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Padrões e processos de organização de comunidades de plantas lenhosas: nicho, evolução e biogeografia histórica

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“No planalto, o próprio aspecto das paisagens, especialmente quando observadas de avião, confirma a ideia de um crescente aflorestamento natural. Os contingentes mais avançados do mato, tanto na escarpa meridional, como no Vale do Uruguai, do Pelotas e do Rio das Antas, os matos de galeria, os capões, os núcleos de mata virgem insulados cercam de todos os lados os redutos de campo gramináceo... (...) O planalto rio-grandense, em igualdade de clima, de erosão progressiva, e sem a interferência do homem, daqui a alguns milênios mais, apresentaria o aspecto de uma única selva primigênia.”

Balduíno Rambo

(A Fisionomia do Rio Grande do Sul, 1956)

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Sumário

Resumo

Abordagens funcionais e filogenéticas têm sido amplamente utilizadas no estudo de ecologia de comunidades e têm propiciado um melhor entendimento de como atributos funcionais e sua evolução influenciam padrões ecológicos observados atualmente na natureza. A incorporação da variabilidade intraespecífica em estudos recentes de ecologia de comunidades vegetais tem demonstrado que, apesar de a variabilidade intraespecífica de um atributo ser normalmente menor do que sua variabilidade interespecífica, estudos que consideram a variabilidade intraespecífica inferem mecanismos de organização de comunidades com mais acurácia. Além disso, abordagens analíticas que incluem a variabilidade intraespecífica em estudos de comunidades possibilitam integrar as escalas de populações e comunidades em ecologia. Abordagens filogenéticas recentes permitem a avaliação da interação entre composição filogenética de bancos regionais de espécies e a estrutura filogenética local de comunidades, o que permite a inferência de processos históricos e ecológicos que estruturam comunidades atuais. O objetivo geral desta tese foi avaliar padrões e inferir processos de organização de comunidades de plantas lenhosas da escala local à regional. Para isso, utilizei abordagens baseadas em atributos funcionais para avaliar o nicho de indivíduos (capítulo 2) e das espécies (capítulo 2 e 3) e abordagens filogenéticas para avaliar como a evolução influencia a similaridade funcional entre as espécies (capítulo 3), a formação de bancos de espécies locais (capítulo 3) e regionais (capítulo 4) e a estruturação de comunidades locais (capítulo 4). No capítulo 2, avaliei qual a importância relativa da substituição (*turnover*) de espécies e da variabilidade intraespecífica nas respostas médias e de dispersão de área foliar específica no nível de comunidade a um gradiente de abertura de dossel em uma metacomunidade de árvores juvenis. Nesse capítulo, concluí que a variabilidade intraespecífica é fundamental para a organização de comunidades lenhosas em florestas e arbustais, pois a área foliar específica dentro da mesma espécie varia conforme o ambiente e o contexto local de espécies interatoras. Essa plasticidade permite o estabelecimento de espécies em uma porção maior do gradiente de abertura do dossel. No capítulo 3, avaliei se espécies ocorrentes tanto na floresta quanto no campo diferem de espécies restritas à floresta ou ao campo quanto a resposta de seus atributos a espécies coocorrentes e ao gradiente ambiental. Concluí que uma ação combinada entre área foliar específica, espessura foliar e densidade de folhagem ajuda a explicar a organização de comunidades de plantas lenhosas em ecótonos floresta-campo. A plasticidade nesses atributos permite a colonização do campo por espécies que também ocorrem na floresta. No capítulo 4, avaliei se há associação entre a estrutura filogenética local (agrupamento ou repulsão) de comunidades de árvores e a distribuição geográfica de grandes linhagens de angiospermas no Neotrópico e Afrotrópico. A conclusão foi que diferenças regionais de composição filogenética entre o Neotrópico e o Afrotrópico são provavelmente um resultado de taxas diferenciais de especiação e extinção que seguiram a separação de Gondwana e atualmente influenciam a estrutura filogenética local de comunidades de árvores de florestas pluviais nos dois reinos.

Palavras-chave: Atributos α e β; Atributos funcionais; Biogeografia histórica; Ecótonos floresta-campo; Ecologia filogenética de comunidades; Florestas pluviais tropicais; Organização de comunidades; Plasticidade fenotípica; Variabilidade interespecífica; Variabilidade intraespecífica.

Abstract

Functional and phylogenetic approaches have been widely used in community ecology studies and have provided a better understanding of how functional traits and their evolution influence ecological patterns that are currently observed in nature. The incorporation of intraspecific variability in recent plant community ecology studies have demonstrated that, despite intraspecific variability of a given trait extent be usually lower than its interspecific variability, studies that account for intraspecific variability more accurately infer mechanisms of community assembly. Moreover, analytical approaches that incorporate intraspecific variability in community ecology studies enable integrating population and community scales in ecology. Recent phylogenetic approaches permit evaluating the interaction between the phylogenetic composition of regional species pools and local phylogenetic structure of communities, which enables the inference of historical and ecological processes structuring current communities. The general aim of this dissertation was to evaluate and infer assembly processes of woody plant communities from local to regional scales. For this, I used trait-based approaches to assess the niche of individuals (chapter 2) and species (chapter 2 and 3) and community phylogenetics approaches to evaluate how evolution influences the trait similarity between species (chapter 3), the formation of local and regional species pools (chapter 3 and 4, respectively) and the structuring of local communities (chapter 4). In chapter 2, I evaluated what is the relative importance of species turnover and intraspecific variability to the variation in trait mean and spread responses of specific leaf area at the community level across a canopy openness gradient in a tree juvenile metacommunity. In this chapter, I conclude that intraspecific variability is essential to woody community assembly in forests and shrublands, since specific leaf area within the same species varies according to the environment and local context of interacting species. This plasticity permits species establishment in a wider portion of the canopy openness gradient. In chapter 3, I evaluated whether species both in forest and grassland differ from species restricted to either forest or grassland regarding their trait-based responses to co-occurring species and environmental gradient. I concluded that an interplay between specific leaf area, leaf thickness and foliage density help explaining the assembly of woody plant communities in forest-grassland ecotones. The plasticity in these traits enables the colonization of the grassland by species that also occur in the forest. In chapter 4, I evaluated whether there is association between local phylogenetic structure (clustering or overdispersion) of tree communities and geographical distribution of major angiosperm lineages in the Neotropics and Afrotropics. In this chapter, I concluded that regional differences in phylogenetic composition between the Neotropics and Afrotropics are likely an outcome of differential rates of speciation and extinction following the breakup of Gondwana and currently influence local phylogenetic structure of rainforest tree communities in both realms.

Keywords: α e β traits; Community assembly; Community phylogenetics; Forest-grassland ecotones; Functional traits; Historical biogeography; Interspecific variability; Intraspecific variability; Phenotypic plasticity; Tropical rainforests.

Capítulo 1. Introdução geral

1.1. TEORIAS ECOLÓGICAS SOBRE A ORGANIZAÇÃO DE COMUNIDADES

Desde o início do século XX, ecólogos têm buscado explicar como as comunidades ecológicas se organizam (Tansley 1920; Gleason 1926; Clements 1928). Desde então, duas visões têm dominado a discussão sobre a natureza das comunidades (Keddy & Weiher 1999; Hubbell 2001): (1) a perspectiva de que as comunidades são organizadas pelas interações determinadas pelo nicho das espécies que as compõem e (2) a perspectiva de que as comunidades são organizadas por padrões derivados da dispersão dos indivíduos. Muitas teorias e conceitos contribuíram para o avanço da teoria em ecologia de comunidades enfatizando essas duas perspectivas. Como parte da primeira perspectiva, pode-se citar o conceito de nicho multidimensional (Hutchinson 1957), o conceito de limitação de similaridade (MacArthur & Levins 1967) e a teoria das "regras de montagem" (*assembly rules* em inglês) (Diamond 1975; Weiher & Keddy 1999). Já a teoria da biogeografia de ilhas (MacArthur & Wilson 1967) e a teoria neutra unificada de biodiversidade e biogeografia (Hubbell 2001) representam avanços importantes no entendimento de como a dispersão influencia padrões de organização de comunidades. Enquanto que por muito tempo a ecologia de comunidades viveu na dualidade representada por defensores de cada uma das perspectivas, vários esforços recentes buscam não somente integrar as teorias de nicho e neutra (Tilman 2004; Kraft et al. 2007; Shipley et al. 2012; Püttker et al. 2014), mas também levar em conta o componente evolutivo que carregam as espécies em seu material genético, o que influencia a similaridade de nicho entre espécies e, por consequência, a organização de comunidades ecológicas (Webb et al. 2002; Kraft et al. 2007; Emerson & Gillespie 2008; Pavoine & Bonsall 2011; Cavender-Bares et al. 2012).

1.2. O PAPEL DO NICHO NA ORGANIZAÇÃO DAS COMUNIDADES

Primeiramente, é importante definir os conceitos de funcionalidade e de atributos funcionais. Atributos funcionais são aqueles que respondem ao ambiente e que impactam o desempenho das espécies em comunidades, isto é, seu crescimento, reprodução e sobrevivência no ambiente natural, o que em consequência influencia seu *fitness* (Pillar & Orlóci 1993; Díaz & Cabido 2001; Violle et al. 2007). Atributos funcionais podem também influenciar processos ecossistêmicos, sendo assim chamados atributos de efeito (Lavorel & Garnier 2002). Nesta tese, utilizarei o conceito de atributos funcionais como atributos funcionais de resposta e não de efeito.

Dentro da perspectiva de organização pelo nicho, há uma dicotomia que se originou de duas linhas de pesquisa com filosofias opostas (Grime 2006). A primeira escola tem antecedentes na teoria da seleção natural de Charles Darwin (Darwin 1859) e prediz que diferenças nas características funcionais de organismos e, em última análise, diferenças na exploração de recursos em comum pelos mesmos, permitem sua coexistência. Essa predição é a base das teorias de limitação de similaridade (MacArthur & Levins 1967) e das ‘regras de montagem’ (do inglês *assembly rules*, Diamond 1975). Ambas teorias podem ser consideradas teorias de coexistência. À despeito da crítica de que há carência de evidências diretas que validem a ocorrência de limitação de similaridade na natureza (Grime 2006; Siepielski & McPeek 2010), a teoria da coexistência tem sido atualizada constantemente com novas evidências de campo ou experimentos bem como com revisões do assunto (Mayfield & Levine 2010; Adler et al. 2013; Kraft et al. 2014). Por outro lado, a segunda escola tem raízes nos primeiros estudiosos da biogeografia, sociologia e fisiologia de plantas [por exemplo, Alexander von Humboldt (1769-1859), Frederic Clements (1874-1945) e Eugenius Warming

(1841-1924), ver McIntosh 1985], e avalia até que ponto membros de uma mesma comunidade frequentemente tendem a exibir similaridade em seus atributos funcionais (Grime 2006). Essa visão foi consolidada pela teoria que utiliza a analogia de ‘filtragem ambiental’ (do inglês *environmental filtering*), em que variáveis ambientais funcionam como ‘filtros ecológicos’ restringindo os tipos e valores de atributos ocorrentes sob sua ação (Keddy & Weiher 1999).

Basicamente, a partir de um banco regional ou local de espécies (Zobel 1997) possuindo diferentes atributos, a ação de filtros ambientais restringe os tipos e valores de atributos que comporão as comunidades locais (van der Valk 1981; Keddy & Weiher 1999). Considerando que somente organismos com atributos similares restarão em um dado sítio, a filtragem ambiental causa convergência de atributos (Weiher & Keddy 1995; Grime 2006; Funk et al. 2008). Como uma força contrária, é em geral aceito que a competição gera divergência de atributos, já que organismos coocorrentes que apresentam similaridade muito grande em seus requerimentos ecológicos serão provavelmente submetidos à exclusão competitiva (MacArthur & Levins 1967; Wilson 1999). Como uma consequência das duas forças opostas, comunidades locais podem exibir tanto um padrão de organização por convergência de atributos, quanto um padrão de organização por divergência de atributos (Grime 2006; Pillar et al. 2009).

Em síntese, teorias de nicho são baseadas nas respostas dos organismos à disponibilidade de recursos, a condições ambientais e a interações bióticas (Keddy & Weiher 1999; Wilson 1999; Tilman 2004; Adler et al. 2013). Dado que essas respostas variam espacialmente, os padrões de organização de comunidades baseados no nicho são em grande parte o resultado de gradientes ambientais (Ackerly 2003; McGill et al. 2006; Adler et al. 2013).

1.3. OS BANCOS DE ESPÉCIES E A ORGANIZAÇÃO DAS COMUNIDADES PELA DISPERSÃO

A perspectiva de organização das comunidades pela dispersão baseia-se no aumento da dificuldade que os organismos enfrentam para se dispersar a distâncias cada vez maiores, isto é, a limitação de dispersão. Essa perspectiva, consagrada por MacArthur & Wilson (1967) através da teoria da biogeografia de ilhas, foi recentemente adaptada pela teoria neutra (Bell 2001; Hubbell 2001), a qual assume que espécies de mesma categoria trófica em uma comunidade são equivalentes funcionais em uma base *per capita*, isto é, elas não diferem nas suas taxas vitais individuais, tais como taxas de nascimento, de mortalidade e de dispersão (Hubbell 2005). Dado tal equivalência funcional, a colonização de certa espécie em um certo local depende essencialmente da abundância relativa das espécies no banco local ou regional, o que por sua vez teria sido determinado por processos históricos como especiação (Hubbell 2001). Em comunidades em que o nicho não é tão importante, as abundâncias relativas no banco regional de espécies e a limitação de dispersão seriam os principais fatores a explicar sua organização, e essas comunidades poderiam ser consideradas neutras. Considerando que a limitação de dispersão é maior quanto maior é a distância entre dois sítios estudados, maior deverá ser o papel da neutralidade em amplas escalas espaciais, como por exemplo as escalas regional e macroecológica (Bell 2001; Bell et al. 2006). De fato, diversos autores atribuem parte considerável dos padrões de comunidades encontrados nessas escalas à influência dos bancos regionais e aos fatores históricos, como a migração da biota, que deve enfrentar o efeito da limitação de dispersão através de grandes distâncias ao longo do tempo evolutivo (p. ex. Ricklefs 1987; Bell 2001).

1.4. A EVOLUÇÃO BIOLÓGICA E O PAPEL DA FILOGENIA NA ORGANIZAÇÃO DAS COMUNIDADES

Um dos avanços mais significativos na ecologia moderna foi a inclusão analítica da informação filogenética nos estudos de organização de comunidades. Desde Darwin (1859), tem-se observado que espécies proximamente aparentadas tendem a competir mais fortemente do que espécies distantes filogeneticamente. Essa tendência gera exclusão competitiva local e tem como consequência um padrão de repulsão filogenética (Webb et al. 2002; Webb et al. 2006). Por outro lado, a ação local de filtros ambientais sobre organismos aparentados gera um padrão de agrupamento filogenético (Webb et al. 2002). Diversos trabalhos têm sido realizados no sentido de avaliar a estruturação filogenética de comunidades em diversos ecossistemas por todo o planeta (Emerson & Gillespie 2008).

Uma importante generalização derivada de estudos de evolução de atributos e linhagens é a da conservação filogenética de nicho (*phylogenetic niche conservatism* em inglês) (Ackerly 2003; Wiens & Donoghue 2004; Donoghue 2008). Considerando que os organismos carregam uma informação genética que restringe os fenótipos que podem ser expressos e que evoluir rapidamente em resposta a mudanças ambientais é difícil, as espécies tendem a "seguir" hábitats semelhantes àqueles aos quais se adaptaram ao longo do tempo evolutivo (Ackerly 2003; Donoghue 2008). Portanto, "é mais fácil mover-se do que evoluir" localmente, ou seja, é mais fácil dispersar ou migrar para um hábitat propício do que se adaptar ao ambiente local que recém mudou (Donoghue 2008). Por outro lado, a seleção natural pode atuar sobre espécies distantemente aparentadas, de modo que leva a uma evolução convergente, ou seja, espécies distantes filogeneticamente convergindo para uma morfologia similar e consequentemente um nicho similar (Ackerly 2009a). A formação de uma biota passa pelo balanço entre processos evolutivos como conservação de nicho e radiação adaptativa (Ackerly 2009b).

1.5. VARIABILIDADE INTRAESPECÍFICA EM ATRIBUTOS FUNCIONAIS E ESTRATÉGIAS DAS PLANTAS

Historicamente, a ecologia focou-se na diferença funcional entre espécies sob o pressuposto de que "para ser útil para a ecologia de comunidades, um atributo deve variar mais entre do que dentro de espécies" (McGill et al. 2006). Recentemente, a incorporação da variabilidade intraespecífica em estudos de ecologia de comunidades vegetais ganhou muita força e um crescente número de trabalhos tem sido publicado ao longo dos últimos anos (Violle et al. 2012). Em geral, esses trabalhos têm demonstrado que, apesar de a variabilidade intraespecífica de um atributo ser normalmente menor do que sua variabilidade interespecífica, estudos que consideram a variabilidade intraespecífica inferem mecanismos de organização de comunidades com mais acurácia (Jung et al. 2010; Cianciaruso et al. 2012; Violle et al. 2012). A variação intraespecífica pode ser originada por diferenças genéticas entre populações (Lavorel et al. 2008) ou por plasticidade fenotípica, que é a capacidade de um organismo com determinado genótipo mudar seu fenótipo em resposta a mudanças no ambiente (Lusk et al. 2008). As implicações da plasticidade fenotípica são fundamentais para o entendimento sobre a organização de comunidades vegetais. Alguns ecólogos têm proposto que a variabilidade intraespecífica aumenta as chances de indivíduos de uma espécie de adequar os valores dos seus atributos a um filtro ambiental ou de se ajustar à competição com vizinhos, o que ocorreria principalmente através da plasticidade fenotípica (Jung et al. 2010). Dessa forma, pesquisadores têm defendido que, estudos de ecologia funcional de comunidades, sempre que possível, deveriam medir atributos morfológicos de todos os indivíduos amostrados ou pelo menos medir valores dos atributos das espécies sob diferentes condições ambientais (Albert et al. 2010; Baraloto et al. 2010; Violle et al. 2012).

A grande quantidade de informações acerca de padrões funcionais de organização de comunidades vegetais produzida ao longo das últimas décadas permitiu generalizações importantes sobre a ecologia das plantas (Grime et al. 1997; Reich et al. 1997; Westoby et al. 2002; Díaz et al. 2004; Wright et al. 2004; Reich 2014). Dentre as generalizações está a de que uma das principais estratégias das plantas tem relação com a captação de luz como recurso para a fotossíntese. Vários trabalhos concordam que a área foliar específica (SLA, do inglês *specific leaf area*) é um dos atributos que melhor sintetiza a estratégia de obtenção do recurso luminoso pelas plantas (Westoby 1998; Westoby et al. 2002; Díaz et al. 2004). SLA é medido pela área foliar fresca dividida pela massa foliar seca, representando investimento em maior área foliar para captar luz para fotossíntese em detrimento do gasto energético para construção de folhas mais densas e espessas (Westoby 1998). O atributo tem correlação negativa com espessura da lâmina foliar, longevidade das folhas e concentração de compostos químicos de defesa contra herbivoria, o que explica seu poder de síntese de dimensões importantes da estratégia das plantas (Westoby et al. 2002).

1.6. FERRAMENTAS PARA AVALIAÇÃO DE PADRÕES FUNCIONAIS E FILOGENÉTICOS E INFERÊNCIA DE PROCESSOS LIGADOS AO NICHO E EVOLUÇÃO NA ESCALA DE METACOMUNIDADES

Nos últimos anos, a literatura sobre ecologia de comunidades tem assistido a uma profusão de abordagens analíticas filogenéticas e funcionais para a avaliação de como indivíduos e espécies se organizam em comunidades ecológicas (Pausas & Verdú 2010; Pavoine & Bonsall 2011). Com relação a abordagens filogenéticas, métricas de estruturação filogenética de comunidades, como é o caso do “índice de parentesco líquido” (NRI, do inglês *net relatedness index*) (Webb 2000; Webb et al. 2002), possuem ampla utilização no estudo de organização de comunidades, especialmente quando não se tem informação sobre os atributos das espécies (Kraft et al. 2007). Abordagens de estruturação filogenética de comunidades como o NRI, no entanto, não fornecem informações sobre a natureza das comunidades, já que não informam como padrões de agrupamento ou repulsão filogenética se relacionam à composição filogenética das comunidades estudadas. Por exemplo, duas comunidades podem apresentar estrutura filogenética semelhante, digamos agrupamento filogenético, mas serem compostas por espécies de linhagens com origens evolutivas completamente distintas.

Nesse sentido, a abordagem analítica filogenética baseada em ponderação difusa contempla não somente a composição de espécies mas também a composição filogenética das comunidades avaliadas (Pillar et al. 2009; Pillar & Duarte 2010; Duarte 2011). A ponderação filogenética da matriz de espécies por comunidades pondera a abundância das espécies por sua similaridade filogenética, gerando uma matriz **P**, que contém composição filogenética de comunidades (Pillar & Duarte 2010). A aplicação de uma ordenação sobre a matriz **P** gera as coordenadas principais de estrutura filogenética (PCPS, do inglês *principal coordinates of phylogenetic structure*; Duarte 2011). Os PCPS são gradientes independentes de composição filogenética ao longo de comunidades. A plotagem dos PCPS mostrando escores tanto de unidades amostrais quanto de espécies permite a observação da representatividade dos clados ao longo de gradientes. Esses gradientes podem ser tanto gradientes ambientais ou gradientes biogeográficos, como em uma região separada por processo de vicariância. A aplicação da abordagem de PCPS a gradientes biogeográficos pode esclarecer padrões de associação entre clados e regiões, possibilitando a inferência de processos históricos estruturadores da biota regional.

É comum na literatura a utilização de índices de diversidade funcional, como a entropia quadrática de Rao (Rao 1982), que mede a dispersão de um ou mais atributos dentro de uma comunidade (de Bello et al. 2009; Pavoine & Bonsall 2009; Ricotta & Moretti 2011). Já as médias de atributo ponderadas na escala de comunidade (CWM, do inglês *community-weighted trait means*) indicam o valor médio do atributo na comunidade (Garnier et al. 2004). A utilização conjunta de CWM e diversidade funcional de Rao permite a avaliação de mudanças nas médias e dispersão do atributo no nível de comunidade ao longo de gradientes, o que permite inferências sobre em que porções do gradiente podem ocorrer mecanismos de nicho importantes para a organização de comunidades, como filtragem ambiental e limitação de similaridade (Ricotta & Moretti 2011; Carlucci et al. 2012). No entanto, como essas medidas sintetizam o comportamento médio ou a dispersão do atributo no nível de comunidade em um único valor, perde-se a informação da identidade de espécies.

A análise atributo-gradiente (em inglês *trait-gradient analysis*; Ackerly & Cornwell 2007) é uma abordagem que possibilita preencher a lacuna existente entre as escalas de comunidade e população em análises funcionais. Essa análise particiona valores de atributos em componentes α e β, seguindo a lógica dos nichos α e β (Ackerly et al. 2006; Silvertown et al. 2006). Em analogia aos componentes da diversidade propostos por Robert Whittaker (Whittaker 1975), o nicho α refere-se a como os atributos diferenciam as espécies de espécies coocorrentes, enquanto o nicho β refere-se a distribuições de espécies através de hábitats ou gradientes geográficos tendendo a ser compartilhado por espécies coocorrentes (Ackerly & Cornwell 2007). A análise atributo-gradiente também permite a avaliação de amplitude de nicho e a quantificação da resposta intraespecífica do atributo ao gradiente ambiental através da “inclinação intraespecífica” da reta de regressão em que os valores de atributo da espécie são preditos pelo gradiente. Medidas de sinal filogenético podem ser aplicadas ao atributo α, atributo β, amplitude de nicho e inclinação intraespecífica para avaliar-se se as respostas das espécies ao gradiente ambiental e a espécies coocorrentes são conservadas, neutras ou convergentes na filogenia. Medidas de sinal filogenético na metacomunidade também podem ser avaliadas pela correlação entre uma matriz **T** definida pelos CWM e a matriz **P** (Pillar & Duarte 2010) ou PCPS derivados da matriz **P**.

1.7. ORGANIZAÇÃO DE COMUNIDADES DE PLANTAS LENHOSAS EM ÁREAS CAMPESTRES DA ESCALA LOCAL À REGIONAL

O sul do Brasil é rico em mosaicos de ecossistemas nativos contrastantes, como campos e florestas (Fig. 1). De maneira geral, as florestas encontram-se dispostas ao redor das áreas campestres, criando campos insulares de diferentes tamanhos, bem como em manchas que acompanham cursos d'água ou que se distribuem isoladamente ao longo dos campos (Rambo 1956). Os principais tipos florestais em contato com campos são a floresta com araucária no Planalto Sul-Brasileiro e a floresta estacional na Serra do Sudeste e demais regiões geomorfológicas do Rio Grande do Sul (Overbeck et al. 2009). Os campos são ecossistemas característicos de um clima pretérito mais frio e seco, e com a tendência de mudança para um clima mais quente e úmido nos últimos três milênios, tem se observado uma progressiva expansão das florestas sobre os mesmos, pelo menos nos Campos de Cima da Serra no Rio Grande do Sul (RS), em Santa Catarina (SC) e no Paraná (PR), na Serra do Sudeste e Campanha Oeste do RS (Behling et al. 2007; Behling et al. 2009). Mais evidências sobre a expansão da vegetação lenhosa são necessárias para as regiões gaúchas da Serra do Sudeste e da Campanha do Sudoeste, mas considerando o padrão em mosaico campo-floresta, os dados paleopolínicos existentes e a tendência global de expansão da vegetação lenhosa sobre áreas campestres em latitudes subtropicais (Archer et al. 1988; Bond 2008; Behling et al. 2009), pode-se assumir que o fenômeno também ocorre nessas regiões.

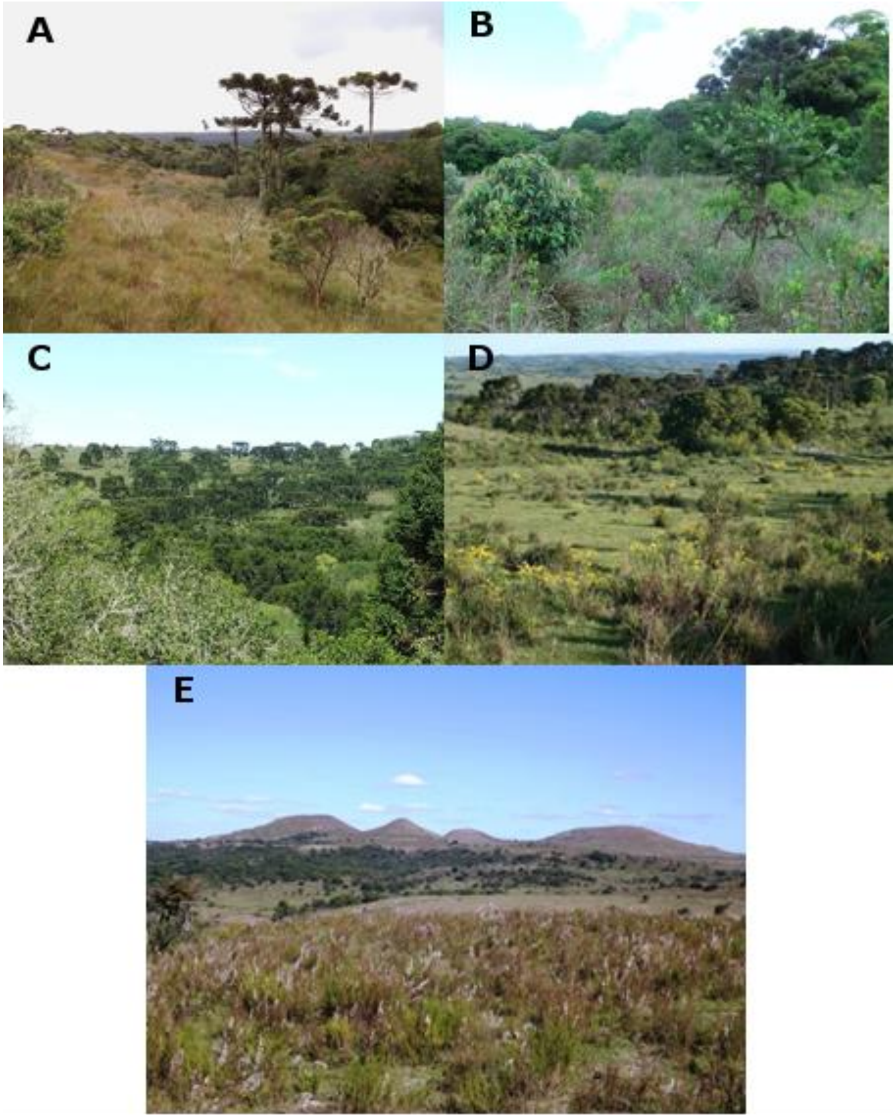

Fig. 1. Paisagens de ecótonos floresta-campo no Estado do Rio Grande do Sul. A. Parque Nacional dos Aparados da Serra, no Município de Cambará do Sul. B. Centro de Pesquisas e Conservação da Natureza Pró-Mata (PUCRS), no Município de São Francisco de Paula. C. Propriedade particular no Município de Encruzilhada do Sul. D. Propriedade particular no Município de Santana da Boa Vista. E. Propriedade particular no Município de Santana do Livramento. Tipos florestais: imagens A-D, florestas com araucária; imagem E, floresta estacional pampeana.

O processo de expansão florestal é mais evidente em áreas excluídas de fogo e de pastejo pelo gado como observado por análise temporal de imagens de satélite (Oliveira & Pillar 2004). A expansão da vegetação lenhosa ocorre basicamente de duas maneiras: por nucleação, a partir de manchas isoladas (Yarranton & Morrison 1974; Duarte et al. 2006a; Duarte et al. 2006b) ou por dinâmica de borda (Oliveira & Pillar 2004; Carlucci et al. 2011b). A nucleação geralmente começa com plantas ou rochas-berçário (do inglês *nurse plants* e *nurse rocks*) que atraem dispersores como aves e melhoram as condições de estabelecimento de plântulas florestais em meio ao campo (Duarte et al. 2006a; Duarte et al. 2010; Carlucci et al. 2011a). Duarte (2011) avaliou a estruturação filogenética de manchas de floresta com araucária em expansão sobre campos e observou que plantas de linhagens com origem evolutiva remota tendem a se estabelecer em manchas maiores, enquanto há uma tendência de que plantas de linhagens com origem evolutiva mais recente ocupem manchas pequenas e expostas ao sol. Em outras palavras, há indícios de que ocorre "filtragem filogenética de hábitat" nessas manchas, já que organismos mais aparentados tendem a ocupar hábitats mais semelhantes (Duarte 2011). Esse padrão é recorrente em diversas regiões de mosaico campo-floresta no sul do Brasil (Debastiani et al. 2014).

1.8. ORGANIZAÇÃO DE COMUNIDADES DE PLANTAS LENHOSAS EM AMPLAS ESCALAS

A formação de bancos regionais de espécies depende da história biogeográfica a que a biota foi submetida ao longo do tempo evolutivo (MacArthur 1972; Cracraft 1994). Alguns dos processos que ocorrem ao longo da história biogeográfica de uma região e que influenciam a formação de bancos de espécies são vicariância (Cracraft 1994), mudanças climáticas (Ackerly 2009b), dispersão de longa distância (Renner 2004) e abundância histórica do hábitat (Zobel et al. 2011). Tais processos ocorreram, por exemplo, após a separação de Gondwana, levando a diferentes taxas de diversificação entre as biotas do Neotrópico e do Afrotrópico (Parmentier et al. 2007). Além disso, a separação dos dois continentes ocasionou o isolamento de suas biotas, submetendo-as a distintas condições climáticas ao longo do tempo, especialmente durante o Cenozóico (Morley 2011). É possível verificar-se a influência da história biogeográfica em padrões locais de comunidades relacionando-se NRI local a eixos de PCPS (descritos anteriormente) de uma série de comunidades cuja composição filogenética reflita a composição filogenética de uma região biogeográfica. Uma relação significativa entre NRI local e o vetor de PCPS descrevendo um gradiente filogenético através de sítios em regiões com diferentes histórias biogeográficas indica que a biogeografia histórica influencia a estrutura local das comunidades através da composição filogenética, dado que a composição filogenética é determinada pela história idiossincrática experimentada por cada biota regional.

1.9. QUESTÕES GERAIS

O objetivo geral desta tese foi avaliar padrões e inferir processos de organização de comunidades de plantas lenhosas da escala local à regional. Para isso, utilizei abordagens baseadas em atributos funcionais para avaliar o nicho de indivíduos (capítulo 2) e das espécies (capítulo 2 e 3) e abordagens filogenéticas para avaliar como a evolução influencia a similaridade funcional entre as espécies (capítulo 3), a formação de bancos de espécies locais (capítulo 3) e regionais (capítulo 4) e a estruturação de comunidades locais (capítulo 4). As questões gerais de cada capítulo da tese foram as seguintes:

Capítulo 2. Qual a importância relativa da substituição (*turnover*) de espécies e da variabilidade intraespecífica nas respostas médias e de dispersão de área foliar específica no nível de comunidade (CWM e Rao) a um gradiente de abertura de dossel em uma metacomunidade de árvores juvenis?

Capítulo 3. Espécies ocorrentes tanto na floresta quanto no campo diferem de espécies restritas à floresta ou ao campo quanto às respostas de seus atributos a espécies coocorrentes e ao gradiente ambiental?

Capítulo 4. Há associação entre a estrutura filogenética local (agrupamento ou repulsão) de comunidades de árvores e a distribuição geográfica de grandes linhagens de angiospermas no Neotrópico e Afrotrópico?

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Capítulo 2. Between- and within-species trait variability and the assembly of sapling communities in forest patches [1]

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Resumo

Questões: Qual a magnitude da variabilidade interespecífica e intraespecífica de área foliar específica (SLA, do inglês *specific leaf area*) em uma metacomunidade de árvores juvenis? Até que ponto a substituição (*turnover*) de espécies e a variabilidade intraespecífica influenciam respostas médias de atributo no nível de comunidade a um gradiente ambiental e padrões de dispersão de atributo ao longo desse gradiente? Qual o papel da variabilidade intraespecífica para a variação nas respostas médias à variação ambiental e para a partição de

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nicho na estruturação de comunidades de árvores juvenis?

Local: Manchas florestais em uma matriz de campo nativo no sul do Brasil.

Métodos: Nós registramos árvores juvenis em parcelas de comunidades ao longo de um gradiente de abertura de dossel em manchas florestais e descrevemos cada um dos 1129 indivíduos utilizando SLA. Primeiramente, particionamos a variação do atributo em variação inter e intraespecífica à despeito da ocorrência em parcelas. Então, utilizando os dados de comunidades, particionamos a variação total de médias do atributo ponderadas no nível de comunidade (CWM, do inglês *community-weighted trait means*) e diversidade funcional de Rao em componentes explicados por abertura de dossel, substituição de espécies e variabilidade intraespecífica. Também particionamos os efeitos da variabilidade intraespecífica entre e dentro de parcelas sobre a variação da diversidade funcional. Finalmente, exploramos as respostas de CWM e diversidade funcional ao gradiente utilizando a variabilidade total do atributo, somente variabilidade interespecífica, ou somente variabilidade intraespecífica.

Resultados: A área foliar específica apresentou uma proporção substancial da variação dentro de espécies (37%), embora o atributo tenha variado mais entre espécies (63%). A substituição de espécies e a variabilidade intraespecífica de SLA explicaram 48% e 19% da variação de CWM ao longo do gradiente, respectivamente. A substituição de espécies e a variabilidade intraespecífica explicaram 51% e 45% da variação da diversidade funcional ao longo do gradiente, respectivamente. SLA variou entre espécies mais ao longo do gradiente do que dentro de comunidades. A variabilidade intraespecífica aumentou as mudanças nos valores de CWM e diversidade funcional ao longo do gradiente. A abertura de dossel foi um preditor significativo de CWM em todas as escalas e também da diversidade funcional, exceto na escala intraespecífica.

Conclusões: As respostas plásticas das espécies refletiram a resposta média das comunidades ao gradiente ambiental. A variabilidade intraespecífica do atributo potencializou as respostas médias das plantas à variação ambiental e à partição de nicho, e foi especialmente importante em permitir o estabelecimento das espécies em uma porção mais ampla do gradiente ambiental. Nosso estudo fornece nova evidência de que fenômenos no nível de população são importantes para a organização de comunidades.

Abstract

Questions: What is the magnitude of between-species trait variability (BSV) and within-species trait variability (WSV) of specific leaf area (SLA) in a sapling metacommunity? To what extent do species turnover and WSV influence community-level mean trait responses to an environmental gradient and trait spread patterns across this gradient? What is the role of WSV for mean plant responses to environmental variation and niche partitioning in structuring sapling communities?

Location: Forest patches within a native grassland matrix in southern Brazil.

Methods: We recorded saplings in community plots across a canopy openness gradient in forest patches and described each of the 1129 individuals by SLA. First, we partitioned trait variation into BSV and WSV irrespective of co-occurrence in plots. Then, using the community data, we partitioned the total variation of community-weighted trait means (CWM) and Rao's functional diversity (FD) into components explained by canopy openness, species turnover, and WSV. We also partitioned the effects of WSV between and within plots on FD. Finally, we explored the responses of CWM and FD to the gradient using the whole trait variability, only BSV, or only WSV.

Results: Specific leaf area presented a substantial proportion of variation within species (37%), although it varied mostly between species (63%). Species turnover and WSV explained 48% and 19% of the variation in CWM across the gradient, respectively. Species turnover and WSV explained 51% and 45% of the variation in FD across the gradient, respectively. Specific leaf area varied within species more along the gradient than within communities. Within-species variability enhanced shifts in CWM and FD across the gradient. Canopy openness significantly predicted CWM at all levels and FD at all but the within-species level.

Conclusions: Plastic responses of species mirrored the average response of communities to the environmental gradient. Within-species trait variability enhanced the mean plant responses to environmental variation as well as niche partitioning, and was especially important in enabling species to establish in a wider portion of the environmental gradient. Our study provides new evidence that population-level phenomena matter for community assembly.

Keywords: Community assembly; Community-weighted trait mean; Environmental filtering; Functional diversity; Interspecific variability; Intraspecific variability; Limiting similarity; Phenotypic plasticity; Trait convergence; Trait divergence

Abbreviations: BSV, between-species trait variability; CWM, community-weighted trait mean; FD, functional diversity; SLA, specific leaf area; WSV, within-species trait variability

Running head: Trait variability and community assembly

Introduction

Functional traits mediate the interaction of individuals with the environment and with other individuals, thereby impacting fitness (Díaz & Cabido 2001; Violle et al 2007) and ultimately species performance across space and time. At the community level, ecologists are interested in understanding the link between the spatial distribution of trait values and community assembly patterns (Weiher & Keddy 1999). According to the environmental filtering approach, the environment acts over a given pool of species by constraining the types and values of traits that will compose local communities (van der Valk 1981; Weiher & Keddy 1995). Only species (or individuals) presenting functional traits within a certain range of values succeed in establishing in a community under the given environmental conditions (Cornwell & Ackerly 2009; Jung et al. 2010). Therefore, environmental filtering restricts the spread of traits at the community level (trait convergence). As a contrary force, competition is expected to result in a higher spread of trait values (trait divergence) at the community level (Cornwell & Ackerly 2009; de Bello et al. 2009), since coexisting organisms that have highly similar ecological requirements are likely to face competitive exclusion (MacArthur & Levins 1967; Wilson 1999). Because of these two opposing forces, a given local community may result from both of these types of processes (Grime 2006; Pillar et al. 2009; Adler et al. 2013).

The mean trait approach, which uses averaged traits of species to study community assembly, has historically dominated the literature of functional ecology (Violle et al. 2012). This approach deals solely with between-species trait variability (hereafter BSV; Jackson et al. 2013), i.e. the trait variability observable between species (Albert et al. 2011). Recent literature has shown an increasing interest in accounting for within-species trait variability (hereafter WSV; Jackson et al. 2013) in community ecology studies (Ackerly & Cornwell 2007; Cianciaruso et al. 2009; Albert et al. 2010; Shipley et al. 2012), i.e. the trait variability observed among individuals of the same species. Empirical evidence has indicated that WSV plays a key role in plant community assembly (Ackerly & Cornwell 2007; Jung et al. 2010; Paine et al. 2011; Cianciaruso et al. 2012; Siefert 2012; Kichenin et al. 2013). Further quantification of WSV across ecosystems and taxa is necessary to better understand the role of within-species processes in community assembly, even though the increasing number of papers being published on this theme has already encouraged the publication of pioneer reviews (Albert et al. 2011; Violle et al. 2012).

Functional ecologists frequently have to ask themselves an essential question: which trait or set of traits should be used? In this study, we chose a unique trait as a model, specific leaf area (SLA), which is the ratio between fresh leaf area and oven-dried leaf mass. It indicates a trade-off between an investment in leaf surface area to capture light for photosynthesis and an investment in constructing more protected tissues to avoid dehydration and herbivory (Westoby 1998; Westoby et al. 2002; Long et al. 2011). SLA is one of the most important traits that synthesizes the light capture dimension of the plant strategy spectrum (Grime et al. 1997; Westoby 1998; Wright et al. 2004). Although SLA is usually quite variable between species (Kazakou et al. 2014), it may be a very plastic trait that responds to environmental factors such as light availability (Lusk et al. 2008). Although within-species variability of SLA is generally assumed to be caused by plasticity, it may be the result of both phenotypic plasticity and genetic variability, especially at regional scales (Scheepens et al. 2010). SLA is a functional trait not only because it responds to the environment, but also because it affects plant performance (Westoby et al. 2002; Poorter & Bongers 2006), especially in small plants such as saplings (Poorter et al. 2008; Wright et al. 2010). These qualities make SLA a very good trait to study community assembly in a framework in which between- and within-species trait variability is taken into account.

When individual-based trait information is available for a community data set, the variability of traits may be constrained in several organizational levels (Messier et al. 2010; Auger & Shipley 2013). Given that trait values are expected to vary both between and within species and both between and within plots (Ackerly & Cornwell 2007), previous studies have evaluated whether accounting for different levels of trait variation is important to infer signals of community assembly (Jung et al. 2010; Siefert 2012). These studies have verified the importance of trait variability among species, subpopulations, and individuals using species-fixed trait means (i.e. species trait means irrespective of habitat), plot-specific trait means (i.e. species trait means specific to different points on the environmental gradient), and trait values for each sampled individual, respectively. In other words, these studies tested for signals of community assembly accounting for BSV (species-fixed means) and BSV plus WSV (plot-specific means or trait values per individual). Lepš et al. (2011) and de Bello et al. (2011) have shown that the variation in community-level trait patterns (mean and spread) based on species-fixed means can only be attributed to species turnover, while the variation in these patterns based on plot-specific means can be due to both species turnover and WSV (see also Cornwell & Ackerly 2009). By discriminating the role of WSV on the variation of community-level trait patterns, the “intraspecific variability effect” can be obtained (de Bello et al. 2011; Lepš et al. 2011).

Recently, we have evaluated trait-convergence and trait-divergence assembly patterns of saplings established across a canopy openness gradient in forest patches using individual-based trait data (Carlucci et al. 2012). We used a method proposed by Pillar et al. (2009) for evaluating trait-convergence and trait-divergence assembly patterns in a metacommunity framework, which permitted the assessment of such patterns along gradients using the whole variability of traits in the sampling design (as we used trait information per individual). We concluded that the assembly of the studied communities likely relied on environmental filtering of SLA along a canopy openness gradient. Divergence patterns suggested that limiting similarity and environmental heterogeneity promoted niche partitioning among individuals in the shade. Nevertheless, we have no information about whether similar patterns would emerge at other levels of organization, i.e. taking only BSV or only WSV into account. Quantifying the importance of WSV to trait mean and spread patterns at the community level should help us infer how various mechanisms, namely environmental filtering, interspecific competition, phenotypic plasticity, and intraspecific competition, operate over individuals to make up ecological communities. While BSV would enable individuals of different species to partition their niches locally, promote coexistence, and occupy different parts of the gradient, WSV due to phenotypic plasticity would enable individuals of the same species to both occupy different parts of the gradient and adjust their trait values to co-occurring individuals, thus enhancing the signals of both environmental filtering and coexistence (Jung et al. 2010).

Here we build on recent advances in functional community ecology to answer the following questions: What is the magnitude of between- and within-species variability of specific leaf area (SLA) in a sapling metacommunity? To what extent do species turnover and WSV influence community-level mean trait responses to an environmental gradient and trait spread patterns across this gradient? What is the role of WSV for mean plant responses to environmental variation and niche partitioning in structuring sapling communities? We hypothesized that WSV would account for a substantial proportion of the variability in SLA, and would be important to the mean trait response to the gradient as well as to trait spread patterns across the gradient.

Methods

STUDY AREA

Data collection was conducted in a forest-grassland mosaic (30.778ºS, 53.07ºW) located in the Santana da Boa Vista municipality, within the Serra do Sudeste region, a geomorphologic complex located in the Pampa biome in southern Brazil. The local climate between the years of 1950 and 2000 was characterized by a mean annual rainfall of 1473 mm and a mean annual temperature of 18.3 ºC (Hijmans et al. 2005). The regional vegetation is a mosaic formed by Campos grassland and seasonal forests (Overbeck et al. 2007). Locally, forests spread mainly along valleys and slopes, but also appear as small isolated patches scattered within the grassland matrix. The conifers *Araucaria angustifolia* (Bertol.) Kuntze and *Podocarpus lambertii* Klotzsch ex Endl. are among the most conspicuous trees in the landscape, but most of the tree species in the area are angiosperms (Carlucci 2011). The study area was comprised of two slopes. The first (hereafter grassland slope) consisted of a grassland matrix containing a large number of small forest patches (area = 90 ± 23 m^2), and the second (hereafter forest slope) was almost entirely formed by a single large forest patch of ca. 35 ha. Further details on the study area can be found in Carlucci et al. (2012).

SAMPLING DESIGN

We collected data of sapling communities in forest plots from January to October 2010. A community was operationally defined as a set of individuals of at least two species found within a sampling plot (Palmer & White 1994). We established 40 circular plots (4.5 ± 0.1 m^2) in forest patches in different successional stages in order to capture the highest variability of the environmental gradient. Considering that the small forest patches scattered in the grassland slope represented initial stages of forest succession and that the forest interior in the forest slope constituted more advanced stages of succession, we placed half of the plots in small patches located in the grassland slope and another half in the forest slope. In the grassland slope, plots were placed within randomly-selected patches. In the forest slope, plots were systematically placed in the forest interior according to spatial coordinates previously defined using a satellite image. The distance between two plots in the grassland slope was on average 171.2 ± 126.1 m and ranged between 12.9 and 517.8 m, while in the forest slope the distance between two plots was on average 312.4 ± 201.6 m and ranged between 49.5 and 781.3 m. Details on the sampling design can be found in Carlucci et al. (2012). In each plot, we recorded all sapling individuals (15-100 cm tall). Overall, 1129 saplings were recorded and identified to the species level in a total sampling area of 180 m^2. We recorded 50 native tree species, among which 48 were angiosperms and two were conifers (Carlucci 2011). Among these 50 species, 25 of them occurred both in the small forest patches and in the large forest patch interior, while the other 25 were restricted to the large patch interior (Carlucci 2011). The abundance of saplings per plot was on average 18.6 ± 4.4 in the grassland slope and 37.8 ± 4.4 in the forest slope. Species richness per plot was on average 5.34 ± 0.6 in the grassland slope and 14.9 ± 1.1 in the forest slope.

TRAIT DATA

We measured specific leaf area (SLA) for each of the 1129 recorded sapling individuals. The procedure of leaf trait collection and measurements for SLA calculation is described in Carlucci et al. (2012) and synthetically explained below. For each sapling, up to six expanded leaves that had no signs of herbivory were collected. We did not sample fully exposed leaves as suggested by standard protocols because we worked with saplings 15- to 100-cm tall that were established under the canopy of forest patches, and therefore most saplings were not fully sun-exposed. For compound leaves, we considered leaflets as the laminar units (Baraloto et al. 2010). We measured fresh leaf area from scanned leaf draws. Due to the time lag between leaf collection and weighing (1-7 days), we maintained all collected leaves in silica gel prior to oven drying at 60°C for 96 h. After drying, the leaves were weighed for calculating SLA. The SLA value of a sapling individual was calculated by dividing the total area of the collected leaves of the individual by the total dry mass of the same leaves. Previous studies have found that ontogeny may influence the SLA of juveniles, especially for deciduous plants (Lusk & Warton 2007). We did not remove the influence of ontogeny on SLA from our analyses, as the vast majority of our individuals were evergreens and ontogeny explained a negligible portion of the variability in SLA (Carlucci et al. 2012).

ENVIRONMENTAL GRADIENT

Canopy openness was measured as a proxy variable for light availability (Nicotra et al. 1999). To obtain canopy openness data, we took hemispheric photos in each plot using a digital camera (Nikon CoolPix 995®, Tokyo, Japan) with a fisheye lens (Nikon FC-E8®, Tokyo, Japan). Canopy openness was calculated using the software GapLight Analyzer v. 2.0 by Frazer, Canham and Lertzman (Simon Fraser University, Canada, and the Institute of Ecosystem Studies, Millbrook, New York, USA; available at http://www.ecostudies.org/gla/).

TRAIT-BASED ANALYSES

In order to reveal the relative contribution of between-species variability (BSV) and within-species variability (WSV) to the total variation in SLA irrespective of co-occurrence in plots, we decomposed the total variation in SLA across individuals using a linear model. We considered values of SLA per individual as the response variable and species identity as a factor. The coefficient of determination (R^2) of this linear model refers to the proportion of variation in SLA between species, while $1 - R^2$ provides the proportion of variation in SLA within species.

We calculated the relative contributions of species turnover and WSV on the variation in community-weighted trait means (Garnier et al. 2004) and functional diversity (Rao's quadratic entropy; Rao 1982), hereafter CWM and FD, respectively. For this, we adapted the method described by Lepš et al. (2011) for CWM and de Bello et al. (2011) for FD. First, it is important to emphasize that we accounted for WSV using trait values per individual rather than plot-specific trait means as originally proposed in the methods for partitioning species turnover *vs*. the effects of WSV on CWM and FD (de Bello et al. 2011; Lepš et al. 2011). By measuring trait information per individual, we captured the totality of the WSV in the sampling design (Carlucci et al. 2012). Then we defined

$$CWM_{BSV} = \sum_{f=1}^{Nsp} p_f x\_fixed_f$$

$$CWM_{whole} = \sum_{i=1}^{Nind} p_i x\_ind_i$$

where p_f is the relative abundance of species f in a given community, Nsp is the total number of species in a community, and x_fixed_f is the fixed trait mean for all sampled communities where the species occurred (here based on the trait mean of all individuals measured for the species). On the other hand, p_i is by definition equal to $1/Nind$, where $Nind$ is the total number of individuals within a community, and x_ind_i is the trait value of the individual i.

The logic behind this partitioning (de Bello et al. 2011; Lepš et al. 2011) is based on two principles. First, variation across the environmental gradient in CWM based on species-fixed trait means (CWM_{BSV}) may only be caused by species turnover. Second, variation in CWM based on the trait values of sapling individuals (CWM_{whole}) may be caused either by species turnover, by WSV, or by both. Then, by subtracting CWM_{BSV} from CWM_{whole}, the "intraspecific variability effect" can be defined (Lepš et al. 2011), which we call CWM_{WSV} (see Appendix S1 for an alternative method for the computation of CWM_{WSV} using deviations in trait values of individuals from the species-fixed trait means, which produces identical results). The partition of the effect of the environmental variable (here, canopy openness) on trait variation is based on three ANOVAs for linear regression using CWM_{whole}, CWM_{BSV}, and CWM_{WSV} separately as response variables. The total sum of squares explained by the ANOVA using CWM_{whole} in this case is taken as the total variation in CWM (Lepš et al. 2011), as it derives both from species turnover and WSV. Finally, the sums of squares are decomposed into the proportion of variation explained by individual components (species turnover, WSV, and covariation between both) and by the environmental variable and residuals. The covariation between species turnover and WSV will be positive when CWM_{BSV} and CWM_{WSV} are positively correlated along the gradient and negative when they are negatively correlated (Lepš et al. 2011).

The partition of the effect of canopy openness on FD was based on the same principles as for CWM (de Bello et al. 2011). For this, we defined functional diversity (Rao) for a given plot as

$$FD_{BSV} = \sum_{f=1}^{Nsp} \sum_{g=1}^{Nsp} p_f p_g \, d\_fixed_{fg}$$

$$FD_{whole} = \sum_{i=1}^{Nind} \sum_{j=1}^{Nind} p_i p_j \, d\_ind_{ij}$$

where d_fixed_{fg} is the trait dissimilarity (Euclidean distance) between each pair of species f and g, using species-fixed trait means ($d\_fixed_{fg} = |x\_fixed_f - x\_fixed_g|$), and p_f and p_g express the relative abundances of species f and g in a given community, respectively. For computing FD_{whole}, d_ind_{ij} is the Euclidean distance between each pair of individuals i and j, using trait values measured for each individual ($d\_ind_{ij} = |x\_ind_i - x\_ind_j|$), and p_i and p_j are both equal to $1/Nind$. Since in this case only one trait was considered, Euclidean distance is the absolute value of the difference in trait values. By definition, Euclidean distances are not squared. Then, if another dissimilarity measure or a different index of functional diversity is used, the trait dissimilarity should not be squared to avoid double squaring during the computation of the sum of squares in the ANOVA, which would overemphasize the differences between FD_{whole} and FD_{BSV} (de Bello et al. 2011). Finally, FD_{WSV} is obtained by subtracting FD_{BSV} from FD_{whole}. Similarly to CWM, the covariation between species turnover and the effects of WSV on FD will be positive when FD_{BSV} and FD_{WSV} are positively correlated along the gradient and negative when both are negatively correlated (de Bello et al. 2011).

We used a procedure analogous to the method described above (de Bello et al. 2011) to quantify the relative contribution of WSV between- and within-plots to variation in FD_{WSV}. To do so, we first obtained $FD_{specific}$, defined as $FD_{specific} = \sum_{f=1}^{Nsp} \sum_{g=1}^{Nsp} p_f p_g d\_specific_{fg}$, in which $d\_specific_{fg}$ is the trait dissimilarity between the pair of species f and g, using plot-specific species trait means ($d\_specific_{fg} = |x\_specific_f - x\_specific_g|$). The plot-specific trait mean of a species f ($x\_specific_f$) is obtained as the mean trait value for the individuals of f recorded in a given plot. $FD_{specific}$ ignores WSV within plots, thereby accounting only for WSV between plots. The effects of WSV between and within plots on FD_{WSV} were obtained by subtracting $FD_{specific}$ - FD_{BSV} and FD_{whole} - $FD_{specific}$, respectively. The contributions of WSV between and within plots to variation in FD_{WSV} were calculated by three separate ANOVAs for linear regression using canopy openness as predictor variable, and total FD_{WSV} along with between- and within-plots effects over FD_{WSV} as response variables. The total sum of squares explained by the ANOVA using total FD_{WSV} in this case was taken as the total variation in FD_{WSV}.

We also used the previously defined linear models considering canopy openness as the predictor, and CWM and FD describing the whole variability (CWM_{whole} and FD_{whole}), between-species variability (CWM_{BSV} and FD_{BSV}), and within-species variability (CWM_{WSV} and FD_{WSV}) of SLA (Fig. 1) as response variables. The statistical significances of regressions using CWM were tested against a null model, in which the SLA values were permuted in the original trait matrix, keeping the community matrix unchanged (Pillar et al. 2009) prior to the generation of CWM. This procedure is equivalent to that used in trait-convergence assembly pattern (TCAP) analysis (Pillar et al. 2009). The statistical significances of regressions taking FD as a response variable were obtained using regular randomization tests, i.e. by randomizing observed values of the response variable (Manly 2007). In both cases, we used regression coefficients (*b*) as the test statistic.

To evaluate if the different numbers of individuals sampled under more open *vs*. more closed canopies would affect the resulting patterns for CWM and FD, we tested whether places with more individuals also had higher trait variability and whether places with fewer individuals had lower trait variability (see Appendix S2). Given that this procedure provided an overview of the mean and spread of traits across communities irrespective of the local abundance of individuals, it complemented the CWM and FD analyses, which helped us infer where along the gradient there was evidence for environmental filtering (restriction of trait spread within the community) and for niche partitioning (higher trait spread within community).

All of the analyses in this study were performed using the software R (R Core Team, v. 3.01, R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org). CWM were calculated using the function ‘matrix.t’ in the R package ‘SYNCSA’ (Debastiani & Pillar 2012). For calculating FD (Rao), we wrote a script for R, which is available in Appendix S3. Analyses partitioning the effect of species turnover *vs*. WSV on variation in CWM and FD across the gradient were performed using the script provided in Lepš et al. (2011). We also used this script to quantify the contribution of WSV between- and within-plots to the variation in FD_{WSV} (using as input data total FD_{WSV} in place of FD_{whole} and between-plots effect over FD_{WSV} in place of FD_{BSV}).

Results

We found a substantial proportion of variation in SLA in the metacommunity occurring within species (37%). Nevertheless, most of the variation in SLA occurred between species (63%).

Overall, species turnover across plots accounted for 48% of the total variation in community-weighted SLA means, while within-species variability accounted for 19% (Table 1). The covariation between species turnover and within-species variability accounted for the remaining 32% of the total variation. The positive sums of squares of covariation indicated that CWM_{BSV} and CWM_{WSV} were positively correlated across the gradient. Canopy openness accounted for 46% of the total community-level variation in SLA (Table 1). The covariation between species turnover and WSV accounted for 21% of the effect of canopy openness on community-level SLA, while species turnover and WSV accounted for 19% and 6% of the total variation, respectively (Table 1).

Species turnover explained nearly half (51%) of the variation in FD across plots, followed by WSV (45%) and the covariation between species turnover and the effect of WSV on FD (4%) (Table 1). Positive sums of squares of covariation indicated that the effects of species turnover and WSV on FD were positively correlated. Canopy openness accounted for 21% of the variation in FD across plots, from which nearly three quarters were explained by species turnover (Table 1). The effect of WSV between plots was more important than the effect of WSV within plots for the variation in FD across the gradient (Table 2). Canopy openness explained a negligible proportion of the variation in FD_{WSV} (Table 2).

The linear regressions indicated significant shifts in trait means across the canopy openness gradient for all levels. Community-weighted SLA means decreased with increasing canopy openness at all levels (Fig. 2). The coefficient of determination in the analysis of trait mean shifts was higher when BSV and WSV were considered together, that is, for the whole-variability level (Fig. 2a). Coefficients of determination were lower when only BSV (Fig. 2b) or only WSV (Fig. 2c) was considered. The relationship between FD and canopy openness was significant for the whole-variability and for the between-species levels, with FD decreasing toward open canopies (Fig. 2d, e). FD was not associated with canopy openness at the within-species level (Fig. 2f), which corroborates the result of variation partitioning into species turnover and WSV.

The scatter plot of all individual SLA values against the canopy openness gradient (Appendix S4) showed a tendency for lower SLA values and for lower spread of SLA under more open canopies, confirming the decreasing pattern of CWM and FD as canopy openness increases. It also revealed a tendency for a higher spread of SLA values under more closed canopies, confirming the trend for high FD in the large forest patch. This pattern was consistent even when we standardized the number of individuals per plot (see Appendix S2). Overall, there was a restriction of trait spread within communities under more open canopies and higher trait spread within communities under dense canopies, although some shady communities showed restricted trait spread (Fig. 2d; Appendix S2).

Discussion

We found evidence that plastic responses of species across the canopy openness gradient mirrored the mean trait response of communities to the gradient. Nearly half of the variation in community-weighted means of SLA was explained by the turnover of species between plots, and this variation was considerably related to canopy openness. The overall tendency was that the plastic response to canopy openness led individuals to exhibit higher SLA under denser canopies of the large forest patch, where community-level SLA was typically higher. Our results are consistent with the idea that the relationship between species trait values and the environment covaries in the same direction as the expected average at the community level, with overall lower WSV than BSV (Cornwell & Ackerly 2009). There was also a positive (although small) covariation between FD_{WSV} and FD_{BSV}, which suggests that conspecific individuals varied more in communities where trait variability was typically high, i.e. in the large forest patch, and less where trait variability was typically low, i.e. in the small forest patches.

We showed that incorporating WSV in the analyses resulted in a stronger mean response of SLA to the gradient (see also Jung et al. 2010). In a previous study analyzing the same data set using individual-based trait analyses (Carlucci et al. 2012), our whole-variability level here, we concluded that convergence for low SLA under open canopies was to a great extent the result of environmental filtering associated with hotter and drier conditions of small forest patches. The new results presented here not only further support that environmental filtering occurs under open canopies, but also that it seems to occur in some communities under dense canopies. It is important to note, however, that a restriction in trait spread might also be a result of competitive exclusion (Mayfield & Levine 2010). Moreover, we found that within-species means at the community level shifted across the canopy openness gradient and that FD_{WSV} was mainly due to WSV between plots without being related to canopy openness. Within-species variability in SLA seems to improve both the ability of species from the forest to colonize the small patches and the ability of species to adjust their traits to the dynamic and complex environment of the large forest patch. In other words, phenotypic plasticity (or genetic diversity) enhanced the mean plant responses to environmental variation as well as niche partitioning. Given that our study was performed at a local scale, we assume that phenotypic plasticity rather than genotypic variability is the most important source for WSV.

Our results suggest that phenotypic plasticity enables species to occur in a wider range of locations along the environmental gradient. Plastic responses of species along the gradient may be a result of the adjustment of the trait values of individuals to the local environment (Jung et al. 2010). Kichenin et al. (2013) have also found a considerable proportion of variation in community-level SLA due to WSV, and have attributed it to the relatively high plastic nature of SLA. Interestingly, we found that FD_{BSV} was negatively associated with canopy openness, but FD_{WSV} was not related to it. In other words, between- and within-species components of variability in FD seem to respond to different factors. The results for the between-species component suggest that niche partitioning is occurring under more closed canopies. High FDs may be the result of community assembly driven by limiting similarity (de Bello et al. 2009). Alternatively, high FDs under dense canopies may arise when niche partitioning is related to a heterogeneous light environment at a fine scale (Carlucci et al. 2012; Adler et al. 2013). The high variability of FD_{WSV} under low canopy openness along with our finding that it was mainly due to WSV between plots but not related to canopy openness indicate that there may be other important gradients, such as those related to soil resources, acting on phenotypic plasticity in the large forest patch. Considering that the large patch is richer in species, high plasticity between plots might alternatively result from an adjustment in SLA in sapling individuals to varying compositions of competitor species between plots in the forest interior. Nevertheless, we have little support for asserting that conspecific individuals are competing and adjusting their SLAs to avoid intraspecific competition exclusion (Jung et al. 2010), since a minor proportion of FD_{WSV} was explained by WSV within plots.

The co-occurrence of half of the species in both sides of the gradient (large forest and small patches) suggests that there is a high degree of plasticity in SLA within these species. Although SLA tends to be higher in the shade (Lusk et al. 2008), we found both high and low SLAs in the large forest patch (Appendix S4). The 'counter-gradient variation' of SLA associated with shade in evergreen forests (Lusk et al. 2008) could be a possible explanation for why both CWM_{BSV} and FD_{BSV} were positively correlated with WSV effects across the canopy gradient. Pioneer species usually exhibit higher SLA than late-successional species under the same light environment in evergreen forests (Lusk et al. 2008). Then, higher CWM_{BSV} and FD_{BSV} under closed canopies of the large patch interior could be explained as follows: (1) the species common to the forest interior and small patches ("pioneers") would have higher SLA in the shade of the forest interior due to phenotypic plasticity and (2) the species restricted to the forest interior ("shade tolerants") would have lower SLA than species common to both sides of the gradient. If the restricted species were really those with lower SLA values, the reason why they do not colonize the small patches is unknown. Two possible explanations are that these species lack the plasticity that permits "pioneers" to establish both in light and shade environments, or that they are limited by dispersal to the small patches (e.g. animal dispersers do not carry seeds from the large forest to the small patches).

Although the variability of SLA between conspecific individuals (37%) was not as high as the variability between species (63%), it was important to both the community trait mean and trait spread responses to the environmental gradient, as demonstrated by CWM and FD partitioning into species turnover and WSV. Other studies in subtropical/temperate vegetation systems have also found more than 50% of variability in SLA occurring between species (Jackson et al. 2013; Kazakou et al. 2014). The relative contribution of BSV and WSV for the metacommunity trait variation is variable among studies (Jung et al. 2010; Lepš et al. 2011) and is likely to depend on the scale of the study (Albert et al. 2011), the system, and the trait (Auger & Shipley 2013). We showed that even though WSV contributed less than BSV to the whole trait variability irrespective of species co-occurrences, this did not mean that WSV was not important for revealing community patterns that otherwise would not be found. This indicates that the mean trait approach’s assumption that a good functional trait should vary more between than within species (McGill et al. 2006) is not sufficient. Just assessing the extent of trait variability accounted for by between- *vs*. within-species components does not replace an evaluation of the importance of these components to community assembly.

We confirmed our general hypotheses that WSV accounts for a substantial proportion of variability in SLA and is important to trait mean and spread responses to the environmental gradient. Our main findings were that plastic responses of species mirrored the average response of communities to the environmental gradient, and that within-species trait variability enhanced both mean plant responses to environmental variation and niche partitioning, being especially important in enabling species to establish in a wider portion of the environmental gradient. Our study brought new evidence that population-level phenomena matter for community assembly.

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Alternative definition of community-weighted trait means using within-species trait information.

Appendix S2. Means and standard deviations of SLA for 1000 null communities with a fixed number of individuals.

Appendix S3. R script for calculating Rao’s quadratic entropy.

Appendix S4. Relationship between trait values of sapling individuals and the canopy openness gradient.

Table 1. Variation partitioning of community-weighted means (CWM) and Rao's functional diversity of specific leaf area measured in forest patch sapling communities. Partitioning approach follows Lepš et al. (2011) and de Bello et al. (2011). The variation in CWM or FD due to species turnover, within-species variability (WSV), or covariation between species turnover and WSV was decomposed to verify the effect of canopy openness. Values are percentages of the total sums of squares.

	Community-weighted means				Rao's functional diversity			
	Species turnover	WSV	Covariation	Total	Species turnover	WSV	Covariation	Total
Canopy openness	19.11	5.77	21.01	45.90	14.27	0.72	6.42	21.41
Residuals	29.30	13.49	11.31	54.10	36.39	44.24	-2.03	78.59
Total	48.41	19.26	32.33	100.00	50.66	44.96	4.38	100.00

Table 2. Variation partitioning of within-species Rao's functional diversity (FD_{WSV}) of specific leaf area measured in forest patch sapling communities. The effect of WSV between plots or within plots (or covariation between them) on the variation in FD_{WSV} across plots was decomposed to verify the effect of canopy openness. Values are percentages of total sums of squares of FD_{WSV}.

	WSV between plots	WSV within plots	Covariation	Total
Canopy openness	1.21	0.03	0.37	1.60
Residuals	84.30	11.11	2.98	98.40
Total	85.51	11.14	3.35	100.00

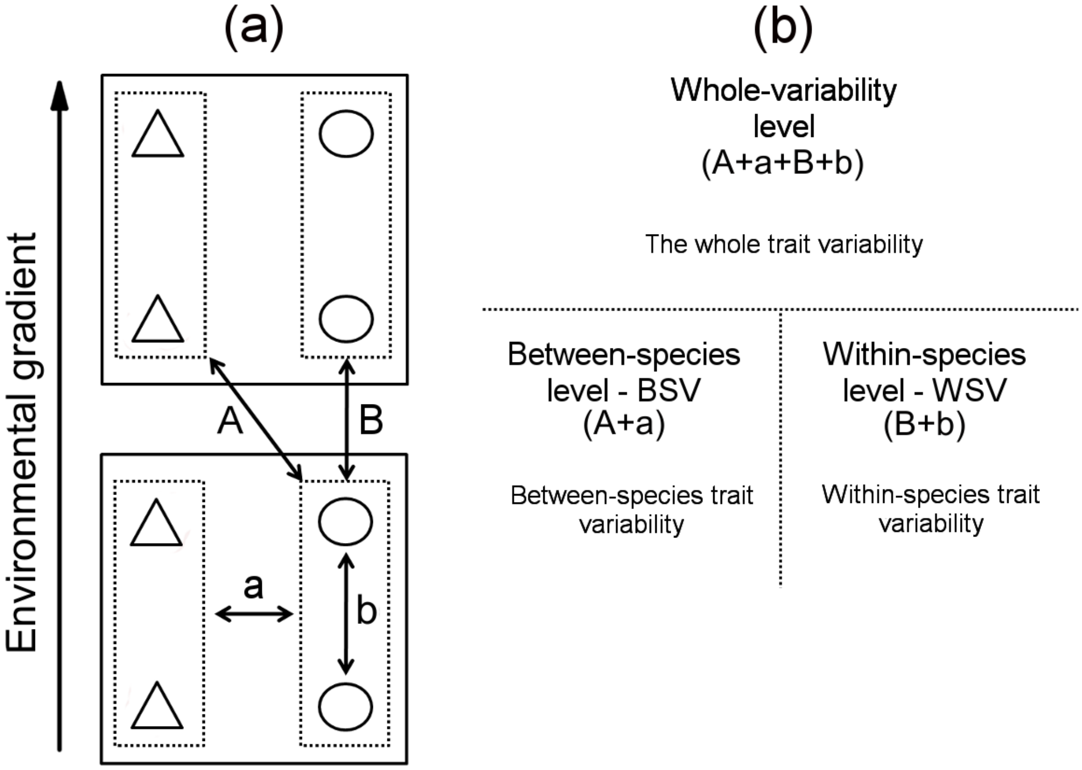

Fig. 1. Trait variation partitioning into organizational levels accounting for between- and within-species trait variability (BSV and WSV) between and within plots across an environmental gradient. (a) Schematic diagram showing two plots (large squares) composed of two species (dashed rectangles), each one having two individuals. Individuals of the same species are represented by the same symbol (triangle or circle). Double-headed arrows represent the following components of trait variability: 'A', between species between plots, 'a', between species within plots, 'B', within species between plots and 'b', within species within plots. (b) The components of trait variability (A, a, B, b) are combined into three levels of trait variability: whole trait variability, BSV, and WSV. For each level, community-weighted means (CWM) and Rao's functional diversity (FD) are calculated using trait information corresponding to the different levels. The mean and spread of trait capturing the whole trait variability (CWM_{whole} and FD_{whole}) are computed using trait values per sapling individual, while mean and spread of trait accounting for only between-species variability (CWM_{BSV} and FD_{BSV}) are computed from species-fixed trait means. Within-species effects over CWM and FD are obtained from the subtractions $CWM_{WSV} = CWM_{whole} - CWM_{BSV}$ and $FD_{WSV} = FD_{whole} - FD_{BSV}$, respectively.

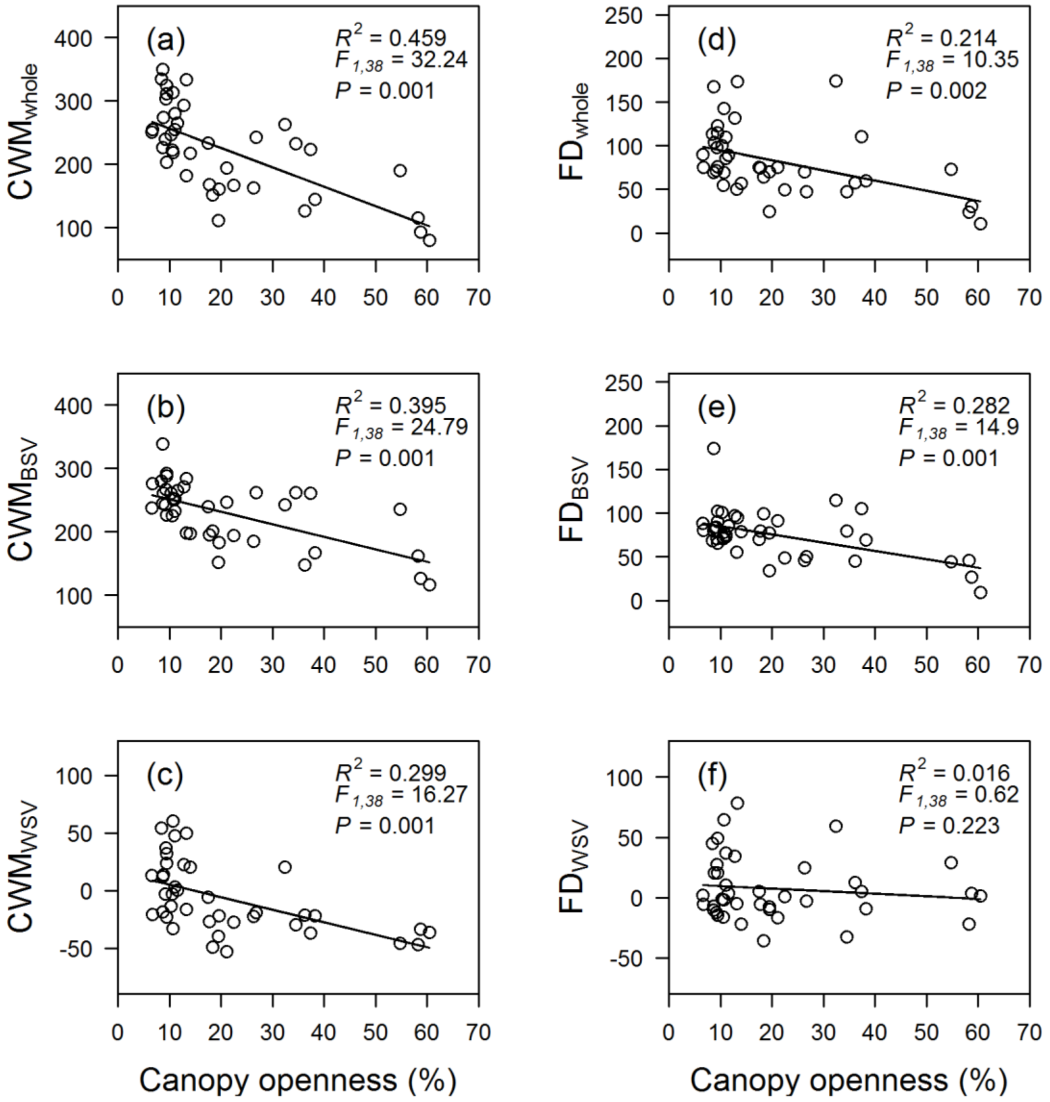

Fig. 2. Shifts in the mean and spread of specific leaf area (SLA) across sapling communities along a canopy openness gradient in forest patches. Community-level mean and spread of SLA were assessed using community-weighted means (CWM) and Rao's functional diversity (FD), respectively. We computed the mean and spread of SLA using the whole trait variability (CWM_{whole} and FD_{whole}; panels a, d), between-species variability (CWM_{BSV} and FD_{BSV}; panels b,e), or within-species variability (CWM_{WSV} and FD_{WSV}; panels c,f). A positive CWM_{WSV} indicates that the SLA of individuals are higher on average locally than expected on average from their species, while negative CWM_{WSV} indicates that the SLA of individuals are lower on average locally than expected on average from their species. A positive FD_{WSV} indicates that there is higher SLA variability among co-occurring individuals than what would be expected if FD was computed from species-fixed SLA means, while a negative FD_{WSV}

indicates that the SLA of co-occurring individuals varied less than what would be expected if FD was computed from species-fixed SLA means. The unit for SLA is $cm^2.g^{-1}$ for all panels.

Supporting information to the paper

Carlucci, M.B., Debastiani, V., Pillar, V.D. & Duarte, L.D.S. Between- and within-species trait variability and the assembly of sapling communities in forest patches

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Appendix S1. Alternative definition of community-weighted trait means using within-species trait information

Alternative definition of community-weighted trait means at the within-species variability level (CWM_{WSV})

An equivalent alternative to compute CWM_{WSV}, other than by subtraction of CWM_{BSV} from CWM_{whole}, is to use deviations of individuals' trait values from their species trait means. Then, we can define

$$CWM_{WSV} = \sum_{i=1}^{Nind} p_i x\_ind\_dev_{i,f}$$

where $x\_ind\_dev_{i,f} = x\_ind_i - x\_fixed_f$, i.e. the deviation of the observed trait mean of the individual *i* from the fixed trait mean of its species *f*. Positive values of CWM_{WSV} indicate that individuals' trait values (x_ind_i) are in average higher than the expected by the species-fixed trait means (x_fixed_f), while negative values indicate that trait values are in average lower than the expected by the species-fixed trait means. High positive or negative CWM_{WSV} values indicate high within-species variability toward the same direction (positive or negative). In other words, a positive CWM_{WSV} would indicate that individuals' trait values were on average larger locally than the expected on average from their species. A negative CWM_{WSV} would indicate the opposite: individuals' trait values are on average smaller locally than the expected on average from their species. Positive or negative values significantly associated with a given environmental gradient indicate that population-level mechanisms, such as phenotypic plasticity (or genetic variability) may be operating. CWM_{WSV} values closer to zero indicate that observed values of x_ind_i are not so different from x_fixed_f values or that x_ind_i values nullified one another around the x_fixed_f values.

Supporting information to the paper

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Appendix S2. Means and standard deviations of SLA for 1000 null communities with a fixed number of individuals.

Testing whether different numbers of individuals affected trait variability within communities

We could expect that places with more individuals had also higher trait variability and places with fewer individuals had lower trait variability. Then, to test whether trait variability patterns depended on the number of individuals, we generated null communities based on our original communities using SLA values that were measured per individual. At each iterative step, we drew 10 individuals by chance to form a null community. For each null community, we calculated the mean and the standard deviation of SLA. We repeated this procedure 1000 times, obtaining a mean of the SLA means, a mean of the standard deviations and a standard deviation of the SLA means (Figs. S2-a,b, below).

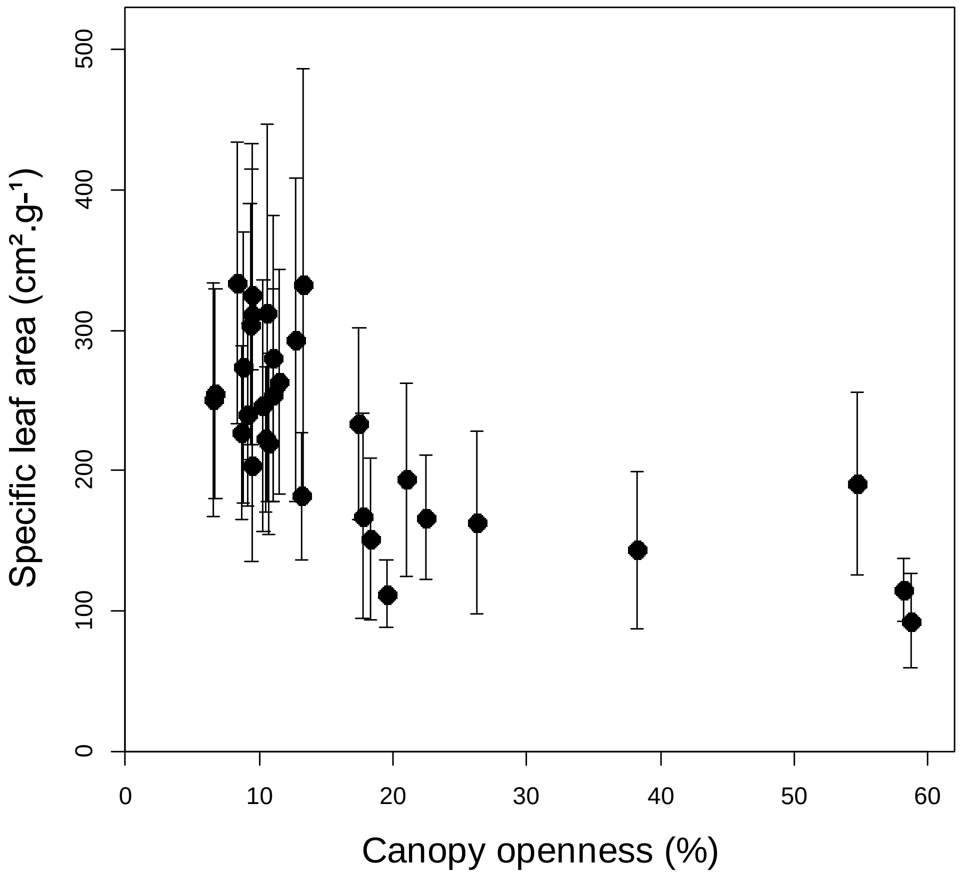

Fig. S2-a. SLA means and means of standard deviations per plot for 1000 iterations in which SLA values were drawn by chance from 10 individuals in each plot.

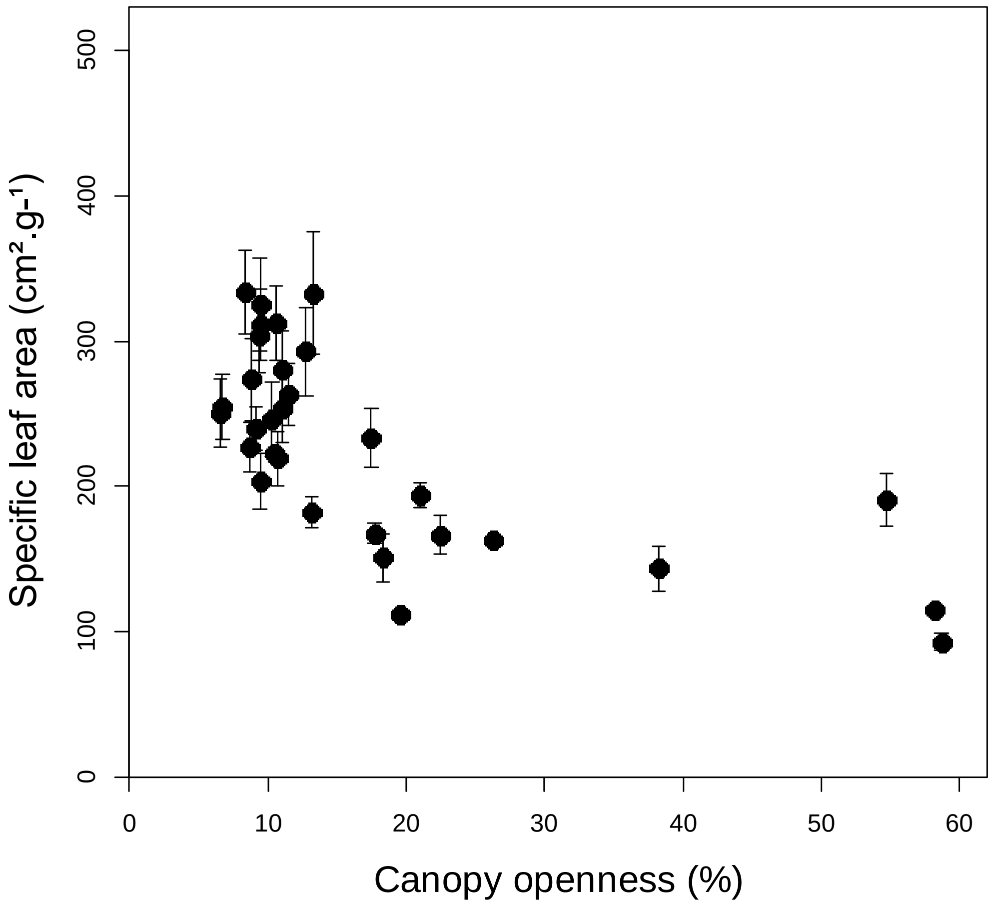

Fig. S2-b. SLA means per plot and their standard deviations for 1000 iterations in which SLA values were drawn by chance from 10 individuals in each plot.

Supporting information to the paper

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Appendix S3. R script for calculating Rao's quadratic entropy.

```
## Script to calculate Rao index as the sum of the relative abundance of species f times the
#relative abundance of species g times the Euclidean distance between trait means of f and g
#without squaring the distance.
#Species can be replaced with individuals or any other OTUs.

rao.diversity<-function(comm,traitsdist=NULL,checkdata=TRUE){
         comm <- as.matrix(comm)
   S <- dim(comm)[2]
   tij1 <- 1 - diag(x = rep(1, S))
   if (!is.null(traitsdist)) {
                  traitsdist<-as.matrix(traitsdist)
                  if (checkdata) {
      if (is.null(rownames(traitsdist))) {
         stop("\n Erro in row names of traitsdist\n")
      }
```

```
                    if (is.null(colnames(traitsdist))) {
        stop("\n Erro in column names of traitsdist\n")
    }
    if (is.null(colnames(comm))) {
        stop("\n Erro in row names of comm\n")
    }
    match.names <- match(colnames(comm), colnames(traitsdist))
    if (sum(is.na(match.names)) > 0) {
        stop("\n There are species from community data that are not on traits distance matrix\n")
    }
    traitsdist <- as.matrix(traitsdist[match.names, match.names])
         }
         tij2<-as.matrix(traitsdist)
}
         comm <- sweep(comm, 1, rowSums(comm, na.rm = TRUE), "/")
         inter<-comm%*%tij1
         SD<-rowSums(sweep(comm,1,inter,"*",check.margin=F))
         if (!is.null(traitsdist)){
                   inter<-comm%*%tij2
                   FRD<-rowSums(sweep(comm,1,inter,"*",check.margin=F))
         }
Res<-list(Simpson=SD)
```

```
   if (!is.null(traitsdist)){
                    Res<-list(Simpson=SD,FunRao=FRD)
   }
return(Res)
}


#################
##Arguments
## comm = A community data, with species (or any OTU) as columns and sampling units as rows.
##This matrix can contain either presence/absence or abundance data.
## traitsdist = A matrix containing trait distance between species (or any OTU).
## checkdata = Logical argument (TRUE or FALSE) to check if species sequence in the community data is the same as in traitsdist matrix (Default checkdata = TRUE).


## Examples
require(vegan)
comm<-matrix(c(0,1,1,1,1,1,0,1,1,0,1,0),4,3)
colnames(comm)=colnames(comm,FALSE,"sp")
rownames(comm)=rownames(comm,FALSE,"com")
comm
trait<-matrix(c(0.5,1,0.75),3,1)
rownames(trait)=colnames(comm)
colnames(trait)="T1"
```

```
trait

dist_eucl_trait<-vegdist(trait,method="euclidean",diag=T)

dist_eucl_trait

rao=rao.diversity(comm,traitsdist=dist_eucl_trait,checkdata=TRUE)

as.matrix(rao$FunRao)
```

Supporting information to the paper

Carlucci, M.B., Debastiani, V., Pillar, V.D. & Duarte, L.D.S. Between- and within-species trait variability and the assembly of sapling communities in forest patches

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Appendix S4. Relationship between trait values of sapling individuals and the canopy openness gradient.

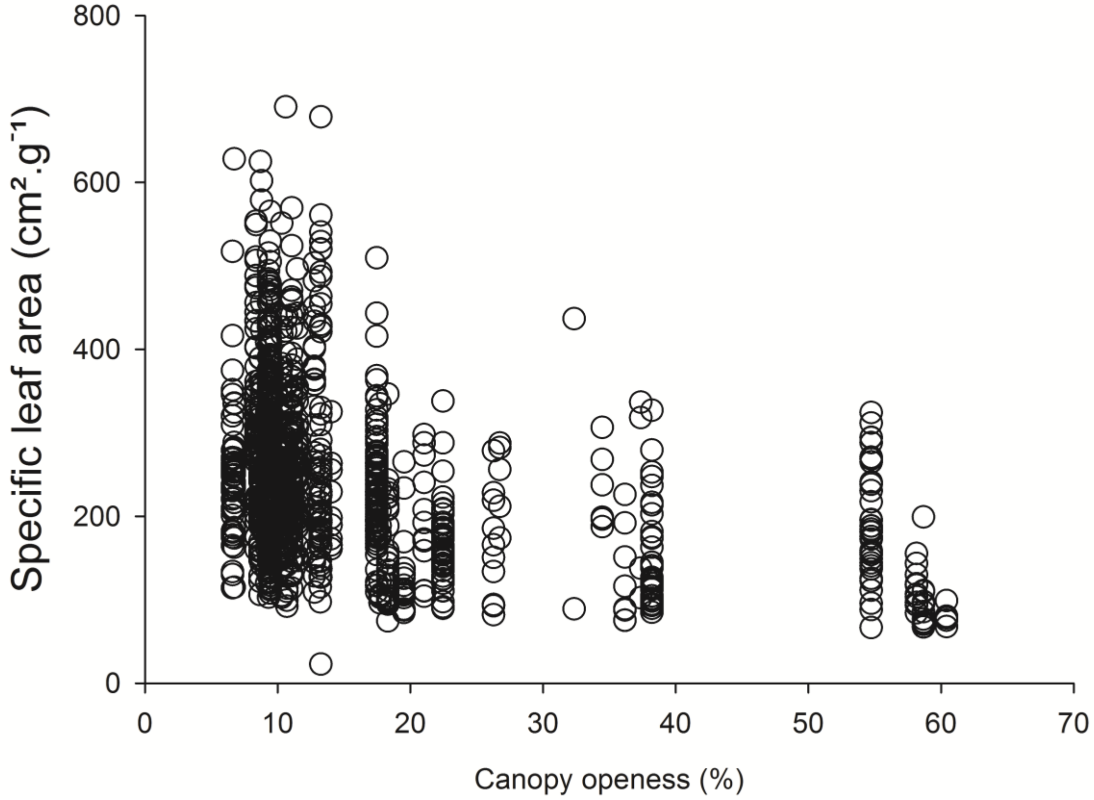

Fig. S4. Specific leaf area of sapling individuals (n = 1129) along a canopy openness gradient in forest patches, southern Brazil. Note that there is a tendency for lower SLA values and for lower dispersion of SLA under more opened canopies.

Capítulo 3. Interplay between leaf traits and architecture mediates forest and shrubland expansion over grasslands [2]

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Running headline: Community assembly in forest-grassland ecotones

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[2] Artigo formatado conforme as regras do periódico *Journal of Ecology*

Resumo

1. Um padrão interessante observado em florestas e arbustais em expansão sobre campos é que algumas espécies lenhosas são comuns à floresta e ao campo, enquanto outras são restritas a floresta ou ao campo. A explicação por trás dessas diferenças de ocorrência entre espécies é desconhecida. Por exemplo, não há informação se o grau de parentesco filogenético ajuda a explicar padrões de variabilidade intraespecífica e distribuições de espécies e seus atributos ao longo do gradiente floresta-campo.

2. Avaliamos se espécies ocorrentes tanto na floresta quanto no campo diferem de espécies restritas à floresta ou ao campo no que se refere a respostas de seus atributos a espécies coocorrentes e ao gradiente ambiental e qual o grau de sinal filogenético nessas respostas funcionais. Respondendo essas questões, inferimos quais atributos e mecanismos potenciais intermediam a expansão de florestas e arbustos sobre campos.

3. Registramos 137 espécies lenhosas em comunidades juvenis em cinco sítios no sul do Brasil. Medimos quatro atributos foliares (área foliar específica, tamanho foliar, conteúdo foliar de matéria seca e espessura foliar) e um atributo de arquitetura da planta (índice de área foliar do indivíduo, uma medida de densidade de folhagem). Particionamos os valores de atributos em componentes α e β e também medimos sua média por espécie, variabilidade intraespecífica, amplitude de nicho e variação intraespecífica como resposta ao gradiente. Comparamos esses atributos entre grupos de espécies que ocorreram tanto na floresta quanto no campo, somente na floresta ou somente no campo. Finalmente, medimos o sinal filogenético nesses atributos.

4. Nossos resultados mostraram que a área foliar específica, espessura foliar e densidade de folhagem são atributos-chave que ajudam a explicar a organização de comunidades de plantas lenhosas em ecótonos floresta-campo. A plasticidade nesses atributos promove a colonização do campo por espécies que também ocorrem na floresta. Os testes de sinal filogenético indicaram ausência de sinal filogenético na média e variabilidade intraespecífica dos atributos vegetativos.

5. *Síntese*. Mostramos que uma ação combinada entre atributos foliares e a arquitetura da planta intermediam a expansão de florestas e arbustais sobre campos subtropicais. Nosso estudo destaca a importância da plasticidade em atributos foliares e arquiteturais para a expansão de formações lenhosas sobre áreas abertas, um fenômeno que tem sido observado globalmente.

Summary

1. An interesting pattern observed in forests and shrublands expanding over grasslands is that some woody species are common to both forest and grassland while others are restricted to either forest or grassland. The reasons behind these differences in occurrence are unknown. For instance, there is no information on whether phylogenetic relatedness helps explaining patterns in intraspecific variability and trait and species distributions across the forest-grassland gradient.

2. We evaluated whether species occurring both in forest and grassland differ from species restricted to either forest or grassland regarding trait-based responses to co-occurring species and environmental gradient and whether these trait-based responses are conserved, neutral or convergent in the phylogeny. By answering these questions, we inferred which traits and potential related mechanisms mediate forest and shrubland expansion over grasslands.

3. We recorded 137 woody species in juvenile communities in five sites in southern Brazil. We measured four leaf traits (specific leaf area, leaf size, leaf dry matter content and leaf thickness) and one architectural trait (individual leaf area index, a measure of foliage density). We partitioned traits in alpha and beta components and also measured their species mean, intraspecific variability, niche breadth and intraspecific slope across the gradient. We compared these traits between groups of species that occurred both in forest and grassland, only in forest, or only in grassland. Finally, we measured phylogenetic signal in the traits.

4. Our results showed that specific leaf area, leaf thickness and foliage density are key traits that help explaining the assembly of woody plant communities in forest-grassland ecotones. Plasticity in these traits promotes the colonization of the grassland by species that also occur in the forest. Phylogenetic signal tests indicated absence of phylogenetic signal in the mean and intraspecific variability of vegetative traits.

5. *Synthesis*. We showed that an interplay between leaf traits and architecture mediates forest and shrubland expansion over subtropical grasslands. Our study highlights the importance of plasticity in leaf traits and plant architecture to the expansion of woody formations over open areas, a phenomenon that has been observed globally.

Key-words: alpha trait, beta trait, community assembly, foliage density, intraspecific variability, leaf size, leaf thickness, niche breadth, phenotypic plasticity, specific leaf area

Introduction

The traits expressed by plants respond to their current abiotic and biotic context. Nonetheless, expressed trait values may have a phylogenetic signal, i.e. they may have been conserved in plant lineages across evolution (Ackerly 2003; Donoghue 2008). Accordingly, the functional response of a plant to the current environment may have been selected by a past environmental condition. On the other hand, a trait may be labile, presenting a lower phylogenetic signal than expected under neutral evolution, which indicates convergent evolution (Ackerly 2009). In this case, distantly-related species have similar traits, thereby occupying similar environments (Cavender-Bares et al. 2004; Kraft and Ackerly 2010). Besides varying between species and lineages, traits related to resource capture such as leaf traits markedly vary between individuals of a same species (Lusk et al. 2008; Carlucci et al. 2014b). The incorporation of intraspecific variability in plant community ecology studies has recently gained increasing space in the literature (Albert et al. 2011; Violle et al. 2012). Ecologists have proposed that intraspecific variability increases the chances of individuals of a given species to adjust their trait values to environmental filters and to competition with neighbours, which would occur mainly by means of phenotypic plasticity (Jung et al. 2010; Carlucci et al. 2014b). Despite the progress towards understanding the role of intraspecific variability on community assembly in the last few years, there is still no information about how intraspecific variability evolves. For instance, there is no information whether intraspecific variability in key traits for community assembly is conserved, neutral or convergent in the phylogeny. By evaluating the phylogenetic signal in intraspecific trait variability we will be able, not only to know whether species trait means were conserved or not across evolutionary time, but also whether the plasticity that enables the individuals of a species to suit the environment has an evolutionary component.

Forest-grassland ecotones provide an interesting system to study plant community assembly, since the transitional zone between forest and grassland represents an environmental gradient to which plants are subject (Carlucci et al. 2012). Woody vegetation have expanded over grasslands in many parts of the world in the past century (Archer et al. 1995; Bond 2008). In southern Brazil, forests and shrublands expand over grasslands as a consequence of a regional change towards a hotter and wetter climate (Oliveira and Pillar 2004; Behling and Pillar 2007). The forest-grassland gradient imposes a filter to lineages of woody plants establishing in distinct portions of the ecotone, which leads the phylogenetic composition to be spatially structured (Duarte 2011). Among woody plants, the association of magnoliids with the forest interior and asterids and rosids with colonization of the grassland is recurrent across southern Brazil (Debastiani et al. 2014). Besides influencing the phylogenetic composition of communities, the forest-grassland gradient also affects trait distribution across the ecotone. In previous studies, our results have suggested that the highly insolated grassland environment selects plants with low specific leaf area and low leaf size, while the more heterogeneous light environment of forest understorey would promote niche partitioning via diversification of strategies among saplings (Carlucci et al. 2012; Carlucci et al. 2014b). We also found that plastic responses of species mirror the trait pattern at the community level across a canopy openness gradient (Carlucci et al. 2014b). These results provided a general picture of the role of different traits, species turnover and intraspecific trait variability in sapling community assembly in a forest-grassland ecotone. In these previous studies, we have used functional approaches that synthesised the trait distribution at the community level, so that we still have no information about how different species and lineages contribute to woody plant community assembly across the forest-grassland gradient. Specifically, we do not know why some species are restricted to the forest or to the grassland while others are common to both forest and grassland. Moreover, there is no information on whether phylogenetic relatedness helps explaining patterns in intraspecific variability and trait and species distributions across the forest-grassland gradient.

Trait-gradient analysis (Ackerly and Cornwell 2007) provides a useful approach to bridge the gap between the community and population scales in trait-based analyses. Trait-gradient analysis is based on the partitioning of trait values into alpha and beta components, following the rationale of alpha and beta niches (Ackerly et al. 2006; Silvertown et al. 2006a; Silvertown et al. 2006b). The beta trait gives information on the mean location of a species along an environmental gradient, while the alpha trait gives an idea of how the traits of a given species differ from those of co-occurring species (Ackerly and Cornwell 2007). Besides alpha and beta traits, trait-gradient analysis permits the evaluation of niche breadths and intraspecific response to the gradient for each species. Measures of phylogenetic signal can be applied to alpha traits, beta traits, niche breadths and intraspecific slopes, in order to assess the level of phylogenetic signal in species responses to environmental gradients and species co-occurrence.

In this study, we applied the trait-gradient analysis to a set of sites and tested for phylogenetic signal of species mean trait values, alpha and beta traits, niche breadths and intraspecific slopes of species. For this, we used data of juvenile communities of woody plant species in forests and shrublands forming ecotones with grasslands in southern Brazil. We used leaf and architectural traits that are expected to affect plant performance: specific leaf area (SLA), leaf size, leaf dry matter content (LDMC), leaf thickness (LT) and individual leaf area index (LAI_{ind}). We addressed the following specific questions: (1) What is the extent of interspecific and intraspecific variability of various vegetative traits (SLA, leaf size, LDMC, LT and LAI_{ind}) in sapling metacommunities established in forest-grassland ecotones? (2) Do species occurring both in forest and grassland differ from species restricted to either forest or grassland regarding their trait-based responses to co-occurring species and environmental gradient (alpha traits, beta traits, niche breadth, intraspecific slope, species mean trait and intraspecific trait variability)? (3) The phylogenetic composition of communities is structured along the forest-grassland gradient? (4) What is the level of phylogenetic signal in these trait-based responses? (5) Which traits mediate forest and shrubland expansion over grassland? And what are the potential mechanisms associated with these traits that drive woody plant community assembly in forest-grassland ecotones?

We hypothesised that traits in general would present higher variability between than within species, and that high intraspecific variability would explain why some species establish both in forest and grassland. We expected the mean of vegetative traits such as SLA, leaf size and LDMC to present less phylogenetic signal than expected under Brownian motion evolution (Kraft and Ackerly 2010; Baraloto et al. 2012; Cavender-Bares and Reich 2012; Lasky et al. 2014b), but the intraspecific variability in some of these traits to be conserved across the phylogeny, which would help explain the recurrent structuring of the phylogenetic composition of woody plants in forest-grassland ecotones in southern Brazil (Debastiani et al. 2014). We hypothesised that SLA, LDMC, LT and LAI_{ind} play a key role in woody plant community assembly in forest-grassland ecotones. We expected that the beta components of SLA, LT and LAI_{ind} would reveal the turnover of species across the gradient. In particular, we expected to observe small and thick-leaved species occurring in grassland communities, where SLA is typically low and LT high, and large and thin-leaved species occurring in forest communities, where SLA is typically high and LT low (Carlucci et al. 2012; Carlucci et al. 2014a). Leaf photosynthetic capacity decreases with increasing LAI_{ind} because self-shading is higher when the individual has more leaves (Posada et al. 2012). Thus, we expected that plants would accumulate more leaves (high LAI_{ind}) in the grassland where light is not limiting and less leaves (low LAI_{ind}) in the forest where light is limiting. We expected that the alpha component of LDMC would be higher among species that occur in the forest because this trait appears to be important to niche partitioning in forests (Carlucci et al. 2014a; Lasky et al. 2014a).

Materials and methods

STUDY SITES AND SAMPLING DESIGN

Data collection was conducted in five sites representing ecotones formed by native grasslands and distinct forest formations in southern Brazil (Fig. 1), where woody vegetation expansion over grasslands is evident. Climate in the study sites is characterised by annual precipitation from *ca* 1,500 mm.yr^{-1} (sites 3-5) to *ca* 1,850 mm.yr^{-1} (sites 1 and 2) and mean annual temperature ranging *ca* 15-18º C (Hijmans et al. 2005). Frosts occur during the winter and appear to hamper the colonization of southern Brazilian forest by tropical tree species (Oliveira-Filho et al. 2013). In southern Brazil, forests have been expanding over grasslands as a result of regional change to a wetter and hotter climate during the last 3-4 millennia (Behling and Pillar 2007; Jeske-Pieruschka et al. 2013). Palaeo-pollen data indicate that *Araucaria* forests and species of the Atlantic rainforest are expanding southwards following the global warming (Jeske-Pieruschka et al. 2013). In grasslands where disturbances such as cattle grazing and burning are ceased, a fast expansion of forest and shrubland elements through edge dynamics and nucleation becomes evident (Oliveira and Pillar 2004; Duarte et al. 2006; Carlucci et al. 2011). All the sites have been historically subject to cattle grazing and periodic burning, but cattle ranching and fire were cessed in sites 1 and 2 three and two decades ago, respectively. Nevertheless, it is common to observe cattle individuals escaping from adjacent farms in site 1. Substantial evidence of boar (*Sus scrofa*) activity was found in sites 1 and 5, but the species, which is exotic to the region, is probably present in all sites.

Four sites (1, 2, 3, 5) were surveyed from November 2011 to August 2013. In each site, two 79m x 158 m grids were established at least 0.7 km distant from each other. The grids were established in the boundary between forest and grassland, so that half of the grid (79 m x 79 m) comprised the forest (hereafter, forest block) and the other half comprised the grassland adjacent to the forest edge (hereafter, grassland block). In each block, the grid located 49 11.3 m x 11.3 m quadrats. We randomly selected 15 out of the 49 quadrats of each forest block for survey. We also selected quadrats of grassland blocks by random, but we gave priority for those quadrats with evidence of woody expansion over grassland, i.e. quadrats containing at least one woody individual with diameter at ground height (DGH) ≥ 5 cm. Then, if a randomly selected quadrat did not present an individual with DGH ≥ 5 cm, we kept drawing quadrats until this requirement was met. In the selected quadrats, we used circular plots to register and identify to the species level every tree, treelet and shrub juvenile individuals 30-130 cm tall. To include only species belonging to these life forms, we recorded only individuals pertaining to species for which we had previous information that its individuals grew DGH ≥ 5 cm. We used 6.25-m^2 plots in the forest block. Juveniles were sparsely distributed in clumps in the grassland. Thus, we used 100-m^2 plots to guarantee sampling of a sufficient number of individuals in the grassland block. In the four sites (1, 2, 3, 5), we surveyed 750 m^2 in forests and 12,000 m^2 in grasslands.

In other site (4), we also used a dichotomic sampling design stratifying forest and grassland plots (Carlucci et al. 2012). In this site, we registered and identified to the species level tree, treelet and shrub juvenile individuals 15-100 cm tall in 40 circular plots (ca. 4.5 m^2). Twenty plots were systematically placed in the forest (range of distance between two plots, 50-781 m), while the other 20 plots were established in randomly-selected small forest patches in a grassland matrix (range of distance between two plots, 13-518 m). Site 4 was surveyed from January to October 2010.

JUVENILE TRAITS

Leaf traits

We measured specific leaf area (SLA) and leaf size for 137 species in all five sites (Table S1). Leaf dry matter content (LDMC) was measured for 111 species in three sites (1, 3, 5). For each species in each plot, we collected six expanded leaves (including petioles) without evidence of herbivory. When the species had only one individual in the plot, six leaves were collected from this individual; when the species had more than one individual in the plot, we made a composite sampling collecting leaves from as many individuals as possible. When less than six leaves were available, all available leaves were collected. We considered leaflets as laminar units for compound leaves (Baraloto et al. 2010). We measured fresh leaf area through leaf scans using the software ImageJ 1.43u (by W. Rasband, National Institutes of Health, USA). We maintained all collected leaves in water-saturated hermetic plastic bags under ca. 10ºC for 1-3 days between leaf collection and measurements. We measured fresh leaf mass before drying leaves in the oven under 60^{o}C during 72 h. SLA was computed as the ratio between fresh leaf area (cm^2) and dry leaf mass (g). Leaf size was computed as the mean fresh leaf area (cm^2) of the species in the plot. LDMC was computed as the ratio between dry leaf mass (mg) and fresh leaf mass (g). Leaf thickness (LT) was estimated using the formula (SLA x LDMC)$^{-1}$ (Vile et al. 2005). SLA responds to light, rainfall, soil water and nutrient gradients (Fonseca et al. 2000; Cornwell and Ackerly 2009; Carlucci et al. 2012) and is positively correlated with growth rate (Westoby et al. 2002). Leaf size is related to energy balance and hydraulic architecture of plants, with small-leaved plants being associated to dry and sun-exposed open vegetation (Ackerly and Cornwell 2007). LDMC approximates tissue density in plants with little intercellular space (Westoby et al. 2002) and is a good predictor of resource capture and use in plants (Wilson et al. 1999). LT is also related to resource capture and use (Vile et al. 2005) and is positively correlated with leaf photosynthetic capacity due to accumulation of photosynthetic compounds in thick leaves (Niinemets 1999). Leaf density and LT are considered components of SLA because of their influence on dry leaf mass, the denominator of SLA (Niinemets 1999).

Ontogenetic variation in leaf traits was found to be negligible during the juvenile stage of woody plant life (Carlucci et al. 2012). Then, we integrated leaf trait data from the five sites in our analyses.

Architectural trait

In site 4, we measured an architectural trait for 51 species: the individual leaf area index (LAI_{ind}). LAI has been usually measured at the ecosystem level as the total one-sided leaf area per ground surface of a stand, but some studies have assessed it at the individual level (Cournède and de Reffye 2007; Dybzinski et al. 2011; Posada et al. 2012). For obtaining LAI_{ind}, we estimated the total leaf area of an individual multiplying the number of leaves of the individual by its mean leaf area (based on the six collected leaves). We also calculated the crown projection area of an individual as the area of an ellipse formed by two orthogonal radiuses of the crown. The trait LAI_{ind} was computed as the ratio between the total leaf area and the crown horizontal area of the juvenile individual (Posada et al. 2012). Given that LAI_{ind} divides area by area, it is dimensionless. LAI_{ind} is a measure of foliage density, informing how much the leaves of an individual are overlapping.

PHYLOGENY

The phylogenetic tree of sampled species was generated from the megatree R20120829 (available at https://github.com/camwebb/tree-of-trees/blob/master/megatrees/R20120829.new), which is based on the phylogenetic hypothesis proposed by APG III (APG 2009). Given that most of this tree has the resolution at the family level, with few families with phylogenetic relationships between genera, infra-family phylogenetic relationships were removed, keeping polytomies linking species within a genus and genera within a family for the whole tree. Then, relationships within families obtained in several published phylogenies of angiosperm clades were included in the megatree. The branch lengths of the whole megatree (including the species that appeared in our communities) were adjusted through the *BLADJ* algorithm in the software Phylocom 4.2 (Webb et al. 2008), following recently published clade age estimates (Bell et al. 2010). By dating the whole megatree rather than just the tree containing the species of our communities, all intermediary nodes were considered, and a biased interpolation of an *a priori* pruned tree was avoided (G.D.S. Seger, pers. comm.). The phylogenetic tree containing the species that appeared in our communities (Fig. S1) was obtained using the module *Phylomatic 2* in the software Phylocom 4.2 (Webb et al. 2008).

DATA ANALYSES

Firstly, we tested for the correlation between traits using Pearson's product-moment correlation. Then, we evaluated the extent of between vs. within-species variability irrespective of species occurrence in communities using a linear model (Carlucci et al. 2014b). For each trait, we considered species trait values per plot as the response variable and species identity as a factor. The coefficient of determination (R^2) of this linear model refers to the proportion of trait variability between species, while 1 - R^2 provides the proportion of trait variability within species.

We used trait-gradient analysis (Ackerly and Cornwell 2007) to assess the responses of species to environmental gradients and species co-occurrence. Alpha and beta traits are computed for each species relative to abundance-weighted plot mean trait values. The gradient can be expressed by either an environmental variable (Cornwell and Ackerly 2009) or represented by a vector composed of plot mean trait values (Ackerly and Cornwell 2007). The beta trait is computed as the averaged plot mean trait value from the set of communities where a species occurred, providing the mean location of a species along the environmental gradient. The alpha trait is computed as the difference between the species trait mean value and the beta trait, giving an idea of how the traits of a given species differ from those of co-occurring species. An alpha trait can also be computed for each species at each community using plot-specific species trait values instead of species trait means. The mean of plot-specific alpha traits provides the alpha trait of the species. Niche breadth is defined as the range of plot mean trait values for the communities where the species occurred. The intraspecific slope refers to the abundance-weighted least squares regression of species trait values as function of a gradient. The intraspecific slope quantifies the magnitude of intraspecific variability in response to the gradient. In this study, we used vectors of plot mean trait values for each trait to represent the forest-grassland gradient. Previous studies have shown that plot trait mean values reflect gradients in forest-grassland ecotones: regressions of SLA and leaf size as function of canopy openness provided $R^2 =$ 0.46 and 0.15, respectively (Carlucci et al. 2012); regressions of SLA, LDMC and LT as function of the factor forest *vs* grassland provided $R^2 =$ 0.51, 0.26 and 0.52 (Carlucci et al. 2014a). We evaluated whether the trait mean, intraspecific trait variability (measured by coefficient of variation) and responses of traits to the gradient and species co-occurrence differ between groups of species occurring in both forest and grassland and species restricted to either forest or grassland using ANOVA.

We identified the major angiosperm clades associated to forest or grassland using principal coordinates of phylogenetic structure (PCPS, Duarte 2011). For this, a matrix of pairwise phylogenetic similarities between species was obtained from the phylogenetic megatree. This matrix was subjected to fuzzy weighting, generating matrix **Q**, containing degrees of phylogenetic belonging of every species to fuzzy sets defined by each other species. Matrix **Q** was used to weight species abundances in the communities, generating by matrix multiplication **P** = **QW** (Pillar and Duarte 2010). A principal coordinates analysis was applied on matrix **P** using square-root transformed Bray-Curtis dissimilarities to generate the PCPS, which are ordination vectors representing independent gradients of phylogenetic composition across communities (Duarte 2011). The bi-plot of PCPS showing both sampling unit and species scores permits observing the representativeness of clades along the forest-grassland gradient. We used the PCPS package (Debastiani and Pillar 2012) for R (R Foundation for Statistical Computing, Vienna, AT; http://www.R-project.org) to run this analysis.

We used Blomberg's *K* statistics (Blomberg et al. 2003) to test for phylogenetic signal in traits at the species level and trait-based responses to gradient and species co-occurrence. A *K*-value near to one indicates that a trait has as much phylogenetic signal as expected under Brownian motion evolution (Blomberg et al. 2003) and may indicate trait evolution under genetic drift (Revell et al. 2008). A *K* less than one indicates that closely-related species resemble each other less than expected under Brownian motion (Blomberg et al. 2003) and suggests convergent evolution or stabilizing selection (Revell et al. 2008; Ackerly 2009). A *K* higher than one indicates that close relatives resemble each other more than expected under Brownian motion (Blomberg et al. 2003), which authors have interpreted as evidence for phylogenetic trait conservatism (Losos 2008; Cavender-Bares and Reich 2012). Similar levels of phylogenetic signal can be generated by distinct evolutionary processes (Revell et al. 2008), so that here we are interested in estimating the amounts of phylogenetic signal in traits rather than disentangling their underlying processes (Baraloto et al. 2012). We tested for the significance of the phylogenetic signal against two null models (Ackerly 2009; Cavender-Bares and Reich 2012): (1) tip-swap, in which trait values are shuffled across the tips of the phylogeny; (2) Brownian motion, in which evolution of traits under Brownian motion is simulated. We used the fastBM function in phytools package (Revell 2012) for R to simulate Brownian motion evolution. For both null models 999 null K values were generated. We calculated K values using multiPhylosignal function in picante package (Kembel et al. 2010) for R.

Finally, we compared the trait mean, intraspecific trait variability (measured by coefficient of variation) and responses of traits to the gradient and species co-occurrence between the following major clades: conifers, magnoliids and eudicots.

All the analyses in this study were performed in the program R.

Results

Specific leaf area was strongly negatively correlated with LDMC, LT, and LAI_{ind} (Fig. S2b-d). Leaf size was negatively correlated with LDMC (Fig. S2e). Leaf thickness was positively correlated with LAI_{ind} (Fig. S2j). Specific leaf area presented similar proportions of variability between and within species (Table 1). Leaf size and LT varied more between than within species, while LDMC and LAI_{ind} varied more within than between species (Table 1).

Specific leaf area was high among species restricted to the forest, intermediary among species common to both forest and grassland and low among species restricted to the grassland (Fig. 2a). Leaf thickness presented an inverse pattern (Fig. 2g). Species restricted to the grassland tended to present smaller leaves than those occurring in the forest (Fig. 2c). Individual leaf area index tended to be higher among species common to both forest and grassland than among species restricted to the forest (Fig. 2i). Intraspecific variability was higher among species common to both forest and grassland than among restricted species for SLA, leaf size, LT and LAI_{ind} (Fig. 2b, d, h, j). Leaf dry matter content did not differ between species occurrence groups (Fig. 2e).

Species restricted to the forest occurred in communities with typical high SLA and low LT (Figs 3b, n and 4c, d, o, p), while species restricted to the grassland occurred in communities with typical low SLA, low leaf size and high LT (Figs 3b, f, n and 4c, d, g, h, o, p). Species common to both forest and grassland occurred in communities with intermediary SLA and LT and high LAI_{ind} (Figs 3b, n, r and 4d, p). Species restricted to the forest tended to present larger leaves than co-occurring species, while species restricted to the grassland tended to present smaller leaves than co-occurring species (Figs 3e and 4g). Species common to both forest and grassland tended to present larger niche breadth than restricted species (Figs 3c, g, k, o, s and 4b-d, f-h, j-l, n-p, r-t). Plastic responses of species to the gradient tended to be stronger among species common to both forest and grassland than among species restricted to grassland (for SLA, Figs 3d and 4c, d) and to forest (for leaf size, Fig. 3h). Plastic responses of species to the gradient for LDMC tended to be stronger among those species that colonized the grassland (Fig. 3l). Plastic responses of species to the gradient for LT and LAI_{ind} did not differ among species occurrence groups (Fig. 3p, t). The Fig. S3 shows the full scatter plots of species trait values *vs* abundance-weighted plot mean trait values.

The PCPS bi-plot revealed that magnoliids are associated with forests, while eudicots are related to open vegetation, with asterids especially represented in grasslands (Fig. S4). The mean, alpha and beta components of some traits and the intraspecific slope of LT presented significantly more phylogenetic signal than the expected by the tip-swap null model (Table S2). Nevertheless, the mean, intraspecific variability and responses of traits to the gradient and species co-occurrence presented phylogenetic signal lower than the expected under Brownian motion evolution for all traits (Table S2). The exception was the log-transformed abundance-weighted mean of $\mathrm{LAI}_{\mathrm{ind}}$, which presented the highest K found in this study and as much phylogenetic signal as expected under Brownian motion evolution (Table S2).

The Fig. 4 provides examples of how species common to forest and grassland and species restricted to either forest or grassland belonging to major clades of spermatophytes behaved across gradients. The two recorded conifers occurred both in forest and grassland and showed similar responses of SLA and leaf size across the forest-grassland gradient (Fig. 4a,e). We did not find any magnoliid restricted to grasslands, and magnoliids in general occurred in communities typically occupied by juveniles with large leaves (Fig. S4, Fig. 4f). The distinction of strategies between the different species occurrence groups (common *vs* restricted species) as revealed by ANOVA (Fig. 3) was especially evident for SLA and LT among asterid and rosid species (Fig. 4c, d, o, p) and $\mathrm{LAI}_{\mathrm{ind}}$ among angiosperm species (Fig. 4r-t).

The ANOVA comparing the mean, intraspecific variability and responses of traits to the gradient and species co-occurrence between conifers, magnoliids and eudicots was significant only for beta leaf size (Fig. S5).

Discussion

Our results showed that intraspecific variability in key traits explains why some species were able to establish both in forest and grassland. Species common to both forest and grassland presented higher variability in SLA, leaf size, LT and LAI_{ind}, which indicates an interplay between leaf traits and plant architecture in response to varying environmental conditions existing across the forest-grassland gradient. Indeed, we found these traits to be correlated, especially SLA, LT and LAI_{ind}. It is well known that SLA and LT are inversely correlated, because there is a trade-off of investment in leaf area to the detriment of leaf thickness, which usually generates large and thin leaves (high SLA) or small and thick leaves (low SLA) (Niinemets 1999; Wilson et al. 1999; Westoby et al. 2002). The negative correlation of SLA and LAI_{ind} and the positive correlation of LT and LAI_{ind} are less known. As LAI_{ind} and consequently leaf self-shading increase, leaf photosynthetic capacity decreases (Posada et al. 2012). Self-shading may be crucial for plants in open light environments by reducing photoinhibition (Howell et al. 2002). In the low light environment of forests, however, SLA is high and leaf longevity is shorter, which causes lower accumulation of leaves in seedlings (Ackerly and Bazzaz 1995). Our results indicate that species occurring in both forest and grassland present high plasticity in these traits. The juveniles of these species can either present few large and thin leaves in the forest understorey or many small and thick leaves in the grassland.

Low intraspecific variability in SLA, LT and LAI_{ind} seems to restrict several species to either forest or grassland. In evergreen forests, juveniles usually present higher SLA under closed canopy (Lusk et al. 2008). Here we showed that species restricted to the forest present SLA higher than species that colonize the grassland, answering an open question that remained in a previous study (Carlucci et al. 2014b). Species that are restricted to the forest present large and thin leaves and accumulate less leaves than species that colonize the grassland. Considering that leaf accumulation increases self-shading leading to leaf senescence under low light (Ackerly and Bazzaz 1995), we expected that leaf accumulation would be lower in the forest, which was found to be true. The positive correlation between

SLA and leaf turnover leads to fast growth (Reich et al. 1997; Westoby et al. 2002). The interplay between these traits is likely to influence plant performance and coexistence in different light environments (Sterck et al. 2006). The strategy of species restricted to the grassland, however, consists in having small and thick leaves, which have higher longevity (Westoby et al. 2002; Poorter et al. 2009). Plants under full sun such as those colonizing the grassland can grow small leaves and accumulate more foliage, because light is not limiting in the open environment. Moreover, the self-shading promoted by foliage accumulation reduces photoinhibition under full sun (Howell et al. 2002). We did not measure LAI_{ind} of any species restricted to the grassland, but our data for those species that colonize the grassland suggest that high foliage accumulation is an important strategy for colonization of the open vegetation. Cattle grazing is expected to have an influence similar to that luminosity has on leaf traits (Carlucci et al. 2012), i.e. accumulation of many small leaves is a good strategy both to avoid dehydration and photoinhibition and to reduce herbivory (Howell et al. 2002; Westoby et al. 2002). Contrary to what we expected, the alpha component of LDMC did not reveal a difference among species occurring in the forest.

As we have hypothesised, species mean values of leaf traits (and also of LAI_{ind}) presented less phylogenetic signal than expected under Brownian motion evolution. Previous studies have also found low Blomberg's *K* values for SLA, leaf size and LDMC (Kraft and Ackerly 2010; Baraloto et al. 2012; Cavender-Bares and Reich 2012; Lasky et al. 2014b), which indicates absence of phylogenetic conservatism in these leaf traits. In other words, our results suggest that similar strategies among plants to deal with the environment and co-occurring species either evolved repeated times in different clades (convergent evolution) or was subject to stabilizing selection to a single trait optimum. Contrary to our expectation, intraspecific variability in vegetative traits was not conserved in the phylogeny. To our knowledge, this is the first assessment of phylogenetic signal in intraspecific trait variability for community data. Confirming the results for phylogenetic signal, we found no differences between major clades in species trait-based responses to the gradient and co-occurring species. The only significant trait-based difference between clades was beta leaf size, which was higher among magnoliids. This finding indicates that magnoliid species occur preferentially in communities with larger leaf sizes, which reinforces the association of magnoliids with the forest (Duarte 2011; Debastiani et al. 2014). Nevertheless, the mechanisms behind this association were not revealed by the traits used in the present study. Rather, these mechanisms are likely related to ecophysiological traits linked to efficiency in the use of water for photosynthesis (Brodribb and Feild 2010). Studies have shown that magnoliids are less efficient in water usage for photosynthesis than eudicots mainly because of distinct leaf venation (Boyce et al. 2009; Brodribb and Feild 2010), and also stem hydraulics, which is vesselless in Winteraceae (Feild et al. 2002). The limitation of magnoliids in water use would explain why we did not find species of this clade restricted to the grassland, i.e. apparently magnoliids did not specialise to the life in the open environment, where plants are often subject to water deficit.

In this study, we found interspecific variability to be predominant for leaf size and LT, while LDMC and LAI_{ind} presented higher intraspecific variability and SLA showed similar amounts of interspecific and intraspecific variabilities. Even though LDMC presented 69% of its variation within species, intraspecific variability in LDMC was not important to differentiate species restricted to either forest or grassland from species common to both. Nevertheless, intraspecific variability in the other traits was important to differentiate species with different occurrences along the gradient, which reinforces the importance of taking intraspecific variability into account in community assembly studies (Violle et al. 2012).

In conclusion, we showed that an interplay between leaf traits and architecture help explaining the assembly of woody plant communities in forest-grassland ecotones in southern

Brazil. Specific leaf area, leaf thickness and foliage density (measured by LAI_{ind}) are key traits that mediate forest and shrubland expansion over subtropical grasslands. We showed that plasticity in these traits promotes the colonization of the grassland by species that also occur in the forest. Our results suggested that both the mean and intraspecific variability in vegetative traits evolved under convergent evolution or stabilizing selection. Our study highlights the importance of plasticity in leaf traits and plant architecture to the expansion of woody formations over open areas, a phenomenon that has been observed globally.

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Table 1. Proportion of variability between and within species for specific leaf area (SLA), leaf size, leaf dry matter content (LDMC), leaf thickness (LT) and individual leaf area index (LAI_{ind}).

Trait	Source of variability	
	Between species	Within species
SLA	0.528	0.472
Leaf size	0.805	0.195
LDMC	0.31	0.69
LT	0.625	0.375
LAI_{ind}	0.24	0.76

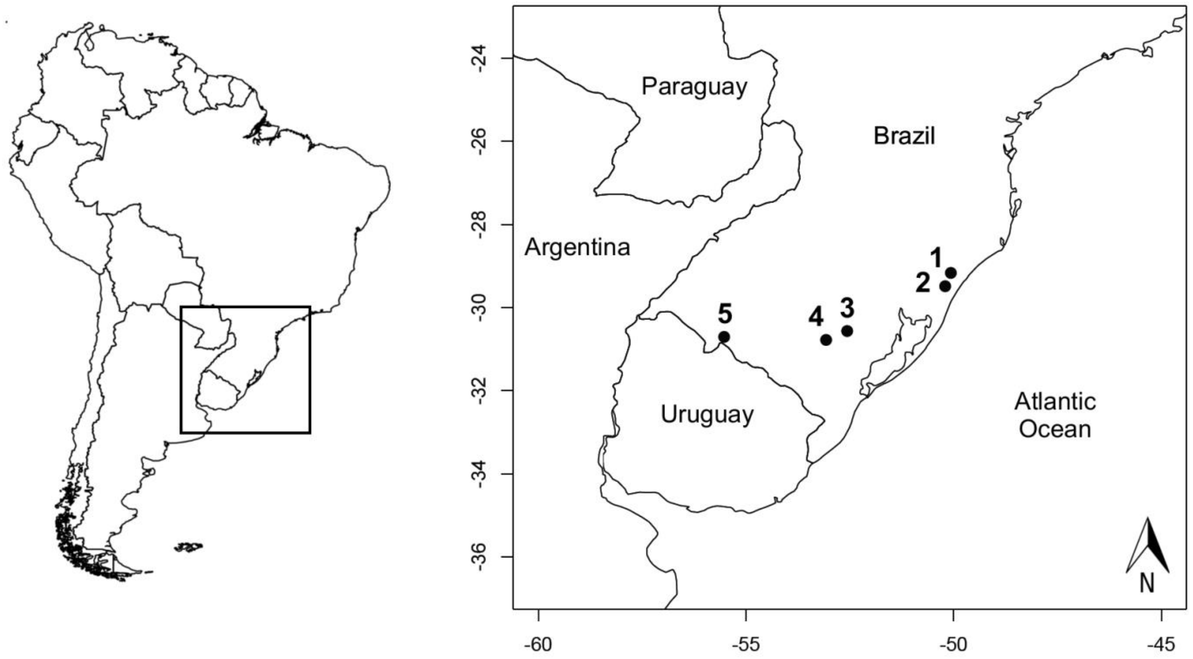

Fig. 1. Location of the five study sites in southern Brazil. Sites 1 and 2 are ecotones formed by *Araucaria* forest and grassland in the Southern Brazilian plateau (900-1,000 m a.s.l.). Sites 3 and 4 are formed by seasonal forest with *Araucaria angustifolia* and grassland in the Serra do Sudeste hills (300-400 m a.s.l.). Site 5 is formed by seasonal forest and grassland in geological remnants of the Southern Brazilian plateau at its southernmost distribution (250-300 m a.s.l.). Site names and coordinates: 1, Aparados da Serra National Park (29.165º S, 50.058º W); 2, Pró-Mata Center for Research and Nature Conservation (29.484º S, 50.205º W); 3, Encruzilhada do Sul (30.561º S, 52.562º W); 4, Santana da Boa Vista (30.778º S, 53.07º W); 5, Santana do Livramento (30.72º S, 55.512º W; near to the Ibirapuitã Environmental Protection Area).

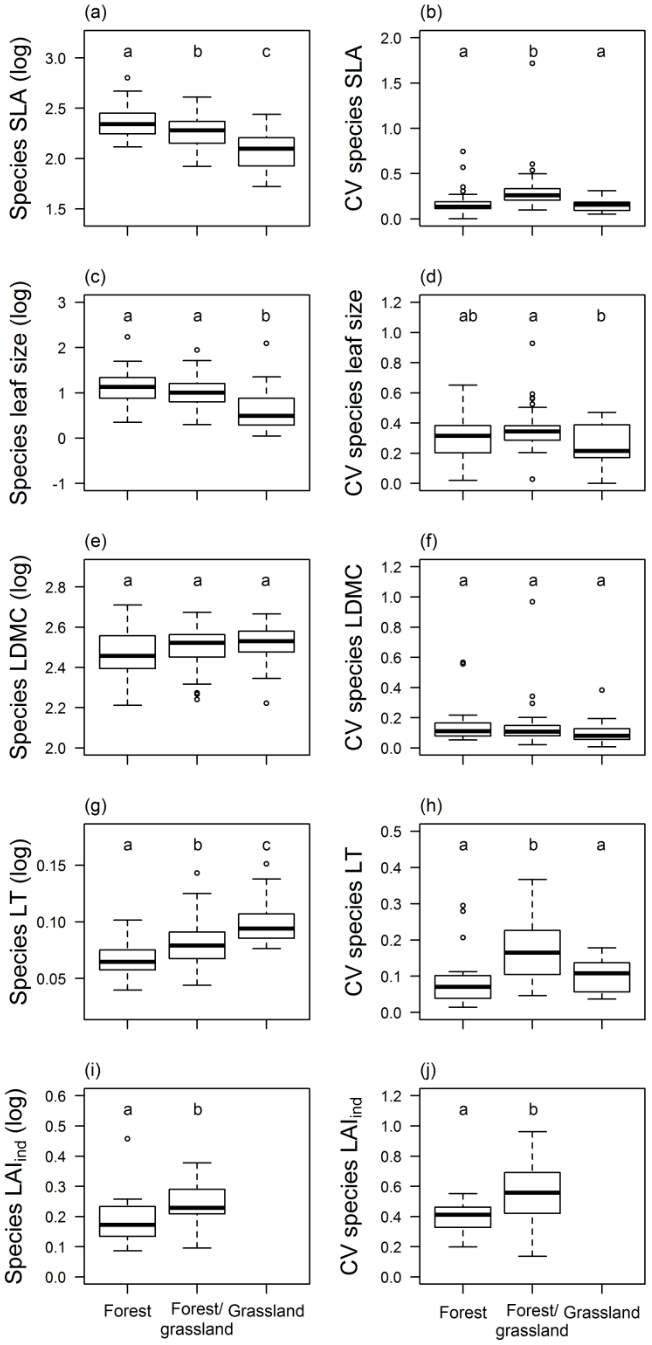

Fig. 2. Results of ANOVA comparing mean trait value and intraspecific variability between species restricted to forest (“Forest”), species common to both forest and grassland (“Forest/grassland”) and species restricted to grassland (“Grassland”). Intraspecific variability was assessed using the coefficient of variation (CV) of each trait within species. Different letters above boxes indicate significant differences ($P \leq 0.05$) between groups of species.

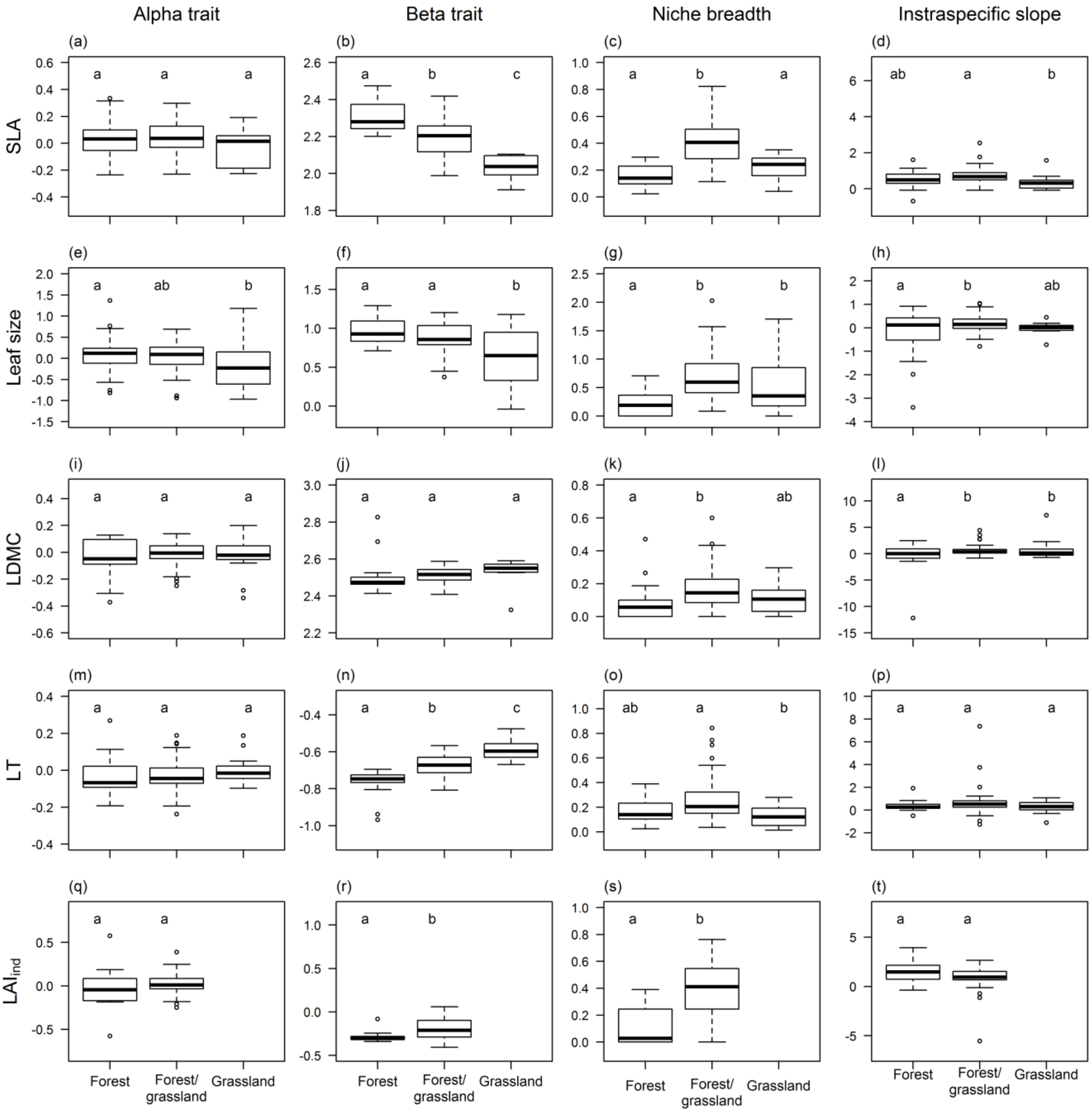

Fig. 3. Results of ANOVA comparing alpha and beta components of traits, niche breadth and intraspecific slope between species restricted to forest ("Forest"), species common to both forest and grassland ("Forest/grassland") and species restricted to grassland ("Grassland"). Beta trait refers to the mean location of species across a gradient represented by plot mean trait values. Alpha trait is the difference between the species mean trait value and its beta trait, indicating how the traits of a given species differ from those of co-occurring species. Niche breadth is the range of community mean trait values where the species occurred. Intraspecific slope quantifies the magnitude of intraspecific variability in response to the gradient. Traits were log-transformed. Different letters above boxes

indicate significant differences ($P \leq 0.05$) between groups of species. Marginally significant comparisons: (d) SLA intraspecific slope - “Forest/Grassland” *vs* “Grassland”, $P = 0.06$; (e) alpha leaf size - “Forest” *vs* “Grassland”, $P = 0.058$.

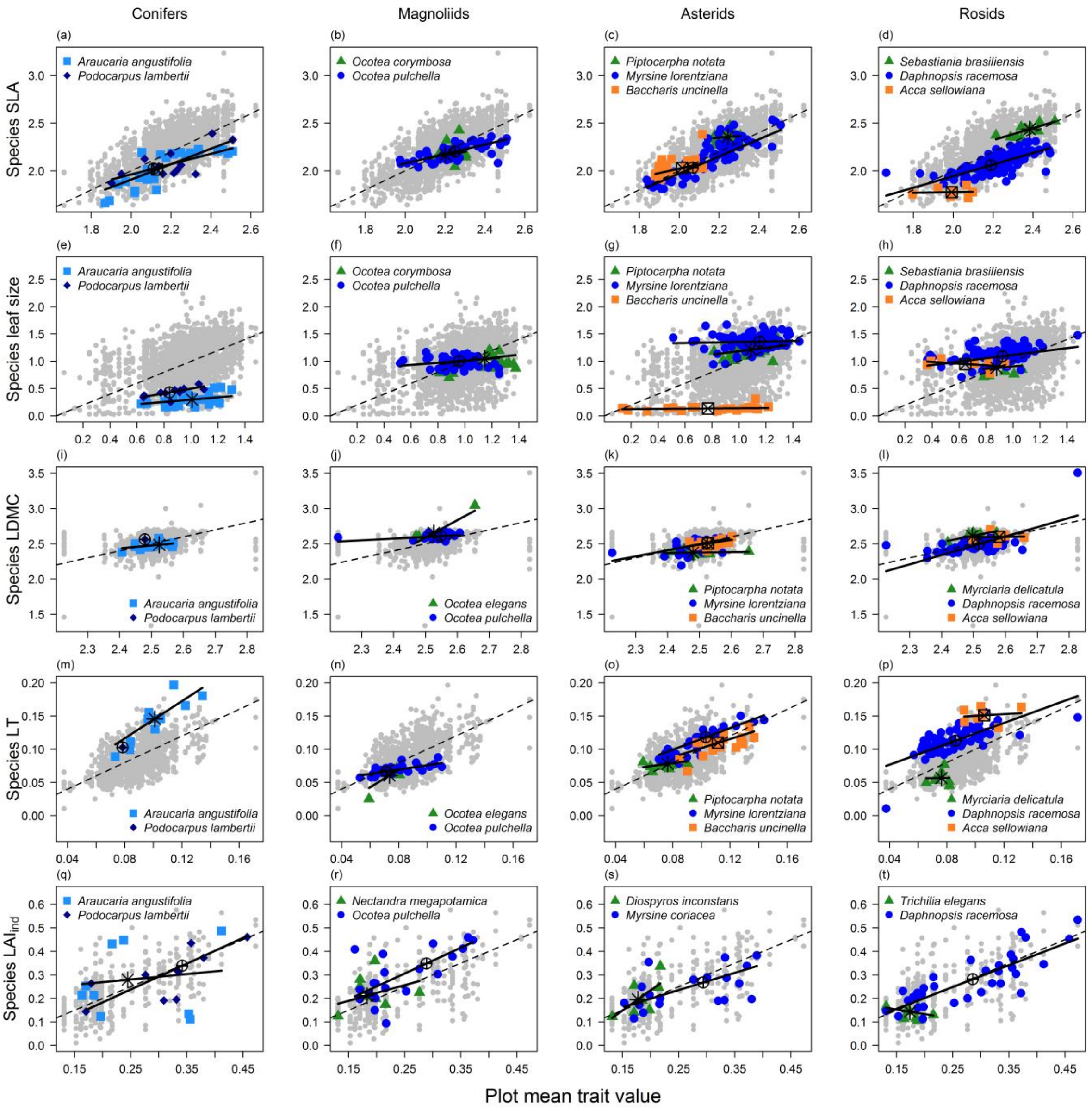

Fig. 4. Examples of how species common to forest and grassland and species restricted to either forest or grassland belonging to major clades of spermatophytes behaved across gradients. Asterisk, crossed circle and crossed square show the mean position of species across the gradient (beta trait) and mean species trait value (on ordinate). The difference between these, or the distance from the X = Y line, is the species alpha trait. The range of occupied plots on the x-axis is the species niche breadth. Regression lines show abundance-weighted least squares regressions of species trait values relative to plot mean trait values. Species trait values in each plot are shown in different colours: in blue, species that occurred both in forest and grassland; in green, species that occurred only in forest; and in orange,

species that occurred only in grassland. The two conifers, *Araucaria angustifolia* and *Podocarpus lambertii*, occurred both in forest and grassland and are shown in different blue intensities. Species highlighted with colours were the most abundant species of each clade representing one of the occurrence groups (common *vs* restricted species) and occurred in at least two sites. Trait values of all other species are shown as little grey points. LAI_{ind} was measured for only one site, where none species was restricted to grassland. Traits were log-transformed.

Supporting Information

Table S1. Occurrence of 137 woody species in forest (Forest) and forest-grassland interface (Grassland) in five sites of forest-grassland ecotones in southern Brazil. It is possible to observe that most species established in the forest-grassland interface. We stress, however, that most juveniles recorded in the grassland were found near adult woody individuals.

Species	Forest	Grassland
Acca sellowiana		X
Agarista minensis		X
Allophylus edulis	X	X
Allophylus guaraniticus	X	X
Aloysia gratissima		X
Annona neosalicifolia	X	
Araucaria angustifolia	X	X
Baccharis dracunculifolia		X
Baccharis uncinella		X
Banara tomentosa	X	X
Berberis laurina	X	X
Blepharocalyx salicifolius	X	X
Brunfelsia australis	X	X
Cabralea canjerana	X	
Calliandra brevipes	X	
Campomanesia xanthocarpa	X	
Campovassouria cruciata		X
Casearia decandra	X	X
Casearia obliqua	X	
Casearia sylvestris	X	X
Cedrela fissilis	X	
Celtis iguanaea	X	X
Cestrum euanthes	X	X
Cestrum strigillatum	X	X
Chrysophyllum gonocarpum	X	
Chrysophyllum marginatum	X	X
Cinnamomum amoenum	X	X
Cinnamomum glaziovii	X	
Citharexylum montevidense	X	X
Citronella paniculata	X	
Citrus x limonia	X	
Clethra scabra	X	
Clethra uleana		X
Cordia americana	X	

Cryptocarya aschersoniana	X	
Cupania vernalis	X	X
Dalbergia frutescens	X	
Daphnopsis fasciculata	X	X
Daphnopsis racemosa	X	X
Dasyphyllum spinescens	X	X
Diospyros inconstans	X	
Discaria americana		X
Drimys angustifolia	X	X
Drimys brasiliensis	X	X
Erythroxylum cuneifolium	X	X
Erythroxylum myrsinites	X	X
Eugenia involucrata	X	
Eugenia uniflora	X	X
Eugenia uruguayensis	X	X
Guettarda uruguensis	X	X
Ilex brevicuspis	X	X
Ilex dumosa	X	X
Ilex microdonta	X	X
Ilex paraguariensis	X	X
Inga lentiscifolia	X	
Lamanonia ternata	X	X
Laplacea acutifolia	X	X
Leandra barbinervis	X	X
Leandra dasytricha	X	
Leandra laevigata	X	
Leandra regnellii	X	X
Lippia ramboi		X
Lithraea brasiliensis	X	X
Lithraea molleoides	X	X
Luehea divaricata	X	
Matayba elaeagnoides	X	X
Maytenus dasyclada	X	
Maytenus evonymoides	X	
Maytenus ilicifolia	X	X
Miconia cinerascens	X	X
Miconia hyemalis	X	X
Miconia pusiliflora	X	
Miconia ramboi	X	X
Moquiniastrum polymorphum	X	X
Myrceugenia alpigena		X
Myrceugenia cucullata	X	
Myrceugenia euosma	X	X
Myrceugenia mesomischa	X	X
Myrceugenia miersiana	X	X

Myrceugenia myrcioides	X	
Myrceugenia oxysepala	X	X
Myrcia guianensis	X	X
Myrcia hartwegiana	X	X
Myrcia palustris	X	X
Myrcia retorta	X	X
Myrcianthes pungens	X	
Myrciaria delicatula	X	
Myrrhinium atropurpureum	X	X
Myrsine coriacea	X	X
Myrsine lorentziana	X	X
Nectandra grandiflora	X	
Nectandra megapotamica	X	
Ocotea corymbosa	X	
Ocotea elegans	X	
Ocotea porosa	X	
Ocotea puberula	X	X
Ocotea pulchella	X	X
Piptocarpha axillaris	X	X
Piptocarpha notata	X	
Podocarpus lambertii	X	X
Prunus myrtifolia	X	X
Psidium cattleianum		X
Psychotria carthagenensis	X	
Psychotria suterella	X	
Quillaja brasiliensis	X	X
Randia ferox	X	
Rhamnus sphaerosperma	X	X
Roupala montana	X	
Rudgea parquioides	X	
Schinus engleri		X
Schinus lentiscifolius	X	X
Schinus longifolia	X	X
Schinus polygamus		X
Scutia buxifolia	X	X
Sebastiania brasiliensis	X	
Sebastiania commersoniana	X	X
Siphoneugena reitzii	X	X
Solanum mauritianum		X
Solanum pseudoquina	X	
Sorocea bonplandii	X	
Strychnos brasiliensis	X	
Styrax leprosus	X	X
Syagrus romanzoffiana	X	
Symplocos tetrandra	X	X

Symplocos uniflora	X	X
Tibouchina sellowiana	X	
Trichilia claussenii	X	X
Trichilia elegans	X	
Vernonanthura discolor	X	X
Vitex megapotamica	X	
Xylosma pseudosalzmanii	X	X
Xylosma schroederi	X	X
Xylosma tweediana	X	X
Zanthoxylum astrigerum	X	X
Zanthoxylum fagara	X	X
Zanthoxylum rhoifolium	X	X

Table S2. Results of phylogenetic signal tests in traits using Blomberg's *K* statistic. Two null models were used for testing the significance of *K*: one based on shuffling trait values across the tips of the phylogenetic tree (tip-swap) and one another based on Brownian motion evolution. P_{TS}, *P*-value for the tip-swap null model; P_{BM}, *P*-value for the Brownian motion null model. *P*-values ≤0.025 or ≥0.975 indicate respectively higher or less phylogenetic signal than expected under the null model considered. Intraspecific variability was assessed through coefficient of variation (CV) of the trait.

		Mean trait value	Mean trait value (log10)	CV	CV (log10)	Alpha trait	Beta trait	Niche breadth	Intraspecific slope (abundance weighted)
SLA	K	0.21	0.14	0.08	0.12	0.17	0.16	0.12	0.28
	P_{TS}	**0.001**	**0.021**	0.696	0.35	**0.004**	**0.009**	0.268	0.050
	P_{BM}	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
Leaf size	K	0.41	0.30	0.12	0.12	0.24	0.18	0.14	0.06
	P_{TS}	0.155	**0.001**	0.335	0.465	**0.003**	**0.003**	0.04	0.922
	P_{BM}	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
LDMC	K	0.32	0.37	0.29	0.23	0.32	0.22	0.12	0.19
	P_{TS}	**0.001**	**0.001**	0.036	**0.003**	**0.001**	**0.022**	0.649	0.207
	P_{BM}	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
LT	K	0.12	0.15	0.12	0.11	0.12	0.17	0.13	0.32
	P_{TS}	0.559	0.167	0.43	0.598	0.453	0.162	0.351	**0.015**
	P_{BM}	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
LAI_{ind}	K	0.42	0.47	0.29	0.27	0.54	0.16	0.29	0.37
	P_{TS}	0.086	**0.004**	0.148	0.342	**0.001**	0.832	0.365	0.143
	P_{BM}	**0.999**	**0.994**	**1.000**	**1.000**	**0.981**	**1.000**	**1.000**	**1.000**

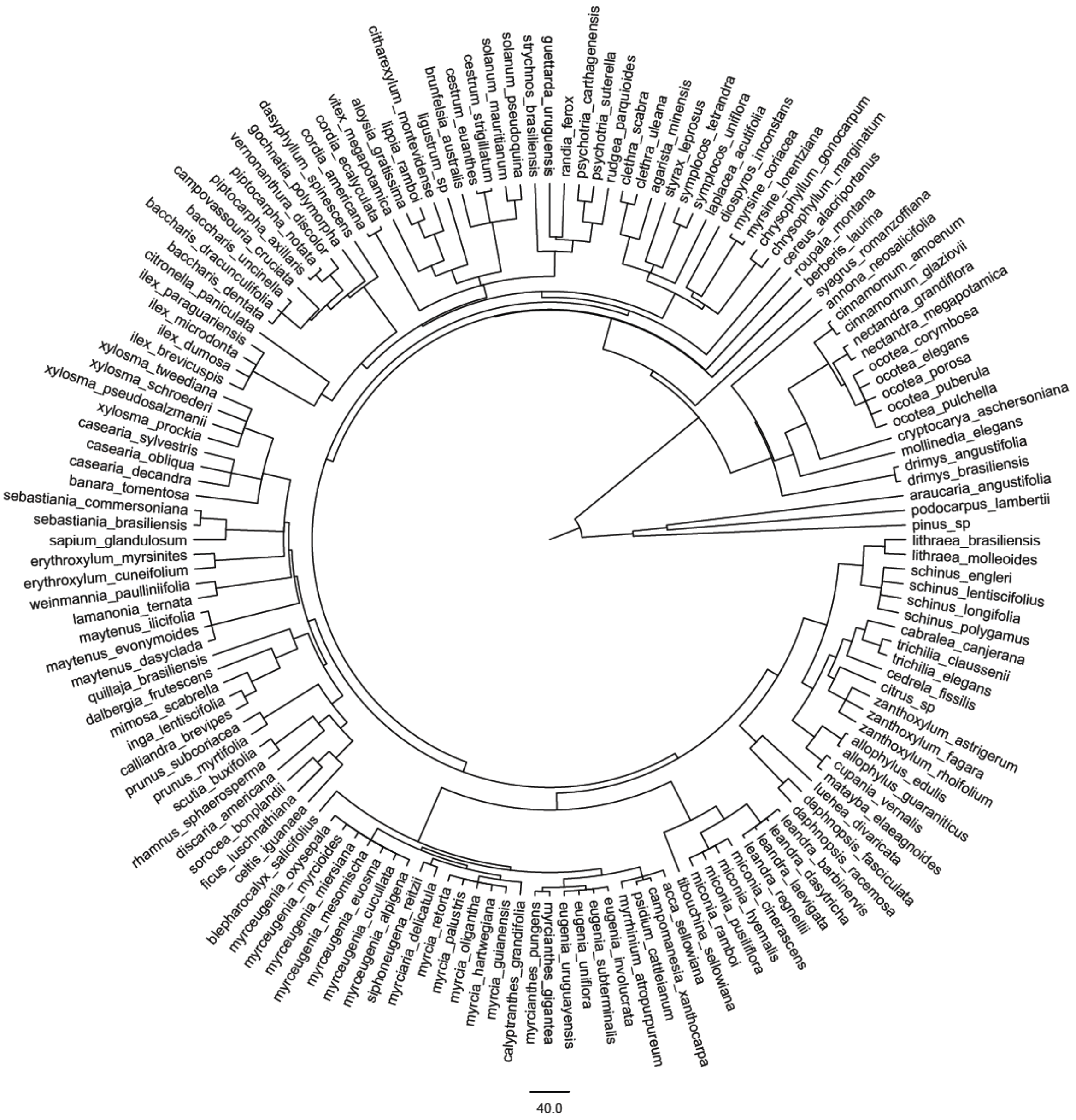

Figure S1. Phylogenetic tree of angiosperm species occurring in forest-grassland ecotones in southern Brazil.

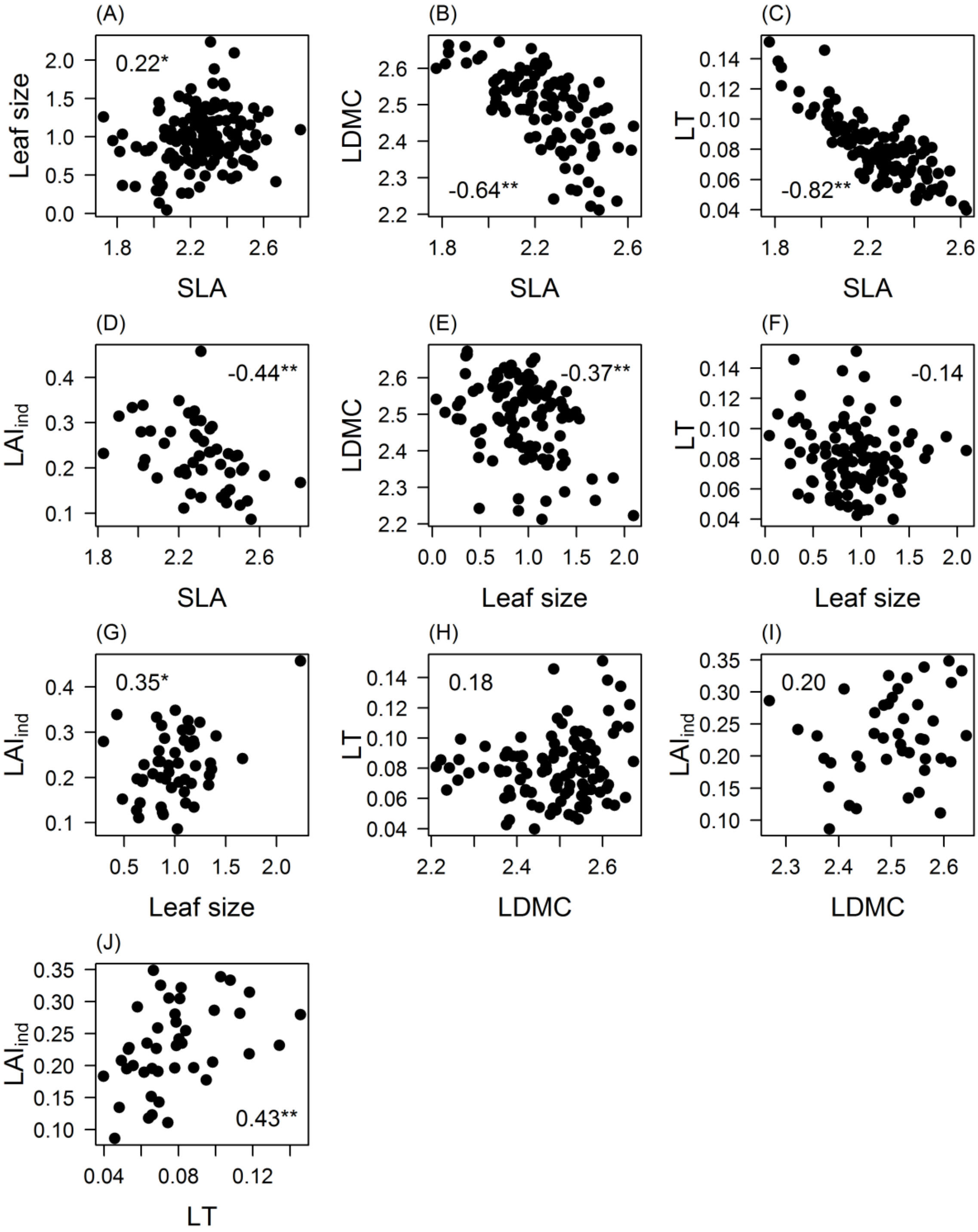

Figure S2. Scatterplots of species mean trait values for all pairwise combinations of SLA, leaf size, LDMC, LT and $\mathrm{LAI}_{\mathrm{ind}}$. Traits were log-transformed. Asterisks indicate that Pearson's correlation coefficients were significant (*P ≤ 0.05; **P ≤ 0.01).

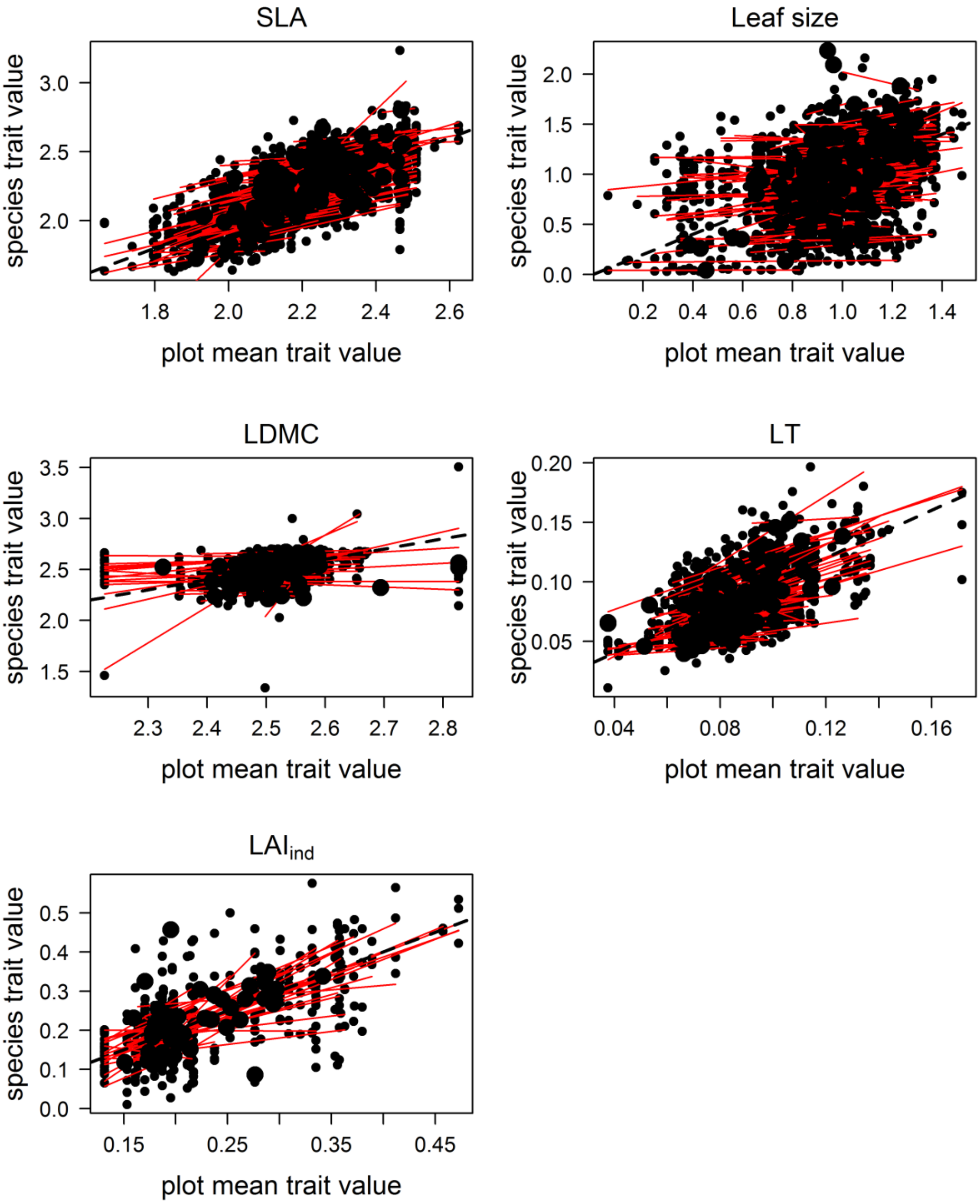

Figure S3. Scatter plots of species trait values *vs* abundance-weighted plot mean trait-values. The large points show the mean position of species across the gradient (beta trait) and mean species trait value (on ordinate). The difference between these, or the distance from the X = Y line, is the alpha trait. The range of occupied plots on the x-axis is the species niche breadth. Regression lines show abundance-weighted least squares regressions of species trait values relative to plot mean trait values.

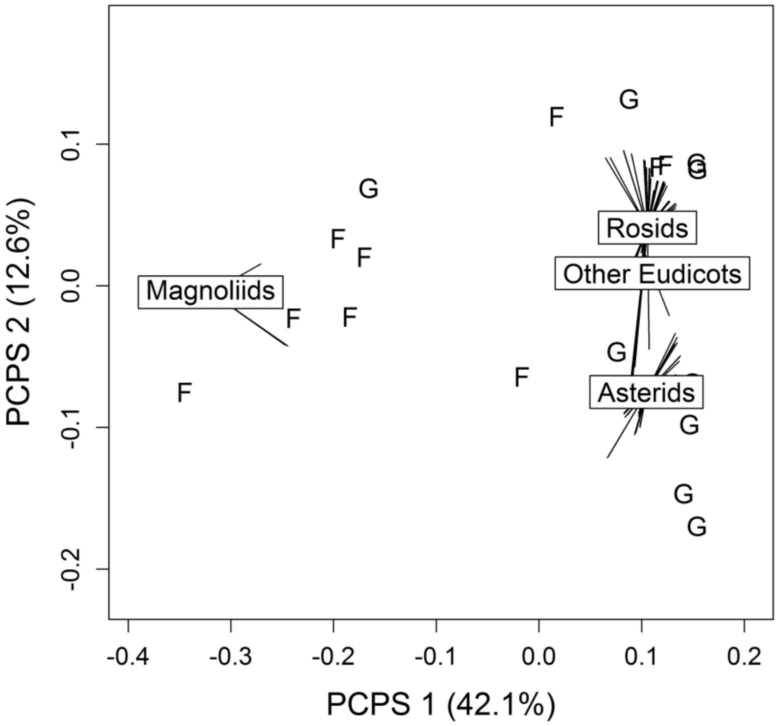

Figure S4. Scatter plot of the two first principal coordinates of phylogenetic structure (PCPS) of juveniles communities of woody species occurring in forest-grassland ecotones in southern Brazil. Plots were pooled to forest (F) and grassland (G) blocks. Segments connect the position of species score to the centroid of the clade, where the clade name is shown.

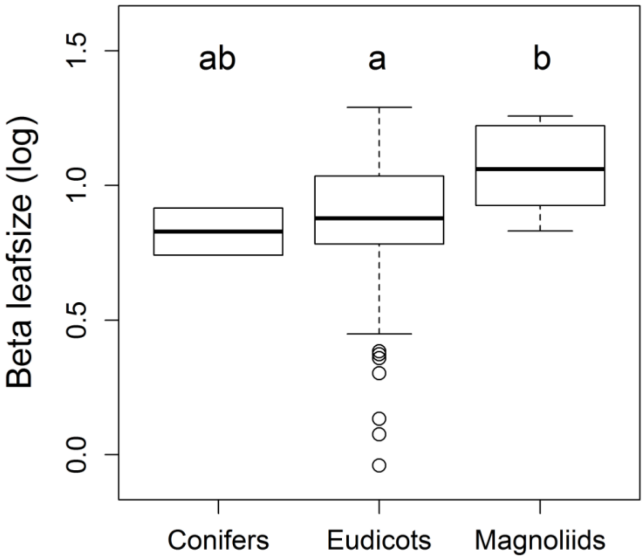

Figure S5. Result of ANOVA comparing the beta component of leaf size between species of conifers, eudicots and magnoliids. Different letters above boxes indicate significant differences ($P \leq 0.05$) between clades.

Capítulo 4. Geographical distribution of angiosperm lineages affects the local phylogenetic structure of tropical tree communities [3]

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Short running head: Lineage geographical distribution affecting local phylogenetic community structure

RESUMO

Objetivo. Responder às seguintes questões: (1) Há associação entre grandes linhagens de angiospermas e os reinos Neotropical e Afrotropical? (2) Há uma tendência de que comunidades locais de árvores neotropicais ou afrotropicais apresentem agrupamento ou repulsão filogenética? (3) Há associação entre a estrutura filogenética local (agrupamento ou repulsão) de comunidades de árvores e a distribuição geográfica de grandes linhagens de angiospermas no Neotrópico e Afrotrópico?

Local. Florestas pluviais tropicais no Neotrópico e no Afrotrópico.

Métodos. Utilizamos dados de abundância de espécies de árvores de uma série de parcelas de 1 ha para sete sítios. A composição filogenética regional através de comunidades foi avaliada por coordenadas principais de estrutura filogenética (PCPS, do inglês *principal coordinates of phylogenetic structure*), que são gradientes filogenéticos ortogonais obtidos a partir da composição de comunidades submetida à ponderação difusa. O índice de parentesco líquido (NRI, do inglês *net relatedness index*) foi utilizado como uma medida da estrutura filogenética local avaliando agrupamento ou repulsão dentro de comunidades considerando-se diferentes tamanhos de bancos regionais de espécies (parcela de 1 ha, reino e global). Comparamos valores de NRI e escores de PCPS entre sítios e entre reinos e avaliamos a relação entre NRI e PCPS.

Resultados. Observamos que a composição filogenética e a estrutura diferem entre o Neotrópico e o Afrotrópico e que diferenças de composição filogenética entre os dois reinos influenciam a estrutura filogenética de comunidades locais. O agrupamento filogenético no Neotrópico foi associado com asterídeas, monocotiledôneas e Magnoliales, enquanto a repulsão filogenética no Afrotrópico foi relacionada a rosídeas e Laurales.

Conclusões principais. As diferenças filogenéticas regionais entre reinos são provavelmente um resultado de taxas diferenciais de especiação e extinção que seguiram a separação de Gondwana. Essas diferenças levaram a probabilidades distintas de se encontrar agrupamento ou repulsão filogenéticas localmente no Neotrópico e Afrotrópico. A utilização conjunta das abordagens de PCPS (para avaliar a variação regional da composição filogenética) e NRI (para avaliar estrutura filogenética local) constitui uma ferramenta útil que pode integrar ainda mais os campos da biogeografia, evolução e ecologia de comunidades.

ABSTRACT

Aim. To answer the following questions: (1) Is there association between major angiosperm lineages and the Neotropical and Afrotropical realms? (2) Is there a trend of Neotropical or Afrotropical local tree communities towards phylogenetic clustering or overdispersion? (3) Is there association between local phylogenetic structure (clustering or overdispersion) of tree communities and the geographical distribution of major angiosperm lineages in the Neotropics and Afrotropics?

Location. Tropical rain forests in the Neotropics and Afrotropics.

Methods. We used data on tree species abundance from a series of 1-ha plots for seven sites. Regional phylogenetic composition across communities was evaluated through principal coordinates of phylogenetic structure (PCPS), which are orthogonal phylogenetic gradients obtained from fuzzy-weighted community composition. The net relatedness index (NRI) was used as a measure of local phylogenetic structure assessing clustering or overdispersion within communities considering different species pool sizes (1-ha plot, site, realm and global). We compared NRI and PCPS scores between sites and between realms and evaluated the relationship between NRI and PCPS.

Results. We found that phylogenetic composition and structure differs between the Neotropics and Afrotropics and that differences in phylogenetic composition between the two realms influence the phylogenetic structure of local communities. Phylogenetic clustering in the Neotropics was associated with asterids, monocots and Magnoliales, while phylogenetic overdispersion in the Afrotropics was related to rosids and Laurales.

Main conclusions. Regional phylogenetic differences between realms are probably an outcome of the differential rates of speciation and extinction following the breakup of Gondwana. These differences lead to different probabilities of finding phylogenetic clustering or overdispersion locally in the Neotropics and Afrotropics. Joining the PCPS approach (to assess regional variation of phylogenetic composition) to the NRI approach (to assess local phylogenetic structure) provides a useful framework that can further integrate the fields of biogeography, evolution and community ecology.

Keywords: Afrotropics, community assembly, historical biogeography, Neotropics, NRI, PCPS, phylogenetic clustering, phylogenetic overdispersion, phylogenetic fuzzy-weighting, tropical rainforest.

INTRODUCTION

Studies have shown that historical factors influence the phylogenetic structure of local communities (Parmentier & Hardy 2009; Leibold et al. 2010; Lessard et al. 2012b), which is likely mediated by regional species pool effects (Ricklefs 1987). The formation of a regional pool of species relies on the biogeographic history to which the biota was subject over the evolutionary time (MacArthur 1972; Cracraft 1994). Some of the processes occurring along the biogeographic history of a region are vicariance (Cracraft 1994), climate change (Ackerly 2009b), long-distance dispersal (Renner 2004) and historical habitat abundance (Zobel et al. 2011). Such historical processes occurred in the Neotropics and Afrotropics after the breakup of Gondwana and have led to different rates of speciation and extinction between the two realms (Parmentier et al. 2007).

Neotropical and Afrotropical biotas have undergone many, if not all, of the above-mentioned biogeographical processes during their history of vicariance. The geological breakup of Gondwana, which started in the Cretaceous (ca. 100 Ma), coincides with the early evolution of many of the currently living families of angiosperms (Bell et al. 2010). The separation of western and eastern Gondwana biotas promoted the isolation of populations, subjecting them to different climatic conditions across time, especially during the Cenozoic (Morley 2011). For instance, there is much stronger support for the role of major dry periods affecting floristic composition in the Afrotropics during the glacial ages of the late Cenozoic than for the Neotropics (Colinvaux et al. 2000; Parmentier et al. 2007). This might have led to high extinction rates in the Afrotropics, while a higher stability coupled with a larger extension of forest would have enabled higher speciation and lower extinction of angiosperms in the Neotropics (Gentry 1982; Parmentier et al. 2007). Although major climatic and historical differences might have played a major role in structuring the species pool of each realm, phylogenetic data indicates that long-distance dispersal promoted the exchange of biota between South America and Africa through the Cenozoic (Pennington et al. 2004), possibly obscuring basal vicariant patterns (Sanmartín & Ronquist 2004).

Ecologists have for long studied floristic connections between Neotropical and Afrotropical rainforests (Raven & Axelrod 1974; Gentry 1982). Their studies typically evaluated species richness of families or genera across sites within a continent or between continents. Currently, the existence of phylogenetic super-trees and the development of novel methodological frameworks enables studying local to regional processes structuring local communities from an eco-evolutionary standpoint (Webb et al. 2002; Cavender-Bares et al. 2009; Pillar & Duarte 2010; Lessard et al. 2012a; Duarte et al. 2014). For instance, the net relatedness index (NRI) is a measure of phylogenetic structure that enables the assessment of local phylogenetic clustering and overdispersion relative to a regional species pool (Webb et al. 2002). By varying the size at which the regional pool is defined to compute NRI (using null models), we can find signals of ecological or biogeographic processes acting from local to regional scales structuring local communities (Swenson et al. 2006; Lessard et al. 2012b). Phylogenetic clustering and overdispersion relative to small species pools are generally interpreted as signal of environmental filtering and biotic interactions such as competition and facilitation (Webb et al. 2002; Eiserhardt et al. 2013), while the same patterns relative to large species pools would indicate that broad-scale, biogeographic and evolutionary processes are more important to the local structuring of communities (Webb et al. 2002; Cavender-Bares et al. 2009).

Nonetheless, NRI provides no information of which lineages are associated to the phylogenetic clustering or overdispersion patterns. For this purpose, principal coordinates of phylogenetic structure (PCPS) can be used (Duarte 2011). PCPS are ordination vectors expressing orthogonal phylogenetic gradients across communities, and have been used to assess phylogenetic composition across sites at local, regional or continental scales (Duarte 2011; Duarte et al. 2012; Brum et al. 2013; Duarte et al. 2014). It is possible to verify the influence of historical biogeography on local community patterns by relating local NRI to PCPS of a set of communities whose phylogenetic composition reflects the phylogenetic composition of the biogeographic region. A significant relationship between local NRI and a PCPS vector describing a phylogenetic gradient across sites in regions with different biogeographic histories indicate that historical biogeography influences local community structure via phylogenetic composition, given that regional phylogenetic composition is determined by the idiosyncratic history experienced by each region.

To our knowledge, studies evaluating inter-continental phylogenetic community structure and composition patterns have not yet been undertaken. In this study, we aimed to assess the influence of biogeographic history on local community structure by evaluating the relationship of regional phylogenetic composition and local phylogenetic structure of rainforest tree communities in the Neotropics and Afrotropics. For this, we built regional pools of tree species based on 96 forest surveys. We addressed the following questions: (1) Is there association between major lineages of angiosperm trees and the Neotropical and Afrotropical realms? (2) Is there a trend of Neotropical or Afrotropical tree communities towards phylogenetic clustering or overdispersion? (3) Is there association between local phylogenetic structure of tree communities and the geographical distribution of major angiosperm lineages in the Neotropics and Afrotropics? We hypothesised that each realm has a characteristic phylogenetic composition and that the broad geographical distribution of phylogenetic lineages, which includes a strong historical component, affects the phylogenetic structure of local communities.

MATERIAL AND METHODS

Study sites

We used tree inventories of the Tropical Ecology, Assessment and Monitoring Network (TEAM) (data sets available at http://www.teamnetwork.org). We selected seven sites containing information of tree composition and abundance in tropical rainforests (Fig. 1). Other TEAM sites were not selected because plant material was not identified by the time we performed this study. The sites were Volcán Barva (La Selva Biological Station and Braulio Carrillo National Park, Costa Rica), Manaus (three different field stations near the city of Manaus, Brazil) and Caxiuanã (Caxiuanã National Forest, Brazil) in the Neotropics; and Korup (Korup National Park, Cameroon), Bwindi (Bwindi Impenetrable National Park, Uganda), Udzungwa (Udzungwa Mountain National Park, Tanzania) and Ranomafana (Ranomafana National Park, Madagascar) in the Afrotropics. For each site, we used the most recent inventory data available, which ranged between Aug 2010 and May 2011. The TEAM Network sampling design for trees consists of sites of rainforest tropical forests with a variable number of 1-ha plots (100 x 100 m), each subdivided in 25 subplots of 400 m^2 (20 x 20 m), where trees with diameter at breast height ≥10 cm were recorded. Plots were placed in closed-canopy moist forest habitats. Each of the selected sites was composed by six plots of 1 ha, except for Korup and Volcán Barva which were composed by five and nine plots, respectively. The data from all these plots were gathered using a defined, shared and therefore comparable method, which follows quality controls, such as including late successional forests with little anthropogenic impact. More details on sampling design and data collection is available in TEAM Network (2010). In this study, we used the data on identity and abundance of angiosperm species per 400-m^2 subplot, which for some analyses were pooled within 1-ha plots. The majority of individuals were identified to the species level. Unidentified individuals were excluded from the data matrix. Each individual identified to the genus level at a given site was regarded as a species particular of that site. All genera were checked and classified into families according to the APG III system (APG 2009).

Regional species pool

We built regional species pools for Neotropical and Afrotropical rainforests, i.e. Central American, Amazonian, Guineo-Congolian and Malagasy rainforests (excluding Neotropical Atlantic rainforests) based on 32 surveys published in the literature and 64 Alwyn Gentry's forest sites (available at <http://www.wlbcenter.org/gentry_data.htm>). See Appendix S1 for the list of published studies and the Gentry's sites used. We standardised the lists by removing non-arboreal species and correcting for nomenclatural synonyms using the online tool Taxonomic Name Resolution Service v3.2 (Boyle et al. 2013). By compiling tree species lists for the rainforests of the Neotropics and Afrotropics, we have defined regional species pools with biogeographic meaning (Lessard et al. 2012b). This enabled testing if the species pool defined by our study sites reflected the species pool of the realm.

Phylogeny

The phylogenetic tree of sampled species was generated from the megatree R20120829 (available at https://github.com/camwebb/tree-of-trees/blob/master/megatrees/R20120829.new), which is based on the phylogenetic hypothesis proposed by APG III (APG 2009). We first standardised the resolution of the tree, because most of this tree has the resolution at the family level, with few families with phylogenetic relationships between genera. Then, we removed infra-family phylogenetic relationships of these families, keeping the resolution at the family level for the whole tree, with polytomies linking species within a genus and genera within a family. We used the module *Phylomatic 2* in the software Phylocom 4.2 (Webb et al. 2008) to build a megatree with all the species present in our global species pool, i.e. including both Neotropics and Afrotropics (Appendix S2). The tree branch lengths were adjusted through the *BLADJ* algorithm in Phylocom 4.2 software (Webb et al. 2008), following recently published clade age estimates (Bell et al. 2010). Undated clades were evenly interpolated between dated clades. Finally, we calculated a matrix of phylogenetic distances (in millions of years) between pairs of terminal taxa for the entire phylogeny.

Phylogenetic composition

The variation of phylogenetic composition, considering the 1-ha plots or 400-m^2 subplots as sampling units, was characterised using principal coordinates of phylogenetic structure, the so-called PCPS approach (Duarte 2011; Duarte et al. 2012; Duarte et al. 2014), which consists of orthogonal vectors expressing phylogenetic gradients across communities. PCPS vectors were extracted by principal coordinates analysis (PCoA) on matrix $\mathbf{P}$ (Appendix S3, Fig. S1) of phylogeny-weighted species composition for each 1-ha and 400-m^2 subplot across all sites (Pillar & Duarte 2010). For computing matrix $\mathbf{P}$, two matrices were necessary: $\mathbf{S_F}$ with pairwise phylogenetic similarities between species, ranging from 0 to 1, which were derived from the above mentioned phylogenetic distances, and $\mathbf{W}$ of communities described by species abundance. The full matrix $\mathbf{S_F}$, with both sides of the main diagonal, was subjected to fuzzy weighting, which consists of standardising phylogenetic similarity values within columns by marginal totals, generating matrix $\mathbf{Q}$, which contains degrees of phylogenetic belonging of every species to fuzzy sets defined by each other species. Matrix **Q** is then used to weight species abundances in the communities, generating by matrix multiplication **P** = **Q** x **W**. The PCPS with the highest eigenvalue describes broad phylogenetic gradients related to the split of deep tree nodes across plots, such as that connecting eudicots and magnoliids; as the eigenvalues of other PCPS vectors decrease, finer phylogenetic gradients related to splits of shallower nodes such as families or genera appear (Duarte et al. 2014). We used square-root transformed Bray-Curtis dissimilarities for performing the PCoA. PCPS scores were compared between sites and between realms using ANOVA. Matrix **P** and PCPS were computed using the package SYNCSA v. 1.3 (Debastiani & Pillar 2012; available at http://cran.r-project.org/web/packages/SYNCSA/) for the R statistical environment (R Core Team 2013).

Phylogenetic structure

Local phylogenetic structure was evaluated using the net relatedness index (NRI; Webb et al. 2002), which is the standardised effect size of mean pairwise phylogenetic distances (MPD) between co-occurring taxa in a community. These distances are measured in millions of years down to the common ancestor of two species and back up to the other tip (Kraft & Ackerly 2010). NRI quantifies overall clustering or overdispersion of taxa in a given community with respect to phylogenetic relatedness between species. Positive values of NRI indicate that taxa are more related than expected by chance (phylogenetic clustering), while negative values indicate that taxa are less related than expected by chance (phylogenetic overdispersion). The significance of NRI is tested through a null model that compares the observed MPD to a null distribution of MPD measured on 999 null communities (Kraft & Ackerly 2010). Given that the null communities are created by randomly drawing an equal number of species from a phylogeny, construction of the phylogeny and an appropriate null model depend on a specified species pool (Hardy 2008; Kembel 2009). In this study, we used the null model *phylogeny.pool* (Kembel et al. 2011), which maintains the species richness and randomises the identity of species occurring in each sampling unit. This null model draws species without replacement from the list of species in the specified phylogeny pool with equal probability of being included in the null communities. For all scales, the NRI values were calculated by weighting species abundances. *P*-values can be considered significant when the observed values are lower or higher than the 2.5% extreme of the null distribution ($\alpha = 0.05$), indicating phylogenetic clustering and overdispersion, respectively. NRI values at the 1-ha plot scale were compared between sites and between realms using ANOVA. The NRI was calculated using the package Picante v. 1.6 (Kembel et al. 2010) in the R statistical environment.

The statistical power of phylogeny-based tests varies according to the spatial scale, community richness and species pool (Swenson et al. 2006; Kraft et al. 2007). To evaluate whether the phylogenetic structure changes according to the spatial scale defining the species pool, we calculated NRI values for each 400-m^2 subplot and each 1-ha plot using varying species pools: 1-ha plot (only for 400-m^2 subplots), site, realm (Neotropics or Afrotropics) and global (Neotropics plus Afrotropics). The effect of the species pool size on NRI values for subplots and plots was tested separately for each site using repeated measures ANOVAs, as compared NRI values were measured for the same sampling units in relation to varying species pool sizes.

Linking local to regional phylogenetic patterns

We used linear regression to link local phylogenetic structure (NRI calculated for 1-ha plots with species pool at the realm scale) and the plot score on the regional phylogenetic composition gradient (first two PCPS eigenvectors). We used NRI as the response variable and PCPS eigenvectors as predictors. PCPS were computed using a phylogenetic tree containing all the species of the seven study sites. To evaluate if this tree reflected the continent-wide phylogenetic tree for the rainforests of Neotropics and Afrotropics, we compared clade relative richness between the species pool of the Neotropical and Afrotropical study sites and the species pool of each realm (based on the 96 surveys). Clade relative richness was calculated as the proportion of species richness (per order) in relation to the regional species richness (represented by the set of TEAM sites within a realm or by the set of surveys from the literature). We compared clade relative richness observed in sites and expected in the realm using a chi-square test. If observed and expected clade relative richness do not differ, we can consider that PCPS gradients reflects the actual regional phylogenetic composition of Neotropical and Afrotropical rainforests.

Linear regressions and ANOVAs were performed using the statistical software SigmaPlot 11.0 (Systat Software©, Inc., 2008, San Jose, CA, USA).

RESULTS

The seven sites together comprised 2069 tree species belonging to 607 genera and 118 families, totalling 29264 individuals (Appendix S3, Table S1). The three sites in the Neotropics had more than twice the number of species of the four sites in the Afrotropics. The clade rosid had the highest fraction of species (57% of total species number), followed by asterids (25.8%), magnoliids (13.1%) and monocots (ca. 1%). The global species pool compiled for the Neotropics and Afrotropics had 4987 species, nearly 2.5 times the species number of the study sites. Considering that the real species pool of the Amazon rainforest harbours ca. 16000 tree species (ter Steege et al. 2013) and that the Afrotropical rainforest have, let us say, one third of this number (Gentry 1982), i.e. ca. 5000 species, our regional species pool would represent nearly 25% of the real species pool (~5000/21000). We can assume that this sample is a good representation of the phylogenetic composition of Neotropical and Afrotropical pool of rainforest tree species. The chi-square test showed that clade relative richness for the set of study sites of each realm did not differ from the clade relative richness considering the realm species pool: for the Neotropics, $\chi^2 = 0.064$; d.f. = 26; $P = 0.999$; for the Afrotropics, $\chi^2 = 0.082$; d.f. = 26; $P = 0.999$. This means that the phylogenetic composition of the study sites in a realm reflects the phylogenetic composition of the rainforests of the realm as a whole. In conclusion, the distribution of clades associated with Neotropical and Afrotropical community scores in the PCPS can be interpreted as the distribution of clades in the continental species pool.

The first two PCPS accounted for ca. 39% of the total variation in phylogeny-weighted species composition; the first eigenvector explained 28.7% of the total variation and the second 10.2% (Fig. 2a). PCPS I represented a phylogenetic gradient separating communities characterised by major angiosperm lineages (Fig. 2b): eudicots (asterids, rosids, Caryophyllales, Santalales and other eudicots) on the left of the chart, monocots on the middle and magnoliids (Magnoliales, Laurales, Canellales and Piperales) and Chloranthales on the right. PCPS II described a phylogenetic gradient within these clades, separating Neotropical and Afrotropical communities. Neotropical communities were characterised mainly by asterids, monocots and Magnoliales, while Afrotropical communities were characterised by rosids, Santalales and Laurales (Fig. 2). Considering more specific site-clade affinities, Volcán Barva was associated with monocots and Ranomafana with Laurales. Overall, the phylogenetic composition did not differ on PCPS I (Fig. 3a), but significantly differed on PCPS II between Neotropics and Afrotropics considering the 1-ha plot level (Fig. 3b). PCPS analysis of the 400-m² subplots generated no clear pattern of ordination of the sampling units in relation to the realms (Appendix S3, Fig. S2).

NRI values for 1-ha plots significantly differed between Neotropics and Afrotropics showing a clear tendency of phylogenetic clustering in the Neotropics (Fig. 4), especially in Manaus and Caxiuanã, where the clustering pattern was consistent for all pool sizes considered (Fig. 5). The other sites presented NRI median values closer to zero when the species pool was defined at site and realm scales (Fig. 5). The exception was Ranomafana, whose communities tended to be more overdispersed in relation to the realm species pool than in relation to site species pool (Fig. 5, 6). Three out of the four Afrotropical sites (Korup, Bwindi and Udzungwa) slightly increased their NRI values from site to global scales of definition of the species pool size (Fig. 5, 6). NRI values for 400-m² subplots have also showed a consistent pattern of phylogenetic clustering for all species pool sizes in Manaus and Caxiuanã (Appendix S3, Fig. S3). Korup also presented a tendency for positive (but low) NRI values for all pool sizes. The other sites maintained their NRI values near to zero when the species pool was defined at 1-ha plot and site scales. Nevertheless, Ranomafana presented a marked tendency for phylogenetic overdispersion in relation to the Afrotropical and global species pools (Appendix S3, Figs. S3-S4). Bwindi and Udzungwa showed a slight trend towards clustering in relation to the global pool of species. All the pairwise comparisons of NRI across species pool sizes were significant, except the comparison site vs. realm for Korup and Udzungwa using 1-ha plots and Udzungwa using 400-m² subplots. Overall, NRI increased with increasing pool sizes, but the pattern was the opposite for Volcán Barva and

Ranomafana, which are disjunct from their realms. The patterns of increase or decrease across scales of species pool definition were fairly consistent between analyses using 1-ha plots and 400-m² subplots (Fig. 6, Appendix S7).

NRI values were significantly and markedly associated with PCPS I (Fig. 7a). Phylogenetically-clustered communities were related to negative scores of PCPS I, which are characterised by eudicot lineages such as asterids and rosids. On the other hand, phylogenetically-overdispersed communities were associated with positive scores of PCPS I and magnoliid lineages such as Magnoliales, Laurales and Canellales. Association of NRI values with PCPS II was also significant (Fig. 7b). On the one hand, NRI was related to a trend for phylogenetic clustering in Neotropical communities associated with asterids, monocots and Magnoliales (Fig. 2, 7); on the other hand, it was related to a tendency for Afrotropical communities to be phylogenetically overdispersed, which was associated with rosids and Laurales (Fig. 2, 7).

DISCUSSION

Historical processes affect the formation of regional species pools (MacArthur 1972; Cracraft 1994), which in turn influence local community assembly (Ricklefs 1987). Thus, we could expect local patterns of phylogenetic structure to be, in great extent, an outcome of the characteristic phylogenetic composition of the regional species pool (Cracraft 1994). Indeed, we found that the probability of observing local phylogenetic clustering or overdispersion was associated with the regional phylogenetic composition and that both were geographically structured across the Neotropics and the Afrotropics. As expected, we found no relationship between the split of basal nodes (e.g. eudicots and magnoliids) and the two realms, suggesting that transatlantic dispersal homogenised Neotropical and Afrotropical rainforest tree communities at this deep phylogenetic level (Sanmartín & Ronquist 2004). Nevertheless, at the order level, we found association of asterids, monocots and Magnoliales with the Neotropics and rosids and Laurales with the Afrotropics. Vicariance per se, i.e. the breakup of Gondwana, is not likely to be the major cause of such associations as long-distance dispersal played a significant role in structuring Neotropical and Afrotropical floras (Pennington et al. 2004). Rather, these associations were likely caused by the different biogeographic histories experienced by each region during millions of year of isolation (Ghazoul & Sheil 2010; Morley 2011).

For instance, lineages of monocots and eudicots appear to have undergone higher diversification in the Neotropics than elsewhere (Richardson et al. 2001; Kissling et al. 2012), which could explain their dominance over the phylogenetic patterns found in the present study. Association of monocots with Neotropics is likely due to the dominance of Arecaceae species in Neotropical forests (ter Steege et al. 2013). Higher diversification of eudicots and monocots in the Neotropics can be explained by the constancy of everwet climates since the Miocene and the uplift of the Andes during the Cenozoic (Gentry 1982; Maslin et al. 2005; Morley 2011). Environmental stability during Late Cenozoic would have also prevented a high extinction rate in the Neotropics (Colinvaux et al. 2000; Maslin et al. 2005). On the other hand, major extinctions in Africa seem to be related to strong episodes of aridity, which have reduced the rainforest to isolated patches (Parmentier et al. 2007; Ghazoul & Sheil 2010). Habitats that are evolutionary more abundant are expected to harbour a richer species pool (Zobel et al. 2011). Thus, the maintenance of large and continuous rainforest areas in the Neotropics likely protected eudicot and monocot tree populations from extinction due to small population sizes, which otherwise would have occurred in Afrotropical refugia during glacial ages (Parmentier et al. 2007). Therefore, even though long-distance dispersal have been important to the formation of Neotropical and Afrotropical floras long after the Gondwanan vicariance (Pennington et al. 2004), historical differences in climatic changes between both continents have led to different speciation and extinction rates between the Neotropics and Afrotropics (Gentry 1982; Parmentier et al. 2007; Ghazoul & Sheil 2010). Hence, these historical processes are likely to have determined major differences of regional phylogenetic composition between Neotropical and Afrotropical floras.

Interestingly, despite the expected increase in phylogenetic clustering as species pool size increased from plot to site level (Swenson et al. 2006), NRI values presented an opposite patterns in two sites. In most sites, increased species pool size led to higher phylogenetic clustering (see also Lessard et al. 2012b), indicating that species inclusion increased the amount of new phylogenetic information in the species pool. This is consistent with the idea that because clades diversify within a region, species in a region tend to be in average more related to each other than to species from other region (Webb et al. 2002). On the other hand, in some sites (Volcán Barva and Ranomafana) increasing species pool led to decreased NRI values, which means that in those sites the addition of species in the phylogenetic pool did not increase the amount of phylogenetic information. If a region is homogeneous regarding the lineages occurring in its communities, changing the species pool from the plot to the region level would just increase the number of species without incorporating new phylogenetic information, augmenting the amount of phylogenetic overdispersion as the species pool size increases. Changes in NRI values as the size of the species pool considered increases supports the role of biogeographic history on the structuring of local communities (Webb et al. 2002; Lessard et al. 2012b).

Species richness and relative abundance per clade, especially genera and family, tend to keep consistently constant over evolutionary time (Wing et al. 2009) and across regions (Ricklefs & Renner 2012), at least in tropical, climatic stable, communities. This is expected to be true especially if major barriers prevent dispersal between regions. Comparing realms, we found a general trend for phylogenetic clustering in the Neotropics, while the Afrotropics tended to have random or phylogenetic overdispersed communities. Looking at a finer scale, we could consider that local phylogenetic structure patterns differed between biogeographic regions: Central American communities, represented by Volcán Barva, presented lower phylogenetic clustering than Amazonian communities (i.e. Manaus and Caxiuanã), while Malagasy communities, represented by Ranomafana, were more overdispersed phylogenetically than Guineo-Congolian communities (i.e. Korup, Bwindi and Udzungwa). Each of these patterns was accentuated under larger definitions of the species pool, i.e. when compared to the whole realm. Central American and Amazonian communities are separated by the Andes. Lower phylogenetic clustering (higher phylogenetic diversity) of Volcán Barva communities in relation to the Neotropical species pool might be explained by a higher importance of clades from Laurasian clades in the west of the Andes (Gentry 1982). Malagasy and Guineo-Congolian communities are separated by the sea and a large extension of dry environments, both in the east of Africa and west of Madagascar. Higher phylogenetic overdispersion in Malagasy communities might be related to the presence of Australasian taxa in Madagascar (Raven & Axelrod 1974). Although we found a pattern structured in biogeographic regions, we should not set it as definitive, as we have no replicates for Central America and Madagascar.

Once a regional pool of species has been formed by biogeographic history, local ecological processes may filter species according to their functional traits (Weiher & Keddy

1995; Zobel 1997; Götzenberger et al. 2012). Under niche conservatism, environmental filtering would select closely-related species with similar traits generating phylogenetic clustering, while biotic interactions such as competition would select distantly-related species with dissimilar traits resulting in phylogenetic overdispersion (Webb et al. 2002; Cavender-Bares et al. 2009). Studies have shown that other biotic interactions such as facilitation and parasitism could also originate phylogenetically overdispersed communities (Verdú et al. 2009; Ricklefs & Renner 2012), while competition could also lead to phylogenetic clustering (Mayfield & Levine 2010). Our resulting patterns suggest that niche-based processes are acting at the local scale, especially at the 1-ha plot scale. Given a regional pool of species whose phylogenetic composition was determined by history, the ecological processes would select species from this "phylogenetic pool" according to their expressed functional traits, which can carry or not a phylogenetic signal (Cadotte et al. 2009). At a finer scale, the 400-m² subplots, complexity and dynamics of the microenvironment summed to the stochasticity in dispersal and neutral birth-death processes (ecological drift) are also expected to play an important role in structuring highly diverse metacommunities (Hubbell 2001; Ricklefs 2012). This is supported by the fact we did not find a distinguishable pattern in the PCPS ordination of 400-m² subplots. Therefore, the variation in phylogenetic structure patterns within region may be due to the complex interplay between presence or absence of phylogenetic niche conservatism in lineages, strength of environmental and biotic filters and neutrality.

In synthesis, we found that differences in phylogenetic composition between the Neotropics and Afrotropics influence the phylogenetic structure of local communities. A more complete and definitive overview of the relationship between regional and local phylogenetic patterns in tropical rainforest communities depends upon the establishment of a higher number of forest plots in different continents using nested designs. Given that the biogeographic history of the region determines the regional phylogenetic composition and that ecological and neutral processes are expected to drive local community assembly, joining the PCPS approach (to assess regional phylogenetic composition) to the NRI approach (to assess local phylogenetic structure) provides a useful framework that can further integrate the fields of biogeography, evolution and community ecology.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Surveys used to build regional species pools.

Appendix S2 Phylogenetic tree for the global species pool.

Appendix S3 Supplementary table and figures.

DATA ACCESSIBILITY

All forest subplot to site data are available at http://www.teamnetwork.org/.

BIOSKETCHES

Marcos B. Carlucci is an ecologist interested in understanding how organisms assemble into communities. In his PhD dissertation, he is using functional and phylogenetic approaches to study the assembly of woody plant communities from local to regional scales. G.D.S.S., V.D.P. and L.D.S.D. are ecologists studying community assembly from functional and phylogenetic perspectives at the Federal University of Rio Grande do Sul, Brazil. The other authors are collaborators of the Tropical Ecology Assessment & Monitoring Network - TEAM (http://www.teamnetwork.org/). Author contributions: M.B.C., G.D.S.S. and L.D.S.D. conceived the ideas; D.S., F.R., I.L.A., J.H., J.C.R., L.V.F., U.G., D.K., B.M., E.M., A.C.A.O., D.C.L., D.T., M.N.S. and G.B.C. collected the data; M.B.C., G.D.S.S. and L.D.S.D. analysed the data; and M.B.C., G.D.S.S., D.S., V.D.P. and L.D.S.D. led the writing.

LIST OF FIGURE LEGENDS

Figure 1. Location of the seven study sites of tropical forests in the Neotropics and Afrotropics. See main text for information on the sites.

Figure 2. Scatter diagram of the two first principal coordinates of phylogenetic structure (PCPS) of tropical tree communities. Ordination axes can be interpreted as gradients of phylogenetic composition of major lineages of angiosperms. (a) PCPS scores for 1-ha plots located in forest sites in the Neotropics (grey) and Afrotropics (white). (b) Association between major clades of angiosperms and PCPS axes. Points represent species plotted according to their correlations to PCPS vectors. Sites are ordered from left to right according to their longitude (west to east). Site acronyms: BIF – Bwindi, CAX – Caxiuanã, KRP – Korup, MAS – Manaus, RNF – Ranomafana, UDZ – Udzungwa, VBA – Volcán Barva.

Figure 3. Comparison of phylogenetic composition between the Neotropics and Afrotropics using ANOVA comparing scores of PCPS. Phylogenetic composition did not differ between realms for PCPS I (a), but differed for PCPS II (b).

Figure 4. The mean phylogenetic structure (for 1-ha plots) significantly differs between Neotropics and Afrotropics as demonstrated by an ANOVA comparing NRI values between groups.

Figure 5. Phylogenetic structure of angiosperm tree communities in Neotropical and Afrotropical forest sites. Net Relatedness Index (NRI) values for each 1-ha plot are represented by white circles. NRI values were obtained considering increasing species pool sizes: (a) site, (b) realm (Neotropics or Afrotropics), and (c) global (Neotropics + Afrotropics). Black circles are NRI median values for each site. Site acronyms in the Fig.2.

Figure 6. Effect of species pool size on NRI values for 1-ha plots in Neotropical (grey) and Afrotropical (white) forests. Repeated measures ANOVAs for each site have shown that changing the species pool from the local to global scales generally altered NRI values (see the main text for detailed results). Standard errors are indicated. Site acronyms in the Fig.2.

Figure 7. Relationship between phylogenetic composition (PCPS) and phylogenetic structure (NRI) in Neotropical (grey) and Afrotropical (white) angiosperm tree communities at 1-ha scale. (a) PCPS I vs. NRI. (b) PCPS II vs. NRI. Site acronyms in the Fig.2.

FIGURES

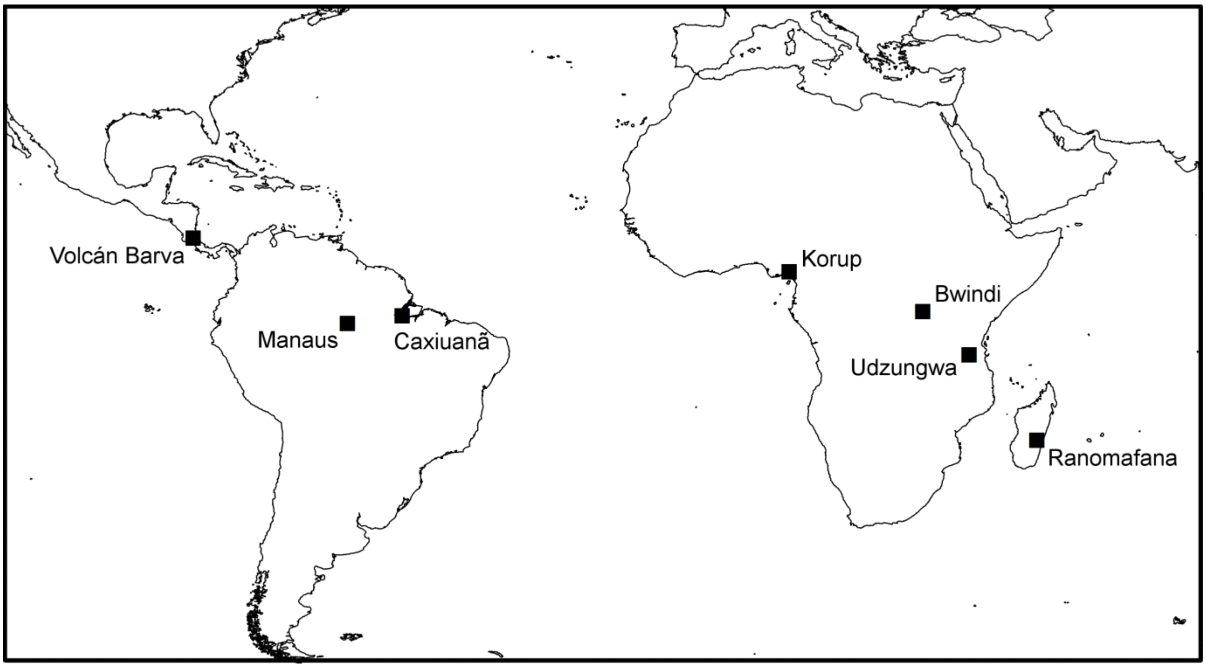


Figure 1

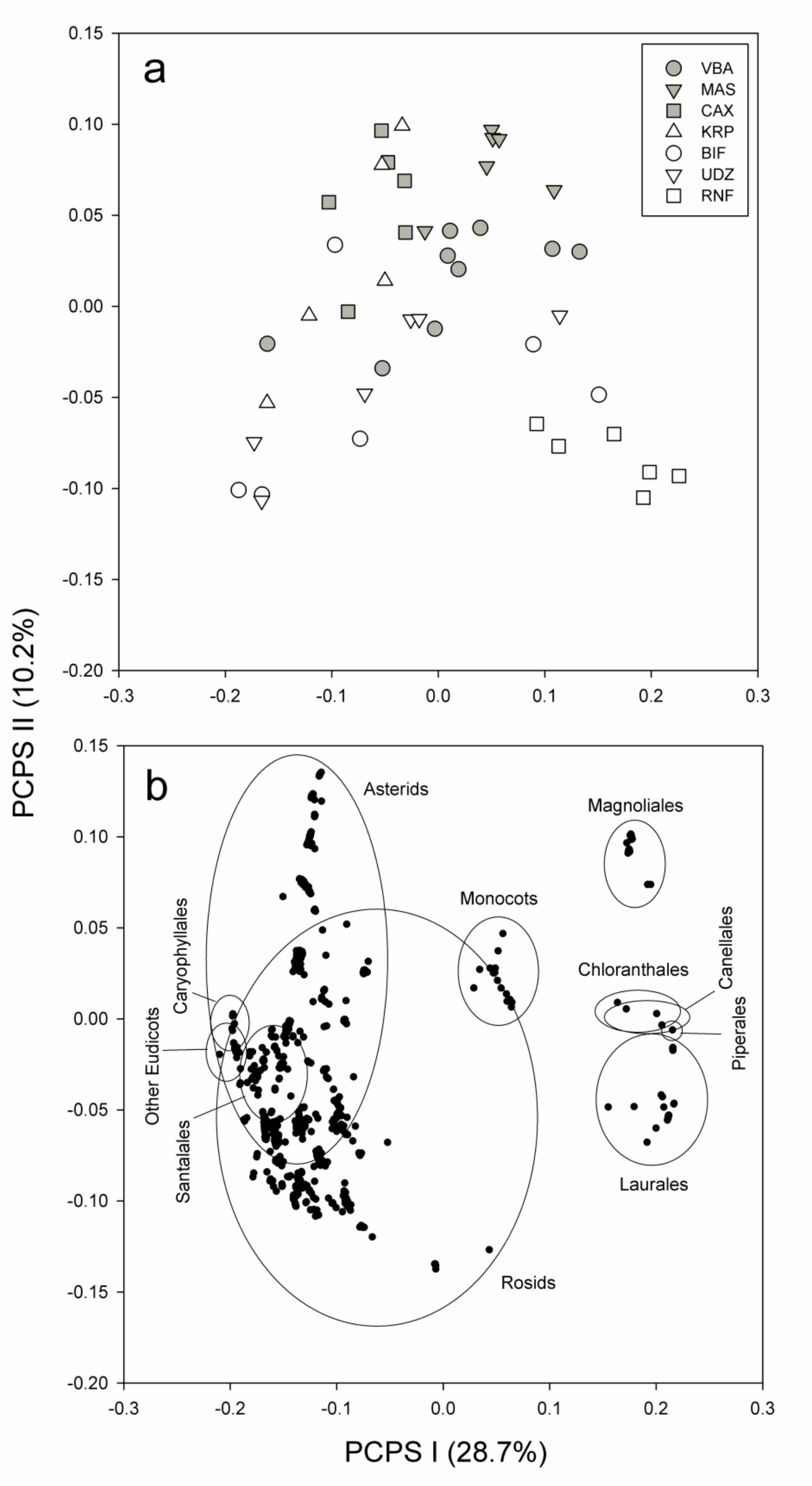

a
● VBA
▼ MAS
■ CAX
△ KRP
○ BIF
▽ UDZ
□ RNF
b
Asterids
Magnoliales
Monocots
Caryophyllales
Chloranthales
Canellales
Piperales
Other Eudicots
Santalales
Laurales
Rosids
PCPS II (10.2%)
PCPS I (28.7%)
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3

Figure 2

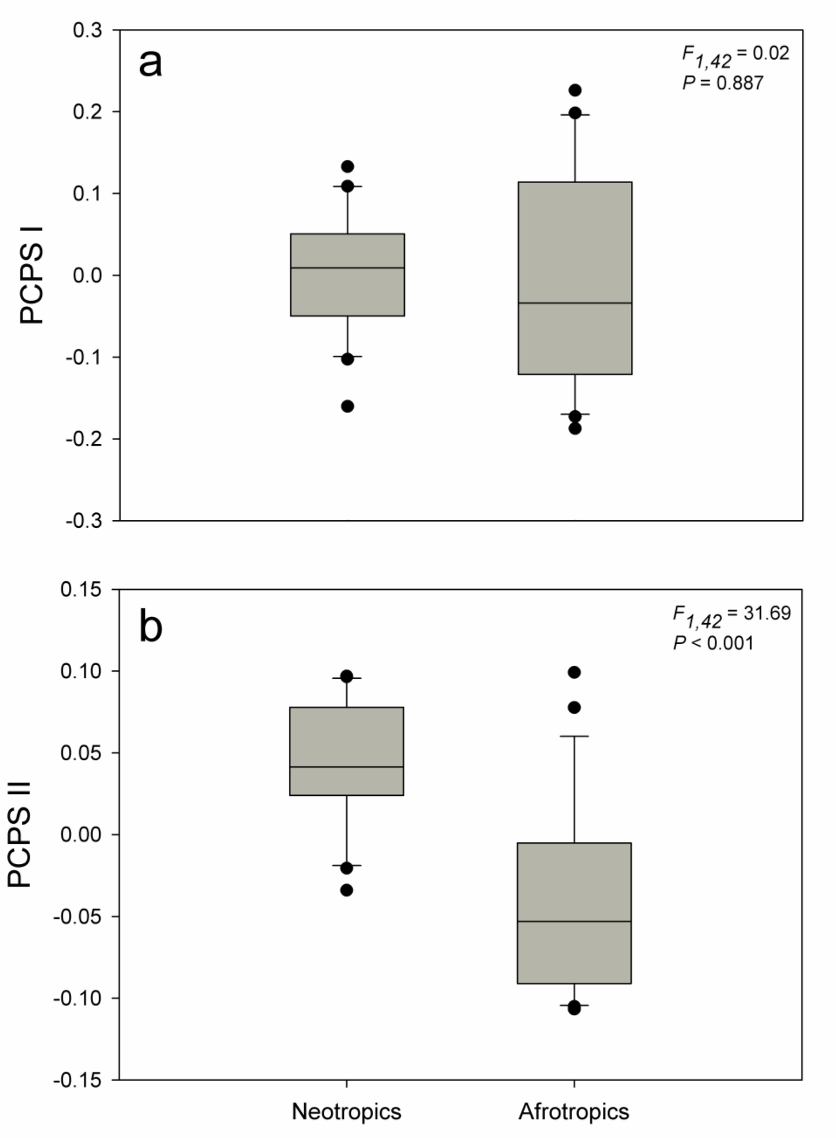

a
F1,42 = 0.02
P = 0.887
PCPS I
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
b
F1,42 = 31.69
P < 0.001
PCPS II
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
Neotropics
Afrotropics

Figure 3

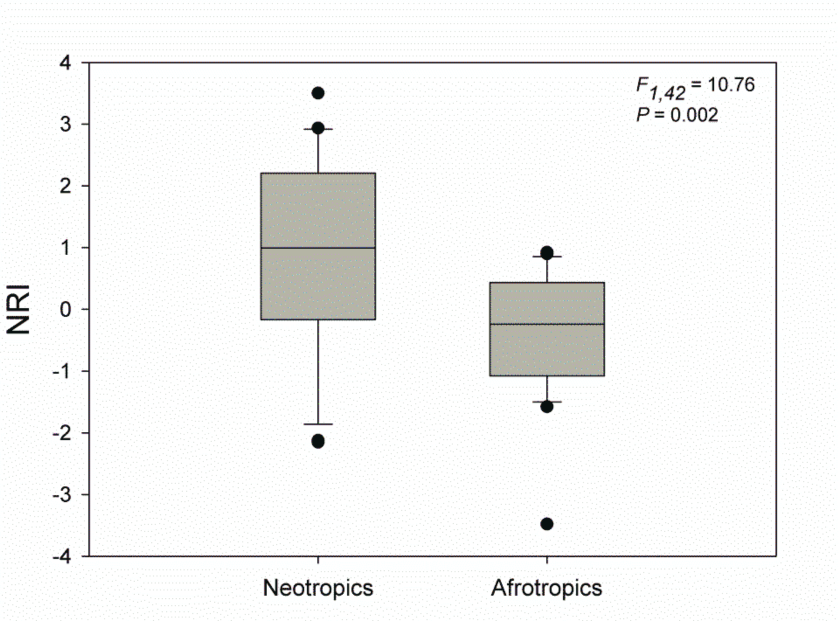


Figure 4

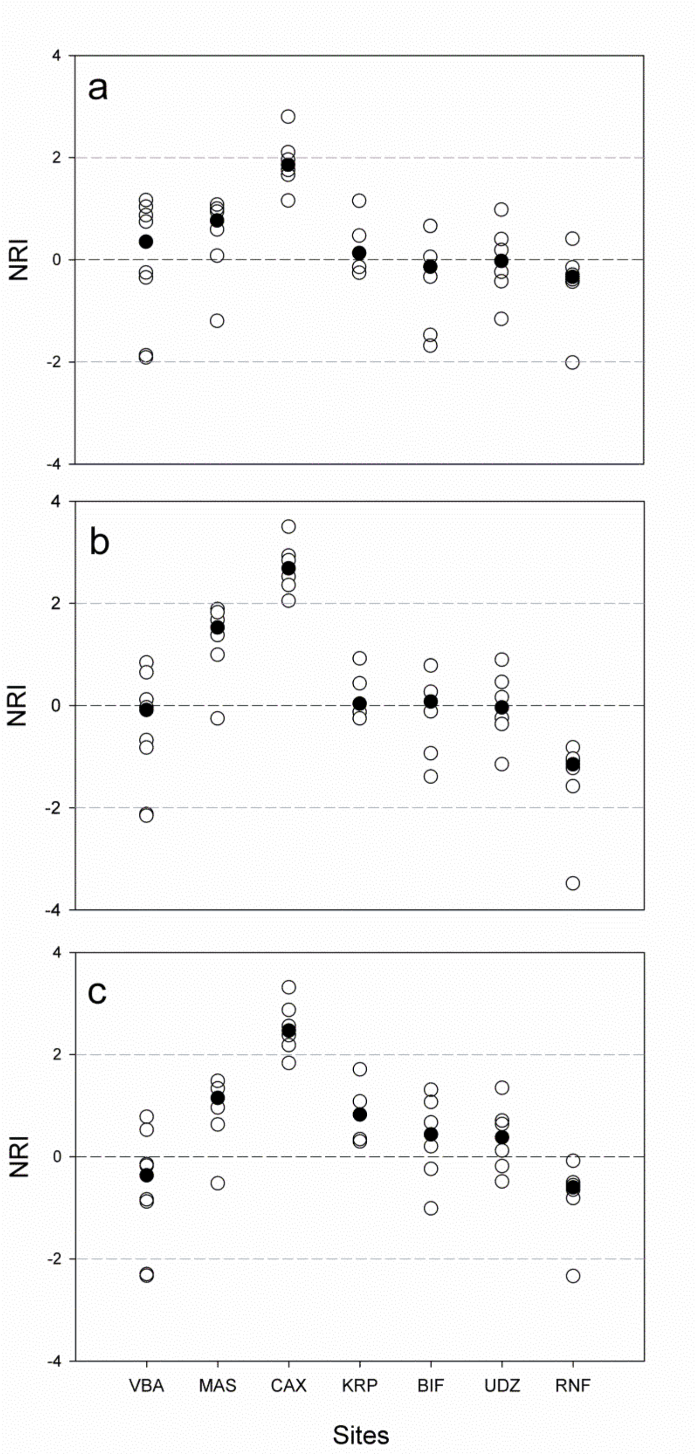
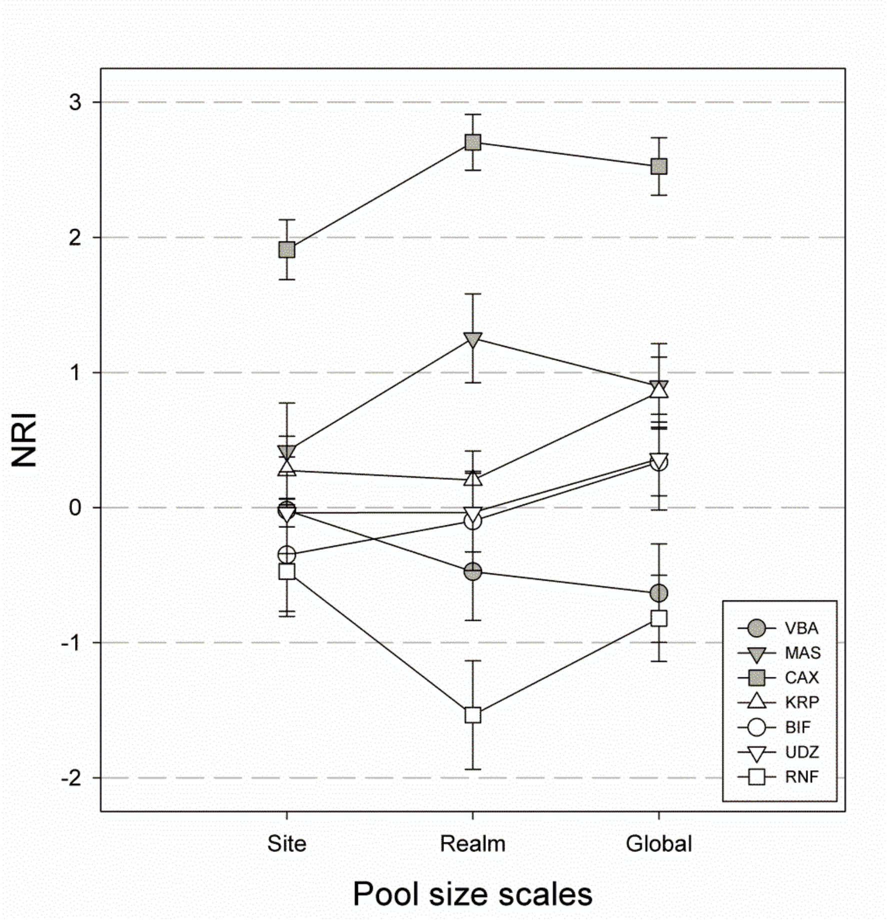


Figure 5



NRI
3
2
1
0
-1
-2
Site
Realm
Global
Pool size scales
VBA
MAS
CAX
KRP
BIF
UDZ
RNF

Figure 6

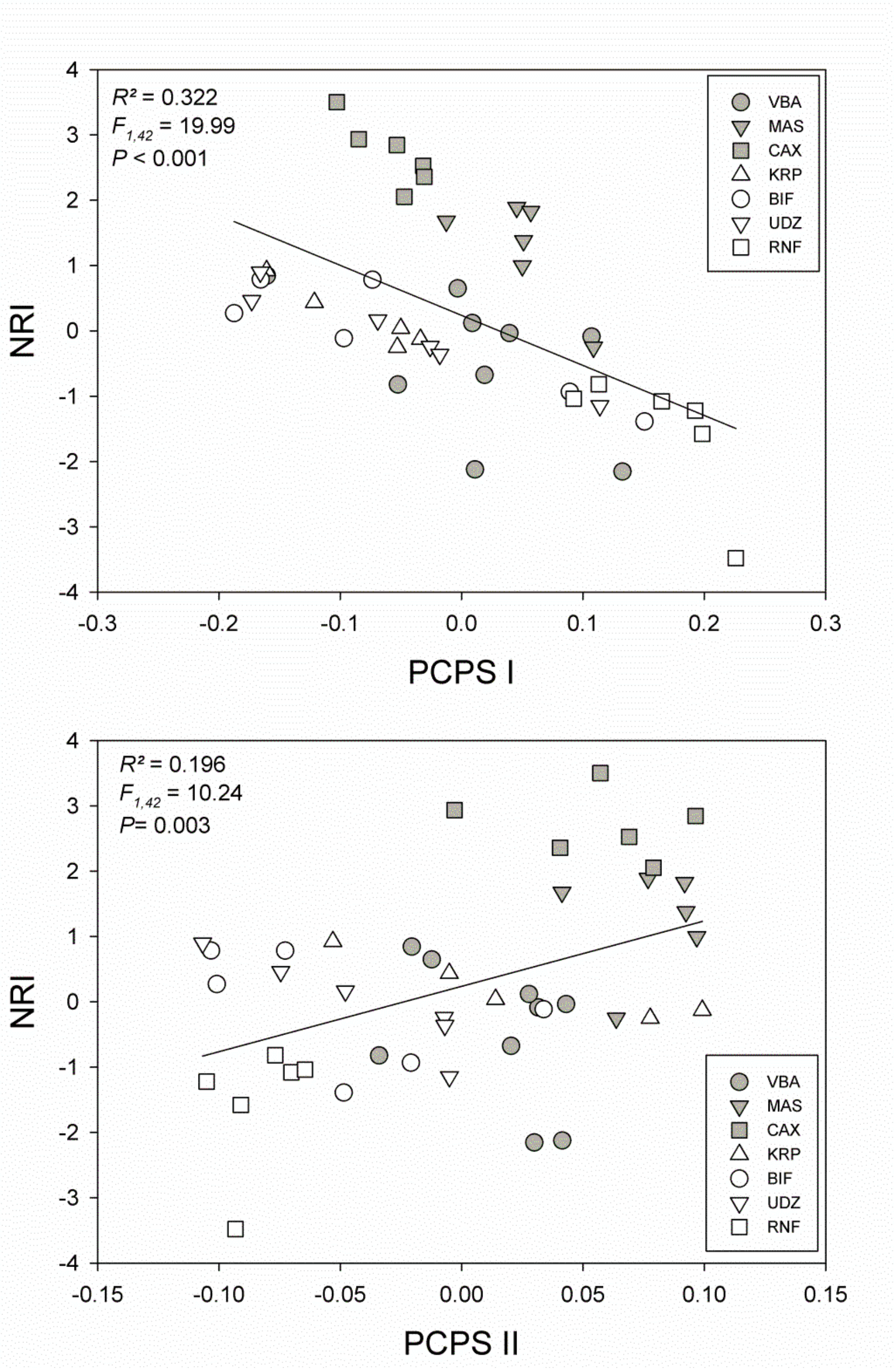

R² = 0.322
F 1,42 = 19.99
P < 0.001
VBA
MAS
CAX
KRP
BIF
UDZ
RNF
NRI
PCPS I
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
4
3
2
1
0
-1
-2
-3
-4
R² = 0.196
F 1,42 = 10.24
P= 0.003
PCPS II
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15

Figure 7

Supporting Information

Appendix S1. Lists of published studies (32 sites) and Gentry's sites (64 sites) used to compile Neotropical and Afrotropical species pools. Each Gentry's site consists in 10 100-m² transects totalling 0.1 ha surveyed per site.

(a) Published studies:

Adekunle, V.A.J. (2006) Conservation of tree species diversity in tropical rainforest ecosystem of South-West Nigeria. *Journal of Tropical Forest Science*, **18**, 91-101.

Alarcón, J.G.S. & Peixoto, A.L. (2007) Florística e fitossociologia de um trecho de um hectare de floresta de terra firme, em Caracaraí, Roraima, Brasil. *Boletim do Museu Paraense Emílio Goeldi (Ciências Naturais)*, **2**, 33-60.

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Batista, F.J., Jardim, M.A.G., Medeiros, T.D.S. & Lopes, I.L.M. (2011) Comparação florística e estrutural de duas florestas de várzea no estuário amazônico, Pará, Brasil. *Revista Árvore*, **35**, 289-298.

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Fashing, P.J. & Gathua, J.M. (2004) Spatial variability in the vegetation structure and composition of an East African rain forest. *African Journal of Ecology*, **42**, 189-197.

Ihenyen, J., Okoegwale, E.E. & Mensah, J.K. (2009) Composition of tree species in Ehor Forest Reserve, Edo State, Nigeria. *Nature and Science*, **7**, 8-18.

Ivanauskas, N.M., Monteiro, R. & Rodrigues, R.R. (2004) Composição florística de trechos florestais na borda sul-amazônica. *Acta Amazonica*, **34**, 399-413.

Jardim, M.A.G. & Vieira, I.C.G. (2001) Composição florística e estrutura de uma floresta de várzea do estuário Amazônico, Ilha do Combu, Estado do Pará, Brasil. *Boletim do Museu Paraense Emílio Goeldi (Série Botânica)*, **17**, 333-354.

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Ojo, L.O. & Ola-Adams, B.A. (1996) Measurement of tree diversity in the Nigerian rainforest. *Biodiversity and Conservation*, **5**, 1253-1270.

Queiroz, J.A.L. & Machado, S.A. (2008) Fitossociologia em floresta de várzea do estuário Amazônico no Estado do Amapá. *Pesquisa Florestal Brasileira*, **57**, 5-20.

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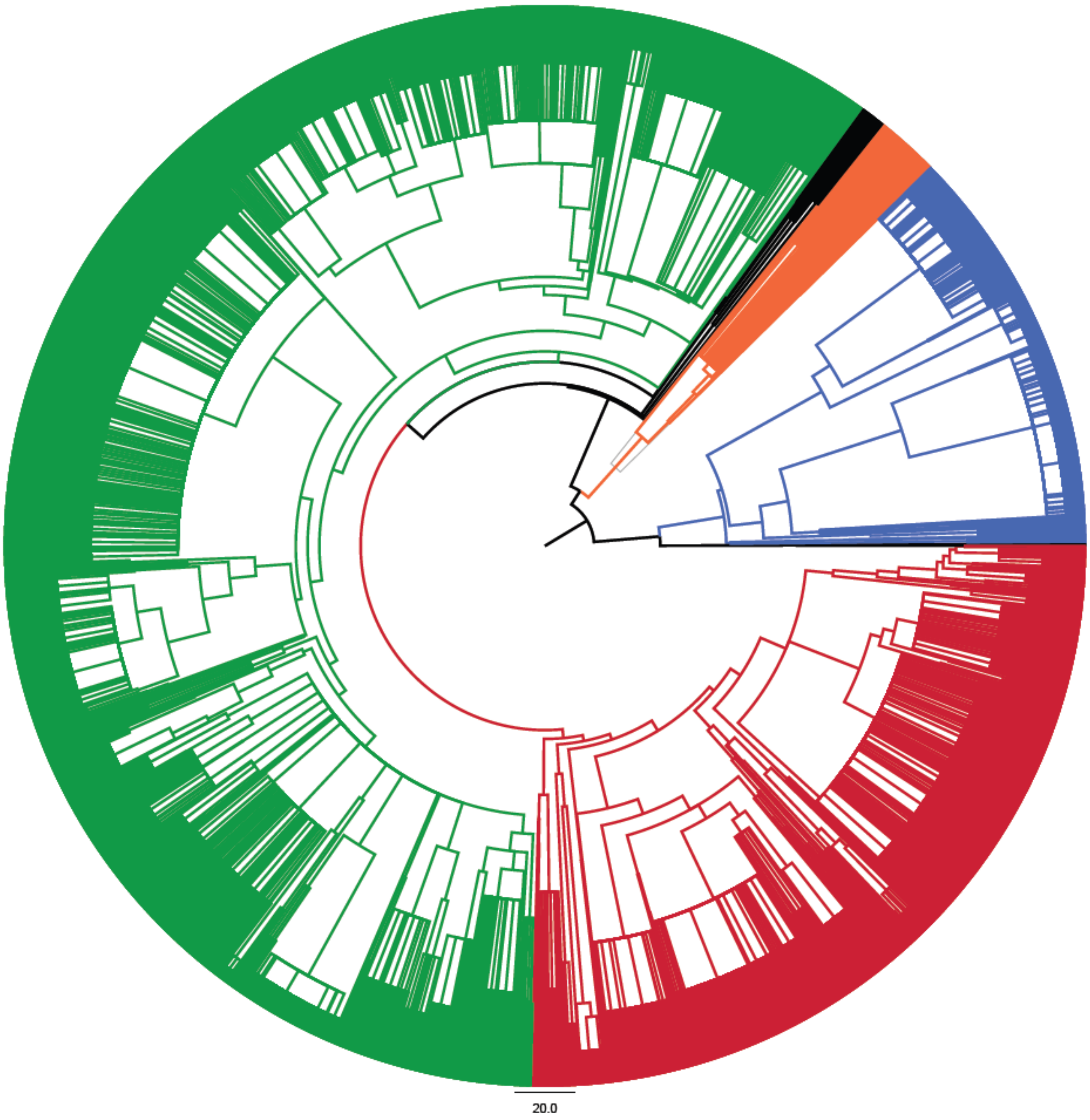
(b) Alwyn Gentry's sites (codes in parentheses): Allpahuayo (SAm89), Alter de Chao (SAm20), Alto de Cuevas (SAm33), Alto de Mirador (SAm35), Alto Madidi (SAm10), Alto Madidi – Ridge Top (SAm11), Anchicayá (SAm36), Antado (SAm37), Araracuara (SAm39), Araracuara - High Campina (SAm38), Bajo Calima (SAm40), Belém-Mocambo (SAm29), Berbice River (SAm87), Bosque de la Cueva (SAm41), Bosque Nacional von Humboldt (SAm90), Cabeza de Mono (SAm91), Candamo (SAm108), Carajas (SAm23), Carara National Park (CAm6), Centinela (SAm70), Cerro de la Neblina 1 (SAm124), Cerro de la Neblina 2 (SAm125), Cerro El Picacho (CAm24), Cerro Olumo (CAm23), Cochacashu (SAm96), Constancia (SAm97),Cuangos (SAm71),Curundu (CAm25), Cuzco Amazónico (SAm99), Dureno (SAm72), Fila de Bilsa (SAm68), Huamaní (SAm75), Indiana (SAm101), Jatun Sacha (SAm76), Jenaro Herrera (SAm102), La Planada (SAm54), Madden Forest (CAm26), Maquipucuna (SAm78), Miazi (SAm79), Mishana - Tahuampa (SAm104), Mishana Old Floodplain (SAm105), Mishana White Sand (SAm106), Murrí (SAm59), Osa-Sirena (CAm8), Pampas del Heath (SAm109), Pipeline Road (CAm27), Quebrada Sucusari (SAm112), Rancho Quemado (CAm7), Río Manso (SAm61), Río Nangaritza (SAm82), Río Palenque 1 (SAm83), Río Palenque 2 (SAm84), Río Távara (SAm110), San Sebastían (SAm85), Saul (SAm86), Shiringamazú (SAm111), Tambopata Alluvial (SAm114), Tambopata Lateritic (SAm116), Tambopata Swamp Trail (SAm115), Tambopata Upland Sandy (SAm113), Tutunendo (SAm65), Yanamono 1 (SAm120), Yanamono 2 (SAm121), Yanamono Tahuampo (SAm119).



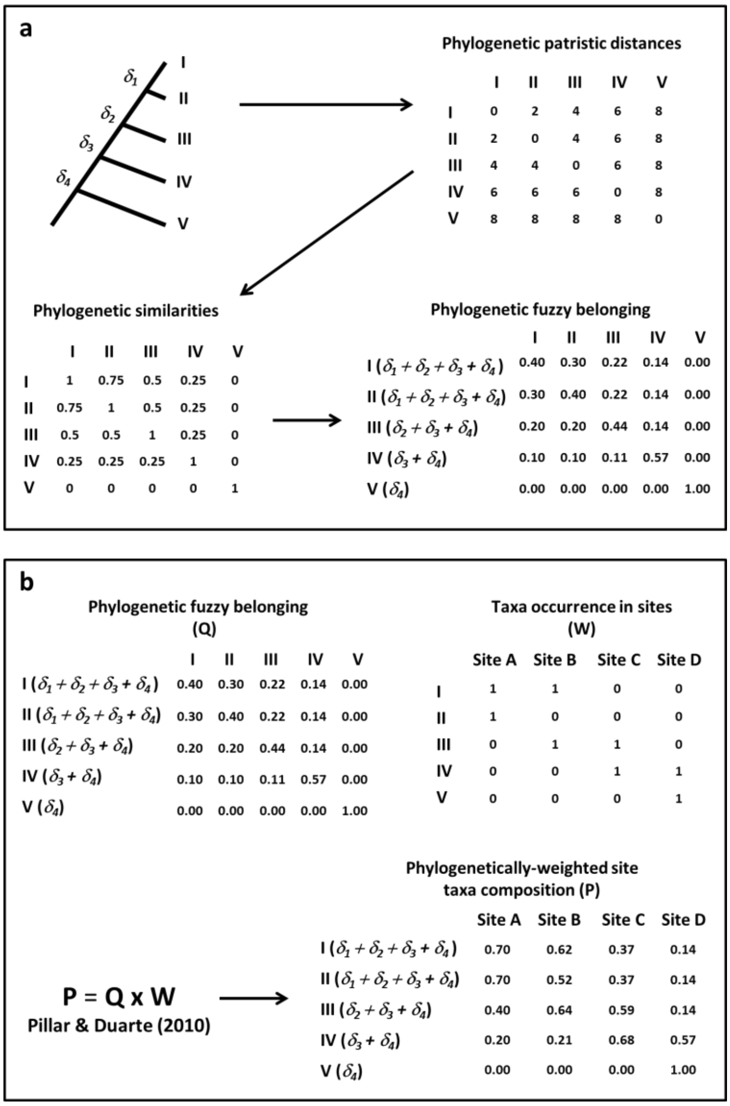
Appendix S2. Phylogenetic tree for tree species occurring in Neotropical and Afrotropical rainforests. Blue, magnoliids; orange, monocots; black, early-diverged eudicots; green, rosids; red, asterids.

Supporting Information

Appendix S3. Supplementary table and figures.

Table S1. Summary of sample sizes and taxonomic richness of trees at Neotropical and Afrotropical forest sites. Each plot had 1 ha; each subplot had 400 m².

Site	Acronym	n plots	n subplots	Families	Genera	Species	Individuals
Neotropics							
Volcán Barva	VBA	9	224	82	197	369	5173
Manaus	MAS	6	150	62	224	879	4055
Caxiuanã	CAX	6	150	49	165	392	2910
Total		21	524	94	347	1453	12138
Afrotropics							
Korup	KRP	5	125	49	149	215	5010
Bwindi	BIF	6	150	51	79	124	2702
Udzungwa	UDZ	6	148	48	92	125	3185
Ranomafana	RNF	6	150	49	104	188	6229
Total		23	573	82	310	618	17126
TOTAL		44	1097	118	607	2069	29264



Phylogenetic patristic distances

	I	II	III	IV	V
I	0	2	4	6	8
II	2	0	4	6	8
III	4	4	0	6	8
IV	6	6	6	0	8
V	8	8	8	8	0

Phylogenetic similarities

	I	II	III	IV	V
I	1	0.75	0.5	0.25	0
II	0.75	1	0.5	0.25	0
III	0.5	0.5	1	0.25	0
IV	0.25	0.25	0.25	1	0
V	0	0	0	0	1

Phylogenetic fuzzy belonging

	I	II	III	IV	V
I ($\delta_1 + \delta_2 + \delta_3 + \delta_4$)	0.40	0.30	0.22	0.14	0.00
II ($\delta_1 + \delta_2 + \delta_3 + \delta_4$)	0.30	0.40	0.22	0.14	0.00
III ($\delta_2 + \delta_3 + \delta_4$)	0.20	0.20	0.44	0.14	0.00
IV ($\delta_3 + \delta_4$)	0.10	0.10	0.11	0.57	0.00
V (δ_4)	0.00	0.00	0.00	0.00	1.00

Phylogenetic fuzzy belonging (Q)

	I	II	III	IV	V
I ($\delta_1 + \delta_2 + \delta_3 + \delta_4$)	0.40	0.30	0.22	0.14	0.00
II ($\delta_1 + \delta_2 + \delta_3 + \delta_4$)	0.30	0.40	0.22	0.14	0.00
III ($\delta_2 + \delta_3 + \delta_4$)	0.20	0.20	0.44	0.14	0.00
IV ($\delta_3 + \delta_4$)	0.10	0.10	0.11	0.57	0.00
V (δ_4)	0.00	0.00	0.00	0.00	1.00

Taxa occurrence in sites (W)

	Site A	Site B	Site C	Site D
I	1	1	0	0
II	1	0	0	0
III	0	1	1	0
IV	0	0	1	1
V	0	0	0	1

Phylogenetically-weighted site taxa composition (P)

	Site A	Site B	Site C	Site D
I ($\delta_1 + \delta_2 + \delta_3 + \delta_4$)	0.70	0.62	0.37	0.14
II ($\delta_1 + \delta_2 + \delta_3 + \delta_4$)	0.70	0.52	0.37	0.14
III ($\delta_2 + \delta_3 + \delta_4$)	0.40	0.64	0.59	0.14
IV ($\delta_3 + \delta_4$)	0.20	0.21	0.68	0.57
V (δ_4)	0.00	0.00	0.00	1.00

Figure S1. Schematic overview of the phylogenetic fuzzy weighting method (Pillar & Duarte, 2010), according to Duarte *et al.* (2014). For computing matrix **P** of phylogenetic fuzzy belonging, two matrices are necessary: $\mathbf{S_F}$ with pairwise phylogenetic similarities between species, ranging from 0 to 1, derived from a matrix of phylogenetic distances, and **W** of communities described by species abundance. (a) Firstly, the full matrix of phylogenetic similarities between species I to V, with both sides of the main diagonal, is subject to fuzzy weighting, which consists in standardising phylogenetic similarity values within columns by marginal totals, generating matrix **Q**, containing degrees of phylogenetic belonging of every species to fuzzy sets defined by each other species. (b) Then, matrix **Q** is used to weight species abundance in the communities, generating by matrix multiplication **P** = **Q** x **W**. The phylogenetic information carried by each species in **P** is represented by phylogenetic tree nodes ($\delta_1 - \delta_4$). The use of this figure was authorised by Duarte *et al.* (2013).

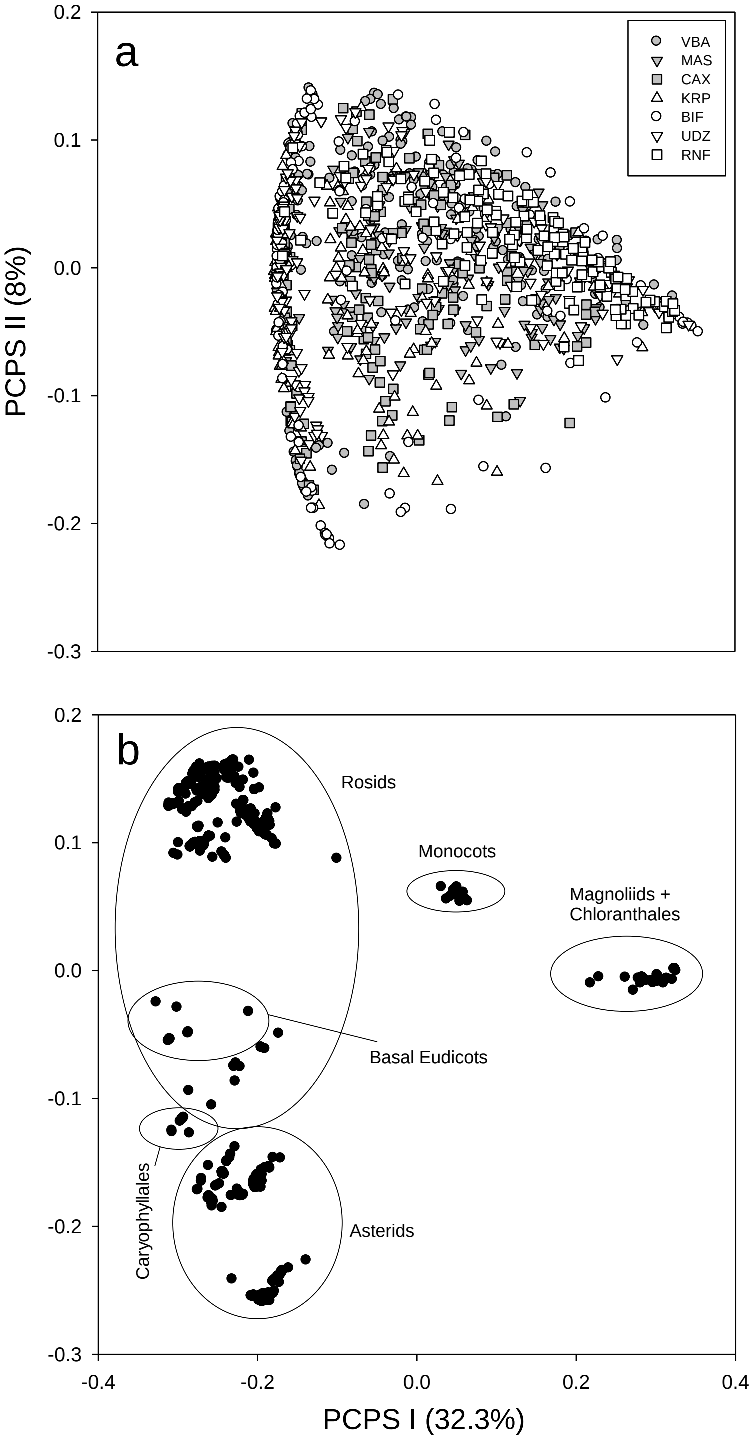


Figure S2. Scatter diagram of the two first principal coordinates of phylogenetic structure (PCPS) of tropical tree communities for 400-m² subplots. Ordination axes can be interpreted as gradients of phylogenetic composition of major lineages of angiosperms. (a) PCPS scores for 400-m² subplots located in forest sites in the Neotropics (grey) and Afrotropics (white). (b) Association between major clades of angiosperms and PCPS axes. Points represent species plotted according to their correlations to PCPS vectors. Site acronyms: BIF – Bwindi, CAX – Caxiuanã, KRP – Korup, MAS – Manaus, RNF – Ranomafana, UDZ – Udzungwa, VBA – Volcán Barva.

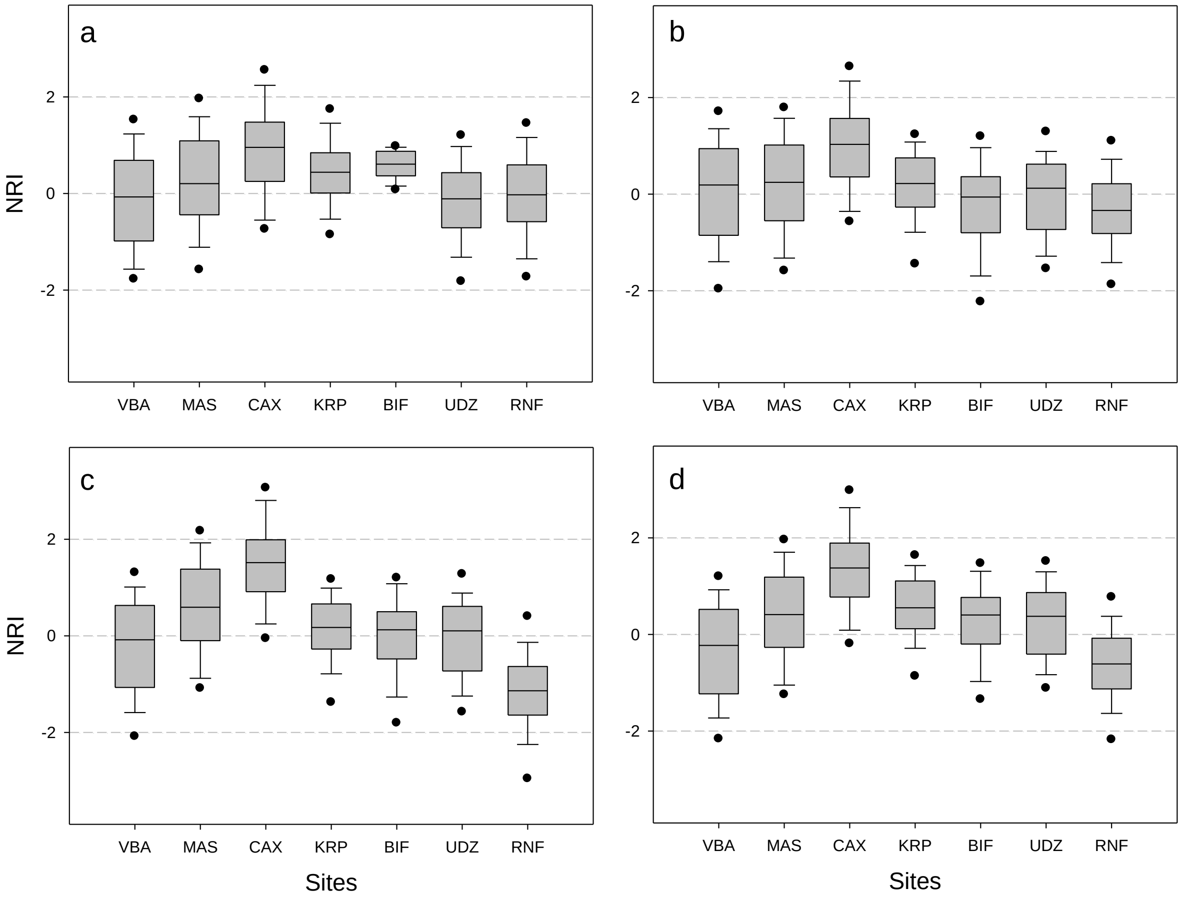


Figure S3. Net relatedness index (NRI) for 400-m² subplots in relation to different sizes of regional species pool: (a) 1-ha plot, (b) site, (c) realm (Neotropics or Afrotropics), and (d) global (Neotropics + Afrotropics). Site acronyms: BIF – Bwindi, CAX – Caxiuanã, KRP – Korup, MAS – Manaus, RNF – Ranomafana, UDZ – Udzungwa, VBA – Volcán Barva.

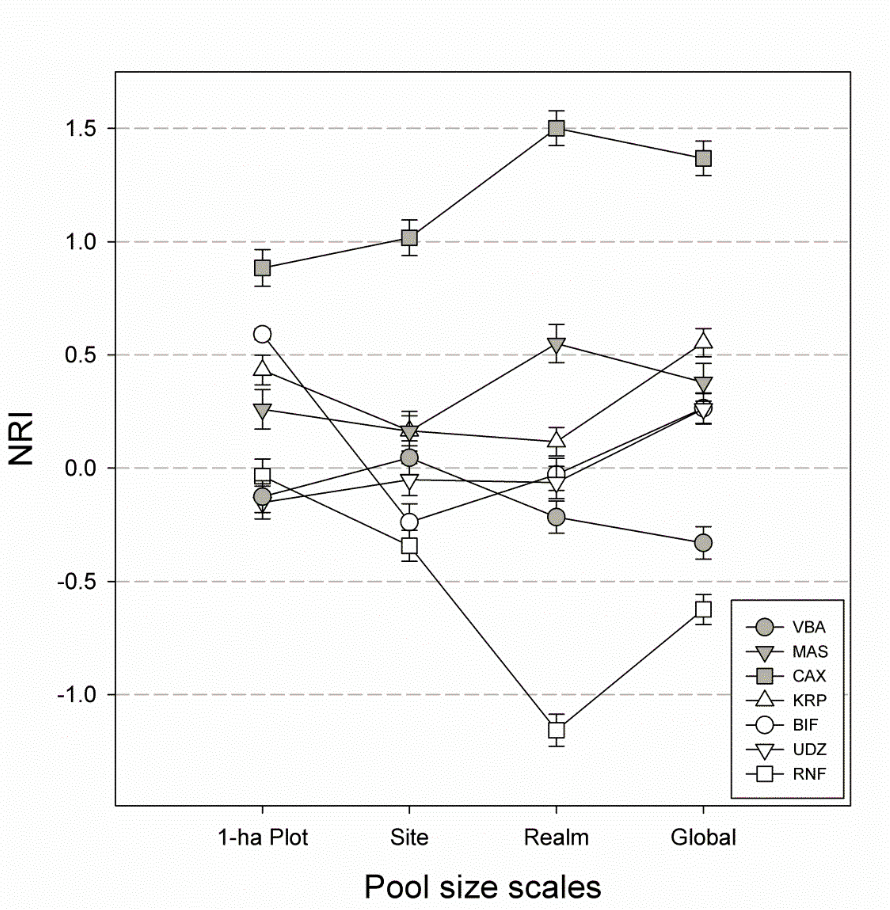


Figure S4. Effect of species pool size on NRI values for 400-m² subplots in Neotropical (grey) and Afrotropical (white) forests. Repeated measures ANOVAs for each site have shown that changing the species pool from the local to global scales generally altered NRI values (see the main text for detailed results). Standard errors are indicated. Site acronyms: BIF – Bwindi, CAX – Caxiuanã, KRP – Korup, MAS – Manaus, RNF – Ranomafana, UDZ – Udzungwa, VBA – Volcán Barva.

Capítulo 5. Considerações finais

Nesta tese, avaliei padrões e processos de organização de comunidades de plantas lenhosas da escala local à regional em diferentes sistemas: ecótonos floresta-campo no sul do Brasil e florestas pluviais tropicais no Neotrópico e Afrotrópico.

5.1. ORGANIZAÇÃO DE COMUNIDADES LENHOSAS DA ESCALA LOCAL À REGIONAL EM DIFERENTES SISTEMAS

No capítulo 2 (Carlucci et al. 2014), utilizei abordagens baseadas em atributos funcionais (CWM e diversidade funcional de Rao) para avaliar a importância relativa da substituição de espécies e variabilidade intraespecífica de um atributo-chave na organização de comunidades de plantas lenhosas, a área foliar específica (SLA). A incorporação da variabilidade intraespecífica nas análises funcionais aumentou a resposta média e de dispersão dos valores de SLA ao gradiente em comparação a análises que consideraram apenas a variação interespecífica. Do ponto de vista biológico, os resultados do capítulo 2 indicaram que a variabilidade intraespecífica aumenta as chances de espécies passarem por filtros bióticos (p.ex. competição) e abióticos (filtragem ambiental), além de permitir seu estabelecimento em uma porção mais ampla do gradiente ambiental, fornecendo nova evidência de que fenômenos no nível de população são importantes para a organização de comunidades.

Como avaliei padrões relativos somente à área foliar específica e com dados de apenas um sítio no capítulo 2, as seguintes questões surgiram: (1) Quais outros atributos seriam importantes para a expansão lenhosa sobre campos? (2) Qual seria o papel da variabilidade intraespecífica desses atributos para a organização de comunidades lenhosas juvenis em ecótonos? (3) Os padrões encontrados no capítulo 2 são generalizáveis para ecótonos floresta-campo no Rio Grande do Sul (RS)? (4) Como diferentes espécies e linhagens estão relacionadas aos padrões funcionais encontrados ao longo do gradiente floresta-campo? Assim, no capítulo 3, utilizei a análise atributo-gradiente (Ackerly & Cornwell 2007) para avaliar as respostas de cinco atributos de espécies de plantas lenhosas a espécies coocorrentes e ao gradiente ambiental em cinco sítios representando ecótonos floresta-campo no sul do Brasil. Mostrei que espécies ocorrentes tanto na floresta quanto no campo diferem de espécies restritas à floresta ou ao campo quanto às respostas de seus atributos a espécies coocorrentes e ao gradiente ambiental. Além disso, os resultados mostraram que área foliar específica, espessura foliar e densidade de folhagem são atributos-chave que ajudam a explicar a organização de comunidades de plantas lenhosas em ecótonos floresta-campo. A plasticidade nesses atributos promove a colonização do campo por espécies que também ocorrem na floresta. Os resultados do capítulo 3 mostraram que os padrões encontrados para o capítulo 2 são gerais para ecótonos floresta-campo no RS. Os testes de sinal filogenético indicaram ausência de sinal filogenético na média e variabilidade intraespecífica dos atributos vegetativos. No capítulo 3, pude generalizar a importância da plasticidade em atributos foliares e arquiteturais para a expansão de formações lenhosas sobre áreas abertas no sul do Brasil, um fenômeno que tem sido observado globalmente.

No capítulo 3, avaliei como a evolução influencia a similaridade funcional das espécies e consequentemente padrões de ocupação de diferentes ambientes através de testes de sinal filogenético em atributos. No capítulo 4, avaliei o que a filogenia pode nos contar sobre como processos históricos de formação de bancos regionais de espécies influenciam a organização local atual de comunidades de árvores em dois reinos biogeográficos. Para isso, utilizei duas abordagens filogenéticas complementares: coordenadas principais de estrutura filogenética (PCPS; Duarte 2011) e índice de parentesco líquido (NRI; Webb et al. 2002) para avaliar, respectivamente, composição e estrutura filogenética de comunidades de árvores em florestas tropicais no Neotrópico e Afrotrópico. Observei que a composição filogenética e a estrutura diferem entre o Neotrópico e o Afrotrópico e que diferenças de composição filogenética entre os dois reinos influenciam a estrutura filogenética de comunidades locais. O agrupamento filogenético no Neotrópico foi associado com asterídeas, monocotiledôneas e Magnoliales, enquanto a repulsão filogenética no Afrotrópico foi relacionada a rosídeas e Laurales. As diferenças filogenéticas regionais entre reinos são provavelmente um resultado de taxas diferenciais de diversificação e extinção que seguiram a separação de Gondwana. Essas diferenças levaram a probabilidades distintas de se encontrar agrupamento ou repulsão filogenéticas localmente no Neotrópico e Afrotrópico. A utilização conjunta das abordagens de PCPS (para avaliar a variação regional da composição filogenética) e NRI (para avaliar estrutura filogenética local) constitui uma ferramenta útil que pode integrar ainda mais os campos da biogeografia, evolução e ecologia de comunidades.

5.2. CONCLUSÕES GERAIS

(1) A variabilidade intraespecífica é fundamental para a organização de comunidades lenhosas em florestas e arbustais, pois a área foliar específica dentro da mesma espécie varia conforme o ambiente e o contexto local de interações com outras espécies. Essa plasticidade permite o estabelecimento de espécies em uma porção maior do gradiente de abertura do dossel.

(2) Uma ação combinada entre área foliar específica, espessura foliar e densidade de folhagem ajuda a explicar a organização de comunidades de plantas lenhosas em ecótonos

floresta-campo. A plasticidade nesses atributos permite a colonização do campo por espécies que também ocorrem na floresta.

(3) Diferenças de composição filogenética entre o Neotrópico e o Afrotrópico são provavelmente um resultado de taxas diferenciais de diversificação e extinção que seguiram a separação de Gondwana e atualmente influenciam a estrutura filogenética local de comunidades de árvores de florestas pluviais nos dois reinos.

5.3. REFERÊNCIAS

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