TESE DOUTORADO

UNIVERSIDADE FEDERAL DO RIO GRANDE DO NORTE

CENTRO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

JOSÉ LUIZ ALVES SILVA

Uso de atributos funcionais para elucidar causas e consequências da estrutura da comunidade vegetal e do funcionamento do ecossistema Restinga

The use of functional traits to elucidate causes and consequences of community structure and ecosystem functioning of the Restinga vegetation

NATAL, RN

2018

Uso de atributos funcionais para elucidar causas e consequências da estrutura da comunidade vegetal e do funcionamento do ecossistema Restinga

JOSÉ LUIZ ALVES SILVA

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Rio Grande do Norte como um dos pré-requisitos para a obtenção do título de Doutor em Ecologia.

Orientador:
Alexandre Fadigas de Souza

Co-orientadores:
Eduardo Luiz Voigt
Juliana Espada Lichston

Universidade Federal do Rio Grande do Norte - UFRN
Sistema de Bibliotecas - SISBI
Catalogação de Publicação na Fonte. UFRN - Biblioteca Setorial Prof. Leopoldo Nelson - -Centro de Biociências – CB

Silva, José Luiz Alves.
Uso de atributos funcionais para elucidar causas e consequências da estrutura da comunidade vegetal e do funcionamento do ecossistema Restinga / José Luiz Alves Silva. - Natal, 2018.
116 f.: il.

Tese (Doutorado) - Universidade Federal do Rio Grande do Norte. Centro de Biociências. Programa de Pós-Graduação em Ecologia.
Orientador: Prof. Dr. Alexandre Fadigas de Souza.
Coorientador: Prof. Dr. Eduardo Luiz Voigt.
Coorientadora: Profa. Dra. Juliana Espada Lichston.

1. Floresta estacional seca - Tese. 2. Ambientes estressantes - Tese. 3. Planícies costeiras - Tese. 4. Bioquímica - Tese. 5. Anatomia foliar - Tese. 6. Produtividade primária - Tese. I. SOUZA, Alexandre Fadigas de et al. II. Título.
RN/UF/BSE-CB CDU 630*18

Dedico este trabalho à minha irmã,

Emmanuelle Silva (Manu),

pelo apoio e incentivos constantes.

AGRADECIMENTOS

Agradeço a UFRN e ao programa de pós-graduação em Ecologia pelo suporte institucional e financeiro. À universidade da Califórnia em Riverside (UCR) pelo acolhimento durante meu doutorado sanduíche.

À Agência Nacional do Petróleo (ANP) pela bolsa concedida no meu primeiro ano de doutorado, a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa concedida durante meu segundo e terceiro ano, e a Fulbright U.S. Student Program pela bolsa sanduíche concedida no meu último ano. Eu recebi destas instituições muito mais do que um apoio financeiro, pois elas me proporcionaram realizar sonhos.

Ao meu orientador, Alexandre Fadigas Souza, por ter acreditado neste projeto desde a sua concepção, pelos inúmeros conselhos e pela sua disponibilidade em momentos importantes. Me espelho na sua humildade e profissionalismo na esperança de colher bons frutos na minha carreira profissional e vida pessoal.

Aos meus coorientadores, Eduardo Voigt e Juliana Espada, e colaboradores, Louis Santiago e Adriano Caliman, pelo inestimável suporte técnico e acadêmico. Sou grato pela troca de ideias, correções de manuscritos e tempo dedicado aos artigos que produzimos em colaboração.

Ao professor Iuri Goulart por gentilmente autorizar o uso de equipamentos em seu laboratório, que foram essenciais para obtenção de dados de anatomia de folhas.

Ao Centro de Lançamento da Barreira do Inferno (CLBI), ao coronel Luiz Medeiros e ao engenheiro Glauberto Leilson, pela permissão de coleta na área de estudo e por mediarem o acesso da equipe ao centro.

À banca examinadora pelos comentários em favor do crescimento deste trabalho.

Ao grupo de pesquisa do professor Alexandre Fadigas, em especial a Karla Juliete e Augusto Silva, pela amizade, conselhos e ajudas nas coletas de campo, dos quais sou imensamente grato. Aos primeiros alunos de iniciação científica que passaram por este grupo e que ajudaram a estabelecer as unidades amostrais e na coleta inicial de dados, além da colega e mestre Amarilys. Um especial obrigado ao amigo Morvan França.

À Gabriel Silva, Ana Basato, Mery Guimarães, Monnaliza Andrade, Elias Silvano, Augusto Silva, Luiza Cantidio, Kassia Galdino, e aos demais colegas que me ajudaram na coleta de dados em dias ensolarados e nublados na restinga. A Danilo Flademir, Ana Avelino, Kionara Sarabella, André Freire, Luiza Cantídio, e aos demais colegas que me ajudaram nos dias cansativos de laboratório. Eu gostaria de retribuir com gratidão tudo o que vocês fizeram por mim, mas qualquer esforço seria pouco. Então o que tenho a dizer além de um muito obrigado seria contem comigo.

Aos amigos que fiz durante meu período no laboratório do professor Louis Santiago, Alleyda, Eleinis, Erika, Antonio, Agustina e Olof. Agradeço pelo acolhimento e por ter me feito sentir como se estivesse em casa.

Agradeço também a família que escolhi para amar, meus queridos Gygy e Thiago. Foram muitas xícaras de café, cervejinhas e viagens compartilhadas que ajudaram a me distrair e passar por fases cansativas e estressantes.

À minha irmã Manu, ao qual dedico este trabalho, e as minhas mães Vânia e Maria, pelo prazer de conviver, aprender e sonhar junto com vocês. Obrigado por apoiarem meus sonhos e estarem comigo sempre, sem requerer nada em troca.

CONTEÚDO DA TESE

RESUMO GERAL

A forma e o funcionamento das plantas dependem de estímulos internos (genética e plasticidade fenotípica) e externos (ambiente) que atuam na folha, lenho e raiz. A escassez de água e nutrientes em solos arenosos da região costeira são citados como os principais estímulos externos às plantas do ecossistema Restinga. Tem sido proposto que a coordenação entre os órgãos das plantas tende a aumentar com a severidade ambiental, devido a redução do espaço de nicho viável e ao aumento dos custos associados à adoção de estratégias ecológicas fora deste espaço de nicho. O primeiro capítulo da tese teve como objetivo testar esta hipótese para a Restinga. Correlações bivariadas entre 21 atributos funcionais de 21 espécies revelaram que o lenho possui maior coordenação interna do que a folha. Além disto, uma análise multivariada revelou uma alta independência entre lenho e folhas, sugerindo que ambientes estressantes não necessariamente possuem plantas com alta coordenação entre os órgãos. Estes resultados foram publicados na Ecology and Evolution. A coordenação funcional está diretamente ligada ao sucesso de ocorrência das plantas e deve interferir na organização da comunidade. Ainda não está claro se os efeitos neutros fracos podem influenciar a distribuição de atributos funcionais, mesmo que a comunidade mostre padrões aleatórios de estrutura composicional e filogenética. Tratamos esta questão no segundo capítulo da tese. A variação funcional na comunidade resultou de respostas fenotípicas de todas as espécies e indivíduos ao invés de conjuntos particulares de espécies ou indivíduos, indicando respostas ambientais, mas não de padrões fortes na distribuição espacial dos atributos. Nesse sentido, aceitamos que a Restinga do nordeste da América do Sul é influenciada por efeitos neutros fracos. Concluiu-se que análises de ocorrência e filogenia podem ser insuficientes para uma compreensão completa da comunidade e devem ser complementadas com análises de atributos. Uma fraca resposta ambiental pode resultar da baixa relevância do particionamento de nicho entre as espécies, que tem sido descrito como o principal mecanismo subjacente às relações entre a biodiversidade e os processos ecossistêmicos. O terceiro capítulo propôs avaliar em que medida facetas da biodiversidade da vegetação e características do meio ambiente influenciam a produção anual de serapilheira e o estoque de biomassa lenhosa, bem como o papel da diversidade de espécies raras versus diversidade de comuns sobre estes componentes de produtividade primária. Encontramos que estes respondem principalmente a aspectos ambientais abióticos e apenas, secundariamente, à riqueza de espécies e a poucos atributos funcionais, mas não a outras facetas da biodiversidade. Também encontramos que a diversidade de espécies raras teve menor influência sobre a produção de serapilheira do que a diversidade de espécies comuns, mas a mesma influência sobre o estoque de biomassa. Em resumo, conclui-se que as diferenças de nicho entre espécies promovem efeitos apenas modestos na estrutura das comunidade e efeitos ainda menores no funcionamento da Restinga. Estes padrões se afastam do esperado na literatura para sistemas estressantes, o que evidencia a relevância de sua biodiversidade.

Palavras-chave: Planícies costeiras, Ambientes estressantes, Floresta estacional seca, Bioquímica, Anatomia foliar, Produtividade primária.

GENERAL SUMMARY

Plant form and function depend on internal stimuli (genetics and phenotypic plasticity) as well as external stimuli (environment) that act in the leaf, stem, and root. Water shortages and poor-nutritional sandy soils in the coastal region are cited as the main external stimuli to plants in the Restinga ecosystem. It has been proposed that coordination among plant organs tends to increase with environmental harshness due to a decrease in the viable niche space and an increase in the costs to adopt ecological strategies out of this viable niche space. The first thesis chapter aimed to test this hypothesis in the Restinga. Pairwise correlations of 21 functional traits of 21 species revealed that the stem had greater internal coordination than the leaf organ. In addition, a multivariate analysis showed high independence between stem and leaves, suggesting that stressful environments do not necessarily have plants with high coordination between organs. Functional coordination is directly linked to the success of plant occurrence and may interfere in the community organization. It is still not clear whether weak neutral effects can influence the distribution of functional traits, even though the community shows random patterns of compositional and phylogenetic structure. We addressed this question in the second thesis chapter. Functional variation in the community resulted from phenotypic responses of all species and individuals rather than particular sets of species or individuals, indicating environmental responses, but not strong patterns in the spatial distribution of traits. In this regard, we accept that the Restinga in the Northeastern South America is influenced by weak neutral effects. We concluded that occurrence and phylogenetic analyses may be insufficient for a complete understanding of the community and should be complemented with functional analyses. The manuscript was submitted to the Journal of Vegetation Science. A weak environmental response may result from low niche partitioning among species, which has been described as the main mechanism underlying the relationships between biodiversity and ecosystem processes. The third chapter assessed the extent to which facets of biodiversity and environmental aspects influence the annual litterfall production and wood biomass storage, as well as the role of rare- and common-species diversities on these components of primary productivity. We found that these components responded mainly to the abiotic environment and just secondarily to species richness and few functional traits, but not to other facets of biodiversity. We also found that rare-species diversity had less influence on litterfall than the diversity of common species, but the same influence on the biomass storage. In summary, I concluded that niche differences among species promote only modest effects on community structure and even lower effects on the ecosystem functioning of Restinga. These patterns deviate from that expected in the literature for stressful ecosystems, which highlights the relevance of its biodiversity.

Keywords: Coastal plains, Stressful environments, Seasonally dry forest, Biochemistry, Leaf anatomy, Primary productivity.

INTRODUÇÃO GERAL

Nas últimas décadas, o número de artigos publicados envolvendo o uso dos atributos funcionais das espécies para elucidar processos sobre a biodiversidade aumentou exponencialmente (Caliman et al. 2010; Cadotte et al. 2011). Atributos funcionais referem-se a qualquer característica morfológica, fisiológica ou fenológica dos organismos que impactam diretamente seu desenvolvimento e sua habilidade de persistência no ambiente (Violle et al. 2007; Díaz et al. 2013). Uma das razões para este crescente interesse é que os atributos funcionais simplificam a formulação de princípios e regras gerais sobre as comunidades independentemente do seu número de espécies e, portanto, permitem a comparação de ecossistemas com biodiversidade muito diferentes (McGill et al. 2006). Princípios gerais explicam como e por quê a biodiversidade varia no tempo e no espaço, além dos efeitos sobre o funcionamento dos ecossistemas associados a estas variações. Atributos que variam em função de gradientes ambientais são chamados de atributos de resposta, enquanto aqueles que criam algum gradiente ambiental ou interferem em fluxos de matéria ou energia (processos ecossistêmicos) são chamados de atributos de efeito (Díaz et al. 2013; Kleyer & Minden 2015).

Explicar sistemas complexos que são moldados por múltiplos fatores exige a investigação simultânea de diversos atributos funcionais, particularmente quando se considera a gama de cenários futuros gerados por mudanças globais. Resumir a informação de múltiplos atributos por meio de eixos ou dimensões que expressem “trade-offs” entre estratégias aquisitivas versus conservativas tem se mostrado a principal abordagem usada para entender o funcionamento das espécies e comunidades (Wright et al. 2004; Chave et al. 2009; Díaz et al. 2016; Méndez-Alonzo et al. 2016). Um “trade-off” significa que o investimento em atributos funcionais associados a aquisição de recursos impede o investimento simultâneo em atributos associados na conservação, e isto cria um compromisso evolutivo e ecológico entre adquirir ou conservar recursos. Por exemplo, plantas podem combinar folhas e lenhos leves, que requerem menos recursos para construção dos atributos (atributos "baratos") e que são pouco duráveis, ou combinar, alternativamente, tecidos densos, "caros" e duráveis (Westoby et al. 2002; Wright et al. 2004, 2007; Chave et al. 2009). Investir em lenho leve e folhas finas tem sido associada a uma estratégia de crescimento rápido (aquisitiva) com vantagem em ambientes com maior oferta de nutrientes e água (Ishida et al. 2008; Baraloto et al. 2010; Vinya et al. 2012). Em contraste, plantas com madeira densa combinam folhas espessas de longa duração para obter maiores taxas de sobrevivência, porque elas toleram melhor o estresse de sombra, vento, seca e herbívoros (Méndez-Alonzo et al. 2016).

Esta abordagem funcional tem chamado a atenção para a necessidade de se entender o funcionamento da planta como um todo, integrando os órgãos de folha, lenho e, se possível, raiz (Kleyer & Minden 2015; Díaz et al. 2016; Méndez-Alonzo et al. 2016). Contudo, a extensão pela qual estas relações representam padrões gerais de coordenação entre características ainda permanece requerendo um maior número de investigações em diversas regiões e tipos de comunidades vegetais. Além disto, uma fonte de variação pouco considerada na dimensão de estratégias funcionais provém da anatomia da folha. A hipótese mais amplamente aceita é a de que existe uma coordenação positiva entre morfologia e anatomia de folhas dado que para se obter uma maior taxa fotossintética faz-se necessário um conjunto de estruturas anatômicas relacionadas a produção, tal como parênquima paliçádico (Wright et al. 2004). A formação de uma folha com maior área foliar específica estaria, portanto, positivamente relacionada a um mesófilo mais fino e rico em parênquima paliçádico, enquanto que negativamente relacionado a estruturas de proteção como uma epiderme espessa, cutícula e cera (Somavilla et al. 2014; Rosatto et al. 2015). Esta combinação de características é amplamente compartilhada por espécies competidoras de ambientes produtivos. Já folhas com muitas camadas de epiderme, com cutícula e cera espessa, cobertas com tricomas ou com estômatos em criptas, são compartilhadas por espécies de ambientes secos para regular a perda de água, principalmente quando elas também têm que lidar com altas taxas de radiação (Yeats & Rose 2013).

A coordenação dos atributos ao longo de eixos funcionais depende de estímulos internos (genética e plasticidade fenotípica) e externos (fatores ambientais) que atuam nas variações inter- e intraespecíficas dos diferentes órgãos (Cornwell & Ackerly 2009; Leps et al. 2011; Auger & Shipley 2013). Geralmente têm se assumido que a variação entre indivíduos é muito baixa e que, portanto, pode ser negligenciada nas investigações de dimensões funcionais (Cornelissen et al. 2003; McGill et al. 2006). Contudo, estudos recentes mostram que esta fonte de variação é maior do que a previamente assumida (revisado em Kichenin et al. 2013) e que quando maior a amplitude do gradiente ambiental, maior é a sua contribuição (Albert et al. 2011; Auger & Shipley 2013). Além disto, a variação intraespecífica esclarece informações relativas à adaptação (variabilidade de genótipos) e plasticidade das espécies (variabilidade de fenótipos dentro de cada genótipo) indispensáveis dependendo do objetivo da pesquisa (Albert et al. 2011).

A escassez de água e nutrientes em solos arenosos da região costeira, combinado com a alta radiação e sazonalidade hídrica, são citados como os principais estímulos e restrições externas às plantas do ecossistema Restinga (Scarano 2002; de Oliveira et al. 2014; Silva et al. 2018). O termo Restinga refere-se à comunidade de plantas que ocorre em planícies arenosas originadas no Quaternário em função de transgressões e regressões marinhas (Scarano 2002). Sistemas abioticamente estressantes como a Restinga geralmente possuem gradientes ambientais curtos. Contudo, manchas de moderado estresse em áreas protegidas do ambiente costeiro, a exemplo de vales interdunares e sotaventos, devem alongar estes gradientes (Fenu et al. 2012; Tissier et al. 2013), assim como aumentar a contribuição intraespecífica na variabilidade funcional e, principalmente, diminuir a diferença entre as variações inter- e intraespecífica (Albert et al. 2011; Auger & Shipley 2013). O entendimento do comprimento do gradiente ambiental e do grau de estresse no qual as plantas estão submetidas é de extrema relevância, pois ambos interferem no grau de coordenação entre atributos funcionais (Westoby & Wright 2006; Dwyer & Laughlin 2017).

Ambientes áridos e semiáridos favorecem plantas com baixa eficiência hidráulica, mas com alta resistência à cavitação hidráulica em tecidos de folha e lenho (Chave et al. 2009). Folhas são geralmente escleróﬁlas, grossas e rígidas, com cutícula e cera também grossas, com grandes quantidades de tecido estrutural e um bem desenvolvido sistema vascular (Somavilla et al. 2014; Rosatto et al. 2015). Em resposta a seca, algumas plantas perdem total ou parcialmente suas folhas como uma estratégia para evitar cavitação. Lenhos possuem geralmente alta densidade por serem constituídos por múltiplos vasos com baixo diâmetro que conferem baixa eficiência hidráulica, mas alta resistência à cavitação (Chave et al. 2009). As várias relações entre características de uso e conservação de água sugerem que a arquitetura hidráulica da planta tem o potencial para estabelecer limites ecológicos importantes por restringir espécies hidraulicamente pouco eficientes à ambientes áridos.

Tem sido proposto que ambientes estressantes exigem uma maior coordenação entre folha, lenho e raiz se comparado a ambientes produtivos (ou menos estressantes). De acordo com esta hipótese, a coordenação funcional tende a aumentar ao longo de gradientes de estresse (Fig. 1), devido a redução do espaço de nicho viável sobre aquelas condições abióticas e ao aumento dos custos associados à adoção de estratégias ecológicas fora deste espaço de nicho (Westoby & Wright 2006; Dwyer & Laughlin 2017). Assim, a variação na severidade do estresse cria um gradiente de comunidades que apresentam espaços de nicho frouxos ou fortemente restritos. Esta hipótese tem encontrado suporte em comunidades de gramíneas entre savanas e desertos na Austrália (Dwyer & Laughlin 2017), embora não tenha sido amplamente testada.

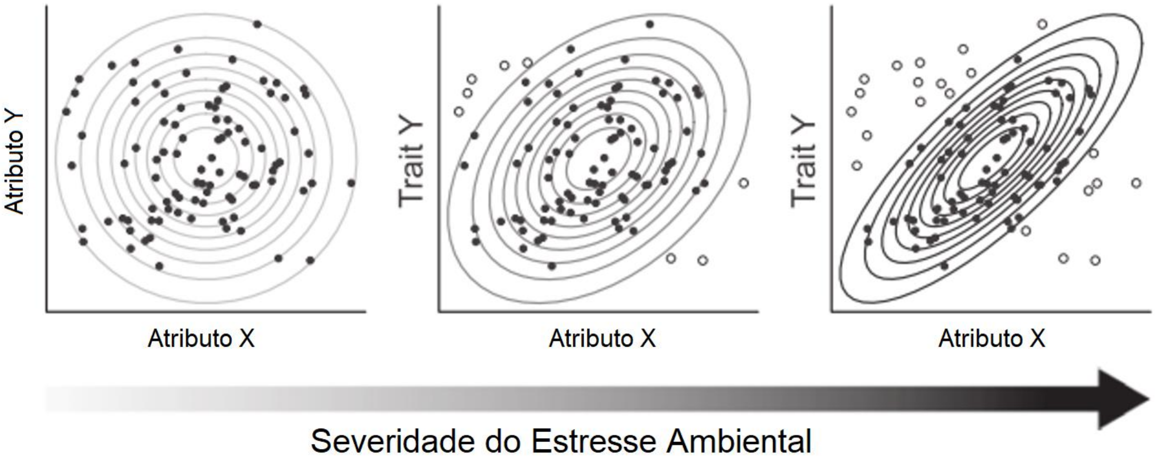

Figura 1. Esquema conceitual adaptado de Dwyer & Laughlin (2017) sobre o aumento da coordenação funcional com a severidade ambiental. Pontos brancos simbolizam estratégias ecológicas fora do espaço de nicho viável para a comunidade.

Entender a contribuição de fatores, tal como o estresse ambiental, que determinam a abundância local das espécies e a maneira como as comunidades estão organizadas ainda permanece no centro de muito debate em ecologia. A visão tradicional, conhecida como teoria determinística do nicho, tem considerado que o ambiente abiótico (filtro ambiental) e as interações bióticas (competição e facilitação) promovem a seleção das espécies em função de diferenças de aptidão entre elas, as colocando sobre vantagem em determinadas condições, mas que fora das quais não mantém indivíduos ou populações viáveis (Gotzenberger et al. 2012). O filtro ambiental deve restringir a variação e diversidade funcional e composicional de uma comunidade local se comparado as demais comunidades locais, criando padrões na distribuição das espécies e de seus atributos funcionais (Ver Fig. 2a-b; Kraft et al. 2008; Cavender-Bares et al. 2009; Cornwell & Ackerly 2009; Conti et al. 2017). Em consequência, espécies ecologicamente mais similares devem co-ocorrer, ou seja, aquelas com maior proximidade filogenética (Fig. 2c; Perrone et al. 2017). Além disto, tem sido proposto que a riqueza de uma comunidade depende do grau de sobreposição de nicho das espécies (Fig. 2d; Violle et al. 2012). Uma maior sobreposição, ou seja, maior similaridade no uso dos recursos limitantes, diminui o número de espécies viável em uma comunidade local (Violle et al. 2012). Por outro lado, as interações bióticas competitivas devem forçar o agrupamento de espécies menos similares, mais distantes filogeneticamente, e provavelmente um maior número de espécies na comunidade local (Perrone et al. 2017). Em resumo, dependendo da força do filtro ambiental e interações bióticas, que são processos não mutuamente excludentes, as comunidades agrupam espécies mais ou menos similares, com a comparação entre elas resultando em uma organização relativamente previsível (Gotzenberger et al. 2012).

Por outro lado, Hubbell (2001) e Bell (2001) propuseram em trabalhos independentes a teoria neutra, a qual postula que comunidades resultam essencialmente da interação entre a dispersão das espécies e flutuações estocásticas na abundância das espécies e não de diferenças de nicho entre elas. Em resumo, a teoria neutra prevê que após a morte de um indivíduo em uma comunidade local, seu lugar pode ser substituído tanto por outros indivíduos da mesma espécie quanto por indivíduos de outras espécies, colocando-as em uma situação de equivalência ecológica. O fator que determina a ocorrência de uma espécie não é, portanto, sua preferência de nicho. Esta teoria contribuiu para gerar um grande debate na ecologia, principalmente sobre o princípio de equivalência, fato que levou a obra de Hubbell a ser amplamente citada e discutida.

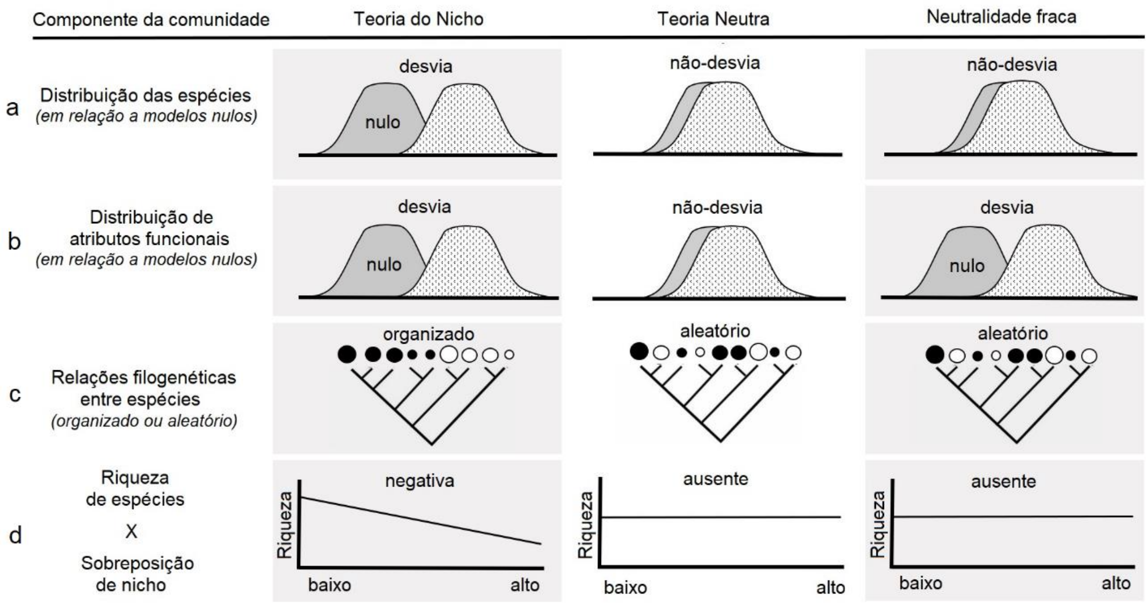

Figura. 2. Esquema conceitual das teorias de nicho, neutralidade e neutralidade fraca e os padrões esperados para a distribuição das espécies (a), distribuição dos atributos funcionais (b), das relações filogenéticas entre espécies (c), e da relação entre a riqueza e o grau de sobreposição de nicho nas comunidades locais (d).

A interpretação da neutralidade fraca tem sido proposta como uma base conceitual que não requer equivalência estrita no desempenho das espécies como predito pela versão forte da neutralidade (Bell 2001). Uma comunidade possui um padrão neutro fraco se filtros ambientais e/ou interações bióticas influenciam os atributos funcionais e o desempenho das espécies (Fig. 2b), mas não suas ocorrências (Fig. 2a), uma vez que a ocorrência tende a ser amplamente influenciada pelas flutuações estocásticas e limitação de dispersão (Tilman 2004; Gravel et al. 2006; Pinto & MacDougall 2010; Beckage et al. 2012). O entendimento destes processos tem avançado através da investigação de padrões filogenéticos, composicionais e funcionais na estrutura das comunidades (Cavender-Bares et al. 2009; Cornwell & Ackerly 2009; Pinto & MacDougall 2010).

Mecanismos estruturadores das comunidades não são apenas importantes para auxiliar no entendimento da maneira com que as comunidades se organizam mais também nas consequências ecossistêmicas da presença e das interações entre as espécies. A complementariedade de nicho tem sido descrita como o mecanismo mediador do impacto da biodiversidade sobre os processos ecossistêmicos. A complementaridade de nicho refere-se aos efeitos conjuntos de facilitação e particionamento de nicho que permitem com que as espécies explorem os recursos e condições disponíveis de forma complementar (Loreau & Hector 2001; Cardinale et al. 2002). Os efeitos de partição de nicho geralmente têm revelado relações positivas entre biodiversidade e os processes ecossistêmicos (Cardinale et al. 2006, 2013; Caliman et al. 2010; Reich et al. 2014; Duffy et al. 2017). Outros mecanismos foram propostos para criar padrões similares, porém não relacionados diretamente à partição de nicho (Huston 1997; Loreau & Hector 2001). O efeito de amostragem, por exemplo, refere-se ao fato de que comunidades mais diversas podem possuir espécies com um desempenho desproporcional em relação às demais e que, portanto, devem elevar as taxas de um determinado processo ou propriedade do ecossistema (Huston 1997; Cardinale et al. 2013). Apesar do notável progresso na avaliação dos efeitos da biodiversidade, ainda não existem evidências suficientes de que estas relações representam florestas tropicais, uma vez que a maioria dos estudos empíricos foram realizados em experimentos de pequena escala na região temperada (Caliman et al. 2010; Clarke et al. 2017).

Nesta tese, discuto três pontos adicionais ao debate sobre as relações entre biodiversidade e o funcionamento dos ecossistemas. Primeiro, questiono se o processo dinâmico da produção de serapilheira pode ser regulado por padrões espaciais de diversidade vegetal e condições ambientais; segundo, se existem efeitos de biodiversidade em uma comunidade que mostra uma organização fraca baseada no nicho;

e terceiro, se o papel da diversidade de espécies raras pode ser comparado ao papel da diversidade de espécies comuns.

OBJETIVOS DA TESE

Esta tese teve como objetivo geral investigar as causas e consequências da estrutura de comunidades e do funcionamento do ecossistema Restinga. Especificamente, objetivou-se entender como mudanças nos atributos funcionais das espécies de plantas refletem respostas conjuntas da comunidade às variações do ambiente costeiro, e como estas mudanças interferem no processo de produtividade da vegetação. Neste sentido, foram questionados se:

1. As espécies de plantas estão condicionadas a terem uma forte coordenação entre os atributos funcionais de folha e lenho para lidar com o estresse hídrico e nutricional do solo no ambiente costeiro?
2. Uma comunidade que possui padrões aleatórios de estrutura composicional e filogenética pode apresentar uma organização na distribuição dos atributos funcionais das espécies?
3. A distribuição dos atributos reflete a influência de interações interespecíficas?
4. Quais características do ambiente abiótico melhor explicam a estrutura funcional da comunidade?
5. Em que medida facetas da biodiversidade da vegetação (diversidade funcional, taxonômica e filogenética) e características do ambiente abiótico afetam a produção anual de serapilheira?
6. Qual o papel combinado da biodiversidade de espécies raras em relação ao papel combinado das espécies abundantes sobre este processo ecossistêmico?

Referências

Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G., & Violle, C. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* 13: 217–225.

Auger, S., & Shipley, B. 2013. Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science* 24: 419–428.

Baraloto, C., Paine, C.E.T., Pooter, L., Beauchene, J., Bonal, D., Domenach, A-M., Herault, B., Patiño, S., Roggy, J-C., & Chave, J. 2010. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* 13: 1338–1347.

Beckage, B., Gross, L., Platt, W., Godsoe, W., & Simberloff, D. 2012. Individual variation and weak neutrality as determinants of forest diversity. *Frontiers of Biogeography* 3: 145–155.

Bell, G. 2001. Neutral macroecology. *Science* 293: 2413–2418.

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

Cadotte, M.W., Carscadden, K., & Mirotchnick, N. 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48: 1079–1087.

Caliman, A., Pies, A.F., Esteves, F.A., Bozelli, R.L., & Farjalla, V.F. 2010. The prominence of and biases in biodiversity and ecosystem functioning research. *Biodiversity and Conservation* 19: 651–664.

Cardinale, B.J., Palmer, M.A., & Collins, S.L. 2002. Species diversity enhances ecosystem functioning through interspecies facilitation. *Nature* 415: 426–429.

Cardinale, B. J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., & Jouseau, C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989–992.

Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., Ruijven, J. Van, Reich, P.B., Scherer-lorenzen, M., & Wilsey, B.J. 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94: 1697–1707.

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

Conti, L., de Bello, F., Lepš, J., Acosta, A.T.R., & Carboni, M. 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. *Journal of Vegetation Science* 28: 762–773.

Cornwell, W.K., & Ackerly, D.D. 2009. Community Assembly and Shifts in Plant Trait Distributions across an Environmental Gradient in Coastal California. *Ecological Monographs* 79: 109–126.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., & Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Clarke, D.A., York, P.H., Rasheed, M.A., & Northfield, T.D. 2017. Does Biodiversity–Ecosystem Function Literature Neglect Tropical Ecosystems? *Trends in Ecology and Evolution* 32: 320–323.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., & Poorter, H. 2003. Handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 308–335.

Cornwell, W.K., & Ackerly, D.D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.

Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P., & Pearse, W.D. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* 3: 2958–2975.

Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., (…) & Gorne, L.D. 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.

Duffy, J.E., Godwin, C.M., & Cardinale, B.J. 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* doi:10.1038/nature23886.

Dwyer, J.M., & Laughlin, D.C. 2017. Constraints on trait combinations explain climatic drivers of biodiversity: the importance of trait covariance in community assembly. *Ecology Letters* 20: 872–882.

Fenu, G., Carboni, M., Acosta, A.T.R., & Bacchetta, G. 2012. Environmental factors influencing coastal vegetation pattern: new insights from the Mediterranean basin. *Folia Geobotanica* 48: 493–508.

Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., (…) & Zobel, M. 2012. Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews* 87: 111–127.

Gravel, D., Canham, C.D., Beaudet, M., & Messier, C. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9: 399–409.

Grime, J.P. 1997. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American naturalist* 111: 1169–1194.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton, NJ, US.

Huston, M.A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449–460.

Ishida, A., Nakano, T., Yazaki, K., Matsuki, S., Koike, N., Lauenstein, D.L., Shimizu, M., Yamashita, N. 2008. Coordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant angiosperms. *Oecologia* 156: 193–202.

Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W., & Freschet, G.T. 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology* 27: 1254–1261.

Kleyer, M., & Minden, V. 2015. Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic and Applied Ecology* 16: 1–9.

Kraft, N.J.B., Valencia, R., & Ackerly, D.D. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322: 580-582.

Leps, J., Bello, F., Smilauer, P., & Dolezal, J. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* 34: 856–863.

Loreau, M., & Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.

McGill, B.J., Enquist, B.J. Weiher, E., & Westoby, M. 2006. Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution* 21: 178–185.

Méndez-Alonzo, R., Paz, H., Cruz, R., Rosell, J.A., & Olson, M.E. 2016. Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93: 2397–2406.

de Oliveira, A.A., Vicentini, A., Chave, J., Castanho, C.D.T., Davies, S.J., Martini, A. M.Z., Lima, R.A.F., Ribeiro, R.R., Iribar, A., & Souza, V.C. 2014. Habitat specialization and phylogenetic structure of tree species in a coastal Brazilian white-sand forest. *Journal of Plant Ecology* 7: 134–144.

Perrone, R., Munoz, F., Borgy, B., Reboud, X., & Gaba, S. 2017. How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. *Perspectives in Plant Ecology, Evolution and Systematics* 25: 29–44.

Pinto, S.M., & MacDougall, A.S. 2010. Dispersal Limitation and Environmental Structure Interact to Restrict the Occupation of Optimal Habitat. *The American Naturalist* 175: 675–686.

Reich, P.B. 2014. The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology* 102: 275–301.

Rossatto, D.R., Rosana, M.K., & Franco, A.C. 2015. Leaf anatomy is associated with the type of growth form in Neotropical savanna plants. *Botany* 93: 507–518.

Somavilla, N.S., Kolb, R.M., & Rossatto, D.R. 2014. Leaf anatomical traits corroborate the leaf economic spectrum: a case study with deciduous forest tree species. *Brazilian Journal of Botany* 37: 69–82.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Annals of Botany* 90: 517–524.

Silva, K.J.P., & Souza, A.F. 2018. Common species distribution and environmental determinants in South American coastal plains. *Ecosphere* 9 e02224.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* 101: 10854–10861.

Tissier, E.J., McLoughlin, P.D., Sheard, J.W., & Johnstone, J.F. 2013. Distribution of vegetation along environmental gradients on Sable Island, Nova Scotia. *Écoscience* 20: 361–372.

Vinya, R., Malhi, Y., Brown, N., & Fisher, J.B. 2012. Functional coordination between branch hydraulic properties and leaf functional traits in Miombo woodlands: implications for water stress management and species habitat preference. *Acta Physiology Plant* 34: 1701–1710.

Violle, C., Navas, M-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., & Messier, J. 2012. The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology and Evolution* 27: 244–252.

Yeats, T.H. & Rose, J.K.C. 2013. The Formation and Function of Plant Cuticles. *Plant Physiology* 163: 5–20.

Westoby, M., & Wright, I.J. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21.

Westoby, M., Falster, D.S., Moles, A.T., Vesk., P.A., & Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornellissen, J.H.C., (…) & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Wright, I. J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Paz, H., Pitman, N.C.A. (…) & Wright, S.J. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99: 1003–1015.

CAPÍTULO I

Weak whole-plant trait coordination in a seasonally dry South American stressful environment [1]

Foto: Morvan França (*in memoriam*)

[1] **[1]** Artigo publicado na revista Ecology and Evolution. Citação: Silva, J.L.A., Souza, A.F., Caliman, A., Voigt, E.L., & Lichston, J.E. 2018. Weak whole-plant trait coordination in a seasonally dry South American stressful environment. Ecology and Evolution 8: 4–12.

Abstract

A core question involving both plant physiology and community ecology is whether traits from different organs are coordinated across species, beyond pairwise trait correlations. The strength of within-community trait coordination has been hypothesized to increase along gradients of environmental harshness, due to the cost of adopting ecological strategies out of the viable niche space supported by the abiotic conditions. We evaluated the strength of trait relationship and coordination in a stressful environment using 21 leaf and stem traits of 21 deciduous and evergreen woody species from a heath vegetation growing on coastal sandy plain in Northeastern South America. The study region faces marked dry season, high soil salinity and acidity, and poor nutritional conditions. Results from Multiple Factor Analyses supported two weak and independent axes of trait coordination, which accounted for 25-29% of the trait variance using phylogenetically independent contrasts. Trait correlations on the MFA main axis fit well with the global plant economic spectrum, with species investing in small leaves and dense stems as opposed to species with softer stems and large leaves. The species' positions on the main functional axis corresponded to the competitor-stress tolerant side of Grime's CSR triangle of plant strategies. The weak degree of trait coordination displayed by the heath vegetation species contradicted our expectation of high trait coordination in stressful environmental habitats. The distinct biogeographic origins of the species occurring in the study region and the prevalence of a regional environmental filter coupled with local homogeneous conditions could account for prevalence of trait independence we observed.

Keywords: Brazil, CSR triangle, Leaf biochemistry, Leaf-shedding behavior, Litterfall production, Plant anatomy.

Introduction

Variation in morphology, physiology, and phenology of leaves, stems, and roots allow plant species to take up different amounts of water and nutrients along temporal and spatial gradients of soil resources and light availability. Variation in plant form and function creates the basis for species coexistence, plasticity, and evolvability (Kleyer & Minden 2015). A core question involving both plant physiology and community ecology is whether multiple traits of different organs co-vary across co-occurring species (hereafter, trait coordination), beyond pairwise correlations between traits (Reich et al. 2003; Reich 2014; Kleyer & Minden 2015). Most research carried out in the last decade has focused on integrative macro-morphological traits such as plant height, leaf area, and wood density (e.g. Westoby et al. 2002; Wright et al. 2006; Díaz et al. 2016). Recently, functional ecology has embraced anatomical and biochemical traits, which are known to play important adaptive roles (Somavilla et al. 2014; Li et al. 2015). For example, the palisade parenchyma layer has been positively correlated with specific leaf area (the ratio of blade area to leaf dry mass content, SLA), which is involved in the leaf's potential for photosynthesis (Markesteijn et al. 2007). In addition, the palisade parenchyma concentrates the largest fraction of leaf nitrogen, and ultimately indicate the leaf's potential for the synthesis of biosynthetic precursors and cellular fuels (Reich et al. 2003; Somavilla et al. 2014; Li et al. 2015). In stems, the negative correlation between xylem vessel diameter and wood density influences the resistance to drought-induced cavitation and the capacity for water storage (Chave et al. 2009).

The notion that traits coordinate along axes of variation has been used to represent the trade-offs underlying ecological strategies (Wright et al. 2006; Chave et al. 2009). Functional variation is central to theories of plant strategy such as that of Grime's (1997)

CSR triangle, which has found growing application in distinct ecosystems (Pierce et al. 2016). The CSR framework defines a triangular trait space between extreme strategies that maximizes resource acquisition in productive environments (competitive strategy), survival in stressful conditions (stress-tolerant strategy), and short lifespan where disturbances are frequent (ruderal strategy). The transition from the competitive to the stress-tolerant strategy in the CSR triangle finds correspondence in the ‘fast-slow’ economic spectrum of leaves, which runs from resource-acquisitive leaves with high specific leaf area, high nitrogen and phosphorous content, fast leaf gas exchange, but short lifespan, to resource-conservative leaves with an opposite set of traits (Wright et al. 2004). Accordingly, the wood economic spectrum ranges from low density stems with tissues that facilitate growth and water movement but have reduced resistance to embolism and physical damages, to slow-growth stems with an opposite set of traits (Chave et al. 2009). The correlation between SLA and deciduousness (Méndez-Alonzo et al. 2016) as well as between SLA and ecosystem productivity (Reich 2014) suggests that litterfall production is correlated to the leaf economic spectrum. Deciduous and evergreen leaves occur at opposite ends of this spectrum (Fu et al. 2012; Méndez-Alonzo et al. 2016).

The strength of within-community trait coordination has been hypothesized to increase along gradients of environmental harshness while niche space decreases, due to the cost of adopting ecological strategies out of the viable niche space supported by the abiotic conditions (Westoby & Wright 2006; Dwyer & Laughlin 2017a; b). Under this hypothesis, environmental harshness variation would drive a gradient of communities presenting loose to strongly constrained niche spaces and, thereby, trait coordination. Evidence supporting many viable combinations of leaf and stem traits within a loose niche space have been found in natural systems such as non-seasonal tropical regions (Baraloto et al. 2010; Fortunel et al. 2012). On the other hand, stronger coordination linking leaf and stem traits within a more constrained niche space has been found in seasonally dry regions (Ishida et al. 2008; Markesteijn et al. 2011; Vinya et al. 2012; Méndez-Alonzo et al. 2016). Here we evaluated the strength of trait relationship and coordination in a heath vegetation community growing on a seasonally dry and soil-poor coastal plain in Northeastern South America. We used 21 leaf and stem traits of 21 deciduous and evergreen woody species, including traits that are missing in the whole-plant economic context, such as anatomical and biochemical traits, and litterfall production.

The Restinga heath vegetation is a mosaic of herbaceous, open scrub, and short dense forests that covers coastal sandy plains of eastern South American, mostly along the Brazilian coast. Heath vegetation communities are recent, an only colonized plains produced by marine transgression in the last 7,000 years (Scarano 2002). They have few endemics species and most constituent species also occur in neighboring species-rich ecosystems such as the semi-arid Caatinga, Cerrado savanna, and Atlantic and Amazon rainforests (Scarano 2002). Colonizing species have reduced productivity (Pires et al. 2006) and display physiological ability to deal with harsh conditions that include seasonal drought, heat stress, and sandy soils with poor nutrients and water retention (Brancalion et al. 2012). We expected the stressful seasonal drought (6 – 9 months long) and nutrient-poor soils to produce highly coordinated traits.

Material and Methods

Study area

Data was collected at the Barreira do Inferno Launch Center, Rio Grande do Norte state, Northeastern Brazil; see Silva et al. (2015) for further details on the study area and a description of the plant community composition. The Launch Center is a 1900 ha coastal area containing tall (ca. 80 m a.s.l.) sandy dunes along the sea line and sandy plains (ca. 40 m a.s.l.) punctuated by short palaeodunes (Muehe et al. 2006). The climate is tropical with a severe dry summer (Aw Köppen climate type, Alvares et al. 2013). Mean annual temperature is 26 ºC and mean annual precipitation is 1746 mm (INMET 2014, http://www.inmet.gov.br/portal/). Myrtaceae is the most abundant botanical family in the study area.

Data collection

We examined 14 leaf and stem traits of the 33 most abundant species in the study area (Supplemental Material Table S1). For 21 of these species, seven additional traits related to leaf anatomy and biochemistry were measured. Leaf and stem samplings were collected from 80 25-m² plots distributed along 16 transects of 100 m-long (five plots per transect). Whenever possible, we collected the organs from the same individuals. Leaves were collected within a two-month interval to reduce temporal variation in leaf biochemistry. To encompass as much phenotypic variability as possible, we sampled plants that were a minimum of 5 m apart, although they were often hundreds of meters to a few kilometers apart.

Leaf dry mass, leaf moisture, leaf area, and SLA were determined for five fully expanded sun leaves with little to no damage from 10 mature individuals per species (Pérez-Harguindeguy et al. 2013). We calculated leaf blade area using the ImageJ program (https://imagej.nih.gov/ij/) from the images of scanned leaves. Three leaves per individual per species were fixed in 70% (v/v) ethanol until anatomical analysis were performed. Freehand transections of each leaf blade were obtained and stained with Alcian Blue and Safranine. Leaf thickness, mesophyll layer, palisade and spongy parenchyma, and cuticle were measured (in µm) using a Nikon Eclipse e200 microscope.

We also measured the content of starch and non-reducing soluble sugars (predominantly sucrose) in 200 mg of fresh leaves for each individual per species using the Antrona method (McCready et al. 1950; Van Handel 1968). The total soluble protein content was estimated by the Bradford's method (Bradford 1976).

Litterfall production and temporal variability were measured in 45 plots as part of a long-term plant phenology project. Six 0.125 m^2 plastic basins were established as litterfall traps in each plot and used for monthly collection from December 2015 to April 2016. The leaf litterfall found in each basin was oven dried at 70 ºC for 72 hours and then sorted by species. Litterfall production has been used as a proxy for primary production of aerial biomass (Clark et al. 2001), and was estimated by dividing the monthly dried leaf mass per species per plot by respective species abundance in the same plot reported in Silva et al. (2015). We considered the temporal variability of litterfall production as an ecological variable related to phenological strategies on how species respond to water stress, and it was measured as the coefficient of variation of species-specific litterfall production per plot for all five months. We evaluated if the employed method adequately represented the litterfall production for both abundant and rare Restinga species by analyzing the correlation between these two variables (temporal variability and mean litterfall production) with the number of litterfall traps in which species were found. Most abundant species (whose litterfall production was captured by a higher number of traps) had similar mean and coefficient of variation values as rare species (captured by a smaller number of litter traps), as suggested by the low coefficients of correlation (Supplemental material Figure S1). To better distinguish the leaf-shedding behavior of species, we visually classified them as evergreen, semi-deciduous or deciduous.

Stem traits were measured in ca. 15 cm-long and 2 cm diameter stem sections collected from five individuals per species at the first lateral bifurcation of each plant

(Pérez-Harguindeguy et al. 2013). Stem density was obtained by dividing the fresh mass by its volume, and stem moisture was obtained by the difference between the fresh and oven dried mass (70 °C for 72 h). Three of these dried stems were divided into two parts. One part was used to evaluate the bark's relative dry mass and the other part to measure vessel anatomical traits. Stems were polished with six sandpapers of different texture grades until the anatomical xylem structures were exposed. We then took photographs using a 3.0x Nikon magnifying glass and processed them using the ImageJ program. The equivalent circle diameter of 100 or more xylem vessels from images of each stem were measured (Scholz et al. 2013). Vessel density was quantified as the number of vessels per mm². A stem vulnerability index was calculated using vessel diameter and vessel density (Scholz et al. 2013). The main-stem length and stem diameter at soil level were obtained from Silva et al. (2016).

Statistical analyses

We first calculated the mean trait values for each species. As some analyses require a full matrix of data, we estimated unobserved trait values (3% of the data) using Multiple Imputation with Chained Equations (MICE) through predictive mean matching with the 'mice' function from the mice package (Van Buuren & Groothuis-Oudshoorn 2011) in R version 3.1.2 (R Core Team, 2013). MICE procedure operates under the assumption that missing data depends only on observed values and not on unobserved values (missing at random data), and it has been reliably considered in ordination analyses (Dray & Josse 2015). All trait distributions were significantly skewed and required log-transformation before further analyses.

Pairwise Pearson correlations were used to test for cross-species relationships among all 21 traits. P-values were adjusted for multiple comparisons using the Benjamini-

Hochberg procedure (Waite & Campbell 2006). Independence between species was assumed by conventional statistical methods to examine trait correlations and functional trade-offs. To avoid the problem of species non-independence, we used the Felsenstein (1985)'s method of phylogenetically independent contrasts (PIC) with the 'apply' function from the ape package (Paradis et al. 2004). A phylogenetic tree was produced using Phylomatic 3 (http://phylodiversity.net/phylomatic/) and the mega tree R20120829. Branch lengths were assigned to the initial megatree using the 'bladj' function in Phylocom 4.2, with angiosperm nodes aged according to Wikström et al. (2001). Single nodes were excluded with the 'collapse.singles' function from the ape package (Figure S2).

Coordination between groups of leaf and stem traits were evaluated by Multiple Factor Analyses (MFA, Pàges 1994) using standardized raw data and PIC values with the 'MFA' function of the FactoMineR package (Lê et al. 2008). PICs values were used to confirm the trait coordination after controlling phylogenetic non-independence. MFA performs a principal component analysis (PCA) for the group of leaf traits and another PCA for the group of stem traits, separately, and then normalizes all its elements using the square root of the first eigenvalues (Pàges 1994). This creates groups of comparable traits by controlling within-group covariance. Finally, the normalized data sets were merged to form a single matrix and then a global PCA was performed. Only significant axes with eigenvalues > 1 were retained.

Species were fitted in the CSR plant strategy triangle according to Pierce *et al.* (2013) using leaf dry mass, SLA and leaf area. This method involves three steps: (1) a principal component analysis (PCA) of three key leaf traits (leaf area, leaf dry mass content, and leaf specific area), (2) a regression of trait values against PCA axes, and (3) using these regression equations to produce ternary coordinates, which summarizes the

PCA dimensions. These dimensions were divided by 100 to determine the proportional contributions of leaf area, leaf dry mass content, and specific leaf area for each species (Pierce et al. 2013, 2016).

Results

Trait values differed across species from 1 (palisade to spongy ratio, bark dry mass, stem vulnerability index, vessel density) to 2 orders of magnitude (leaf dry mass, leaf area) (Tables S2 and S3; Figures S3 and S4). Removing the phylogenetic bias in pairwise trait comparisons using PIC values produced a higher number of significant correlations relative to the raw dataset (Table 1; Figure S5).

Stems presented higher within-organ correlations than leaves (Table 1). Pairwise trait correlations between species using PIC values showed that softer stems had high bark mass and moisture, but low vessel density. Softer stems were correlated with large leaves through bark mass, vessel density, and diameter. In addition, softer stems were correlated to leaves with high protein and sucrose contents that were richer in spongy parenchyma, as indicated by the correlations between stem density, moisture, bark, vessel density, vessel diameter, soluble proteins, sucrose, and palisade to spongy ratio. Softer stems also had a high vulnerability index, which was correlated to the cuticle layer. Deciduousness predominated among large-leaved species, which ranged from 42.85 to 99.14 cm² (Table S2). Despite this, all 21 species showed hypostomatic leaves with reduced spongy-intercellular spaces in the dorsiventral mesophyll. Temporal variability of litterfall production was negatively correlated to vessel diameter, and positively correlated to sucrose.

TABLE 1 Pairwise Pearson correlations between leaf and stem traits, based on raw data (below the diagonal) and phylogenetically independent contrasts (shaded cells above the diagonal)

	Leaf morphology				Productivity		Leaf anatomy				Leaf biochemistry			Stem morphology					Stem anatomy		
	Ldmass	Lmois	Larea	SLA	Litter	Vlitter	Meso	P/S	M/T	Cuticle	Starch	Sucrose	TSP	Smois	Sdens	Bark	Slength	Sdiam	Vdiam	Vdens	Vindex
Ldmass		0.39	**0.97**	−0.23	0.18	−0.31	−0.14	−0.04	0.10	0.36	−0.32	−0.47	−0.46	0.47	−0.46	0.69	0.11	0.16	**0.54**	**−0.52**	0.47
Lmois	0.30		0.44	0.20	0.46	−0.14	0.44	−0.11	−0.11	−0.04	−0.03	−0.22	0.44	−0.01	0.01	0.19	0.12	0.36	0.15	−0.31	0.00
Larea	**0.96**	0.29		−0.05	0.22	−0.28	−0.18	−0.09	0.20	0.36	−0.16	−0.50	−0.47	0.37	−0.35	**0.59**	0.25	0.31	**0.50**	**−0.51**	0.46
SLA	−0.07	0.04	0.14		−0.03	0.17	0.09	−0.38	0.39	−0.05	0.45	−0.09	−0.03	−0.18	0.31	−0.36	0.24	0.28	−0.22	0.17	−0.28
Litter	0.20	0.08	0.17	−0.02		−0.04	0.36	−0.10	0.53	−0.19	**−0.65**	−0.49	−0.21	−0.10	0.15	0.04	0.40	0.45	0.04	−0.07	0.06
Vlitter	−0.05	−0.23	0.02	0.04	−0.21		−0.40	0.21	−0.30	−0.22	0.26	**0.66**	0.04	−0.42	0.43	−0.45	−0.17	−0.15	**−0.51**	0.67	−0.45
Meso	−0.17	0.30	−0.46	−0.50	0.02	−0.29		−0.77	**0.74**	0.18	−0.01	−0.28	**0.64**	0.43	−0.42	−0.11	0.10	**0.47**	−0.15	−0.55	−0.14
P/S	−0.04	0.14	0.04	0.04	0.13	0.16	**−0.61**		−0.79	−0.37	−0.29	0.13	**−0.63**	**−0.63**	0.55	−0.02	0.00	−0.54	0.00	0.81	−0.13
M/T	−0.22	−0.42	−0.17	−0.10	0.13	0.06	0.44	−0.41		0.11	−0.08	−0.31	0.32	0.23	−0.15	−0.18	0.44	0.65	−0.26	−0.55	−0.31
Cuticle	0.26	−0.04	0.09	−0.27	−0.27	0.12	0.39	−0.44	0.13		0.15	−0.34	0.17	0.01	−0.10	−0.24	−0.22	−0.30	0.12	−0.44	**0.64**
Starch	−0.13	0.10	0.15	0.55	−0.36	−0.30	−0.18	−0.22	−0.26	−0.11		0.24	0.18	0.58	−0.54	0.06	−0.50	−0.21	−0.03	−0.27	0.38
Sucrose	0.10	−0.16	0.08	−0.14	−0.08	0.21	−0.08	0.03	0.05	0.36	−0.23		0.20	0.35	−0.34	**0.64**	−0.48	0.11	0.29	0.22	0.03
TSP	−0.18	0.09	−0.41	−0.35	−0.02	−0.20	0.47	−0.41	0.16	0.24	−0.23	0.23		**0.63**	**−0.69**	0.27	−0.43	0.28	0.15	−0.58	0.31
Smois	0.36	0.47	0.31	0.04	−0.02	−0.43	0.07	−0.05	−0.27	0.13	0.33	0.02	−0.03		**−0.91**	0.66	−0.19	−0.05	**0.56**	**−0.50**	**0.57**
Sdens	−0.32	−0.41	−0.26	0.03	0.03	0.42	−0.10	0.07	0.18	−0.21	−0.23	−0.04	−0.02	**−0.95**		**−0.82**	0.37	0.19	−0.70	**0.56**	−0.63
Bark	0.64	0.07	**0.56**	−0.16	0.10	−0.21	−0.13	−0.09	−0.13	0.27	−0.18	0.31	0.09	**0.53**	**−0.61**		−0.24	−0.03	**0.86**	−0.65	0.64
Slength	0.22	−0.05	0.28	0.25	**0.52**	−0.21	−0.43	0.28	0.03	−0.49	0.03	−0.08	−0.23	−0.04	0.13	0.06		0.75	−0.03	−0.12	0.20
Sdiam	−0.06	0.06	−0.04	0.05	0.29	−0.32	0.00	0.13	0.06	−0.20	−0.25	0.35	0.10	0.20	−0.16	0.11	**0.59**		0.25	−0.21	0.41
Vdiam	0.43	0.03	0.39	−0.07	0.15	−0.44	−0.17	−0.03	−0.33	0.17	−0.02	0.16	0.03	**0.52**	**−0.55**	**0.78**	0.24	0.40		**−0.63**	**0.86**
Vdens	−0.36	−0.34	−0.37	−0.15	−0.07	**0.49**	0.04	0.05	0.08	−0.11	−0.15	−0.08	−0.12	**−0.58**	**0.55**	−0.46	−0.18	−0.36	−0.63		**−0.51**
Vindex	0.32	0.04	0.29	−0.12	0.10	−0.38	−0.12	0.02	−0.43	0.29	−0.06	0.14	0.10	**0.55**	**−0.58**	**0.59**	0.33	**0.54**	**0.86**	**−0.57**	

Traits and abbreviations are as in Tables S2 and S3. For all traits, we used n = 33 species, except for leaf anatomical and biochemical traits (n = 21 species). Only significant ($p < .05$) correlations are shown.

Multiple factor analysis produced two independent axes (eigenvalues > 1) using 21 species. The axes accounted for 41% of trait variance using the raw dataset and 53% using phylogenetically independent contrasts (Table 2), where most variables had high loadings on both axes. In accordance with the trait-trait correlations, the first MFA axis showed that short plants with high bark dry mass, moisture and vulnerability to cavitation invested in large leaves with higher synthesis of soluble proteins and sucrose, while plants with longer, dense stems invested in small leaves (Fig. 1). Most anatomical leaf traits, the temporal variability of litterfall production, vessel density, and the stem diameter varied independently from the first MFA axis. The MFA for a higher number of species (n=33) using 14 traits (anatomical and biochemical traits excluded) produced only one significant axis (Table S4). This axis was similar to the MFA's main axis using 21 species, but most variables had stronger loadings.

The species were concentrated at the stress tolerant end of the competitor-stress tolerant side of the Grime's CSR triangle (Fig. 2A and Table S2). The species' positions on the CSR ternary plot corresponded to the main functional dimension created by the MFA (Fig. 2B).

Table 2. Multiple Factor Analysis (MFA) based on raw data and phylogenetically independent contrasts (PICs) for sets of leaf and stem traits of 21 Restinga species.

	raw data		PIC values	
	MFA1	MFA2	MFA1	MFA2
Eigenvalue	1.33	1.04	1.53	1.33
% of var.	23	18	29	25
Leaf				
Ldmass	**0.63**	0.23	**0.55**	0.30
Lmois	0.30	-0.12	0.21	0.31
Larea	**0.62**	0.50	**0.54**	0.35
SLA	0.10	**0.64**	0.08	0.42
Litter	-0.41	0.23	**-0.67**	0.58
Vlitter	-0.13	0.16	0.41	**-0.61**
Mesophyll	-0.21	**-0.85**	0.25	**0.79**
P/S	0.23	**0.73**	-0.42	**-0.82**
M/T	-0.48	-0.32	-0.04	**0.84**
Cuticle	0.32	-0.55	0.12	0.23
Starch	0.11	0.16	**0.60**	-0.06
Sucrose	0.26	-0.2	**0.52**	-0.46
TSP	0.02	**-0.66**	**0.72**	0.39
Stem				
Smois	**0.73**	-0.20	**0.85**	0.36
Sdens	**-0.76**	0.32	**-0.92**	-0.26
Bark	**0.61**	-0.07	**0.57**	-0.20
Vdiam	**0.83**	-0.02	0.44	-0.03
Vdens	**-0.78**	0.14	-0.46	**-0.77**
Vindex	**0.89**	-0.12	**0.60**	-0.15
Slength	-0.31	**0.67**	**-0.81**	0.46
Sdiam	0.32	0.00	0.05	**0.71**

Notes: Significant eigenvalues and percentage of variance explained [Axis features (% of var.)] from the MFA axes are shown. High loadings of traits on the MFA axes are shown in boldface. Traits and abbreviations are as in the Table S2 and S3.

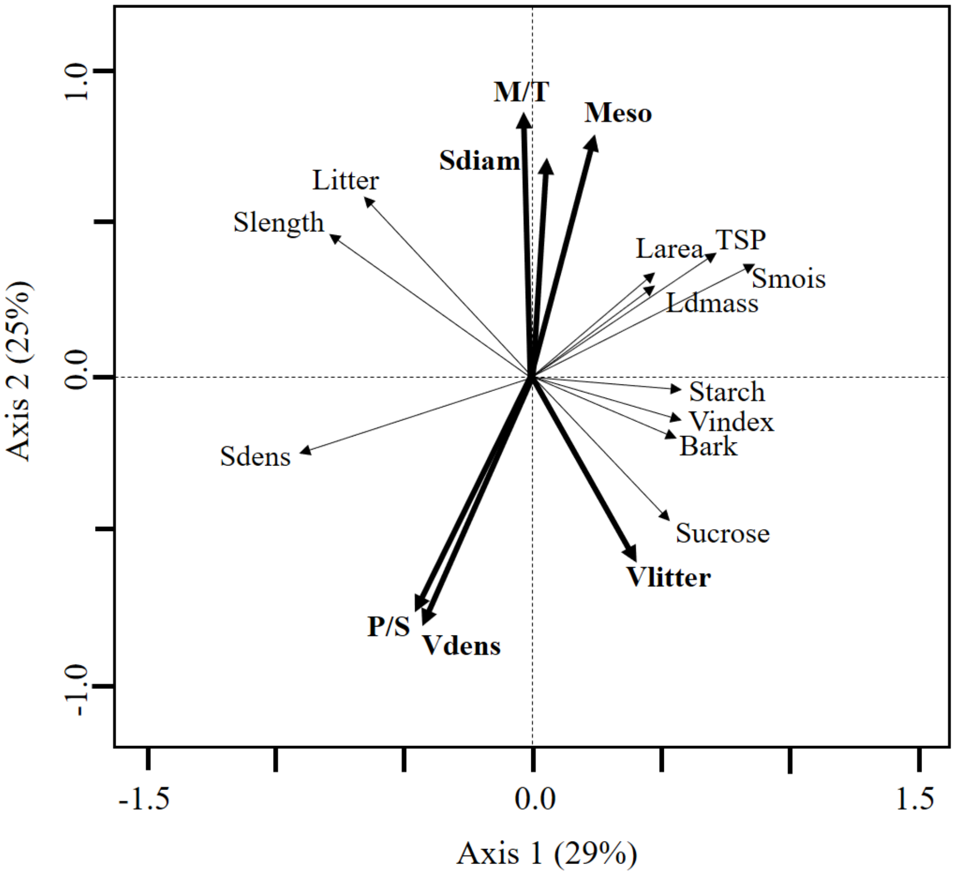

Figure 1. Biplot of functional relationships among leaf and stem traits from multiple factor analysis (MFA) based on phylogenetically independent contrasts (PICs). Traits and abbreviations: Leaf dry mass (Ldmass), leaf area (Larea), litterfall production (Litter), temporal variability in litterfall production (Vlitter), mesophyll layer (Meso), palisade to spongy parenchyma ratio (P/S), mesophyll to total leaf thickness (M/T), starch, sucrose, total soluble protein (TSP), stem moisture (Smois), bark (Bark), stem density (Sdens), vessel density (Vdens), vulnerability index (Vindex), stem length (Slength), and stem diameter (Sdiam). Thin arrows are correlated to axis 1, while thick arrows are correlated to axis 2.

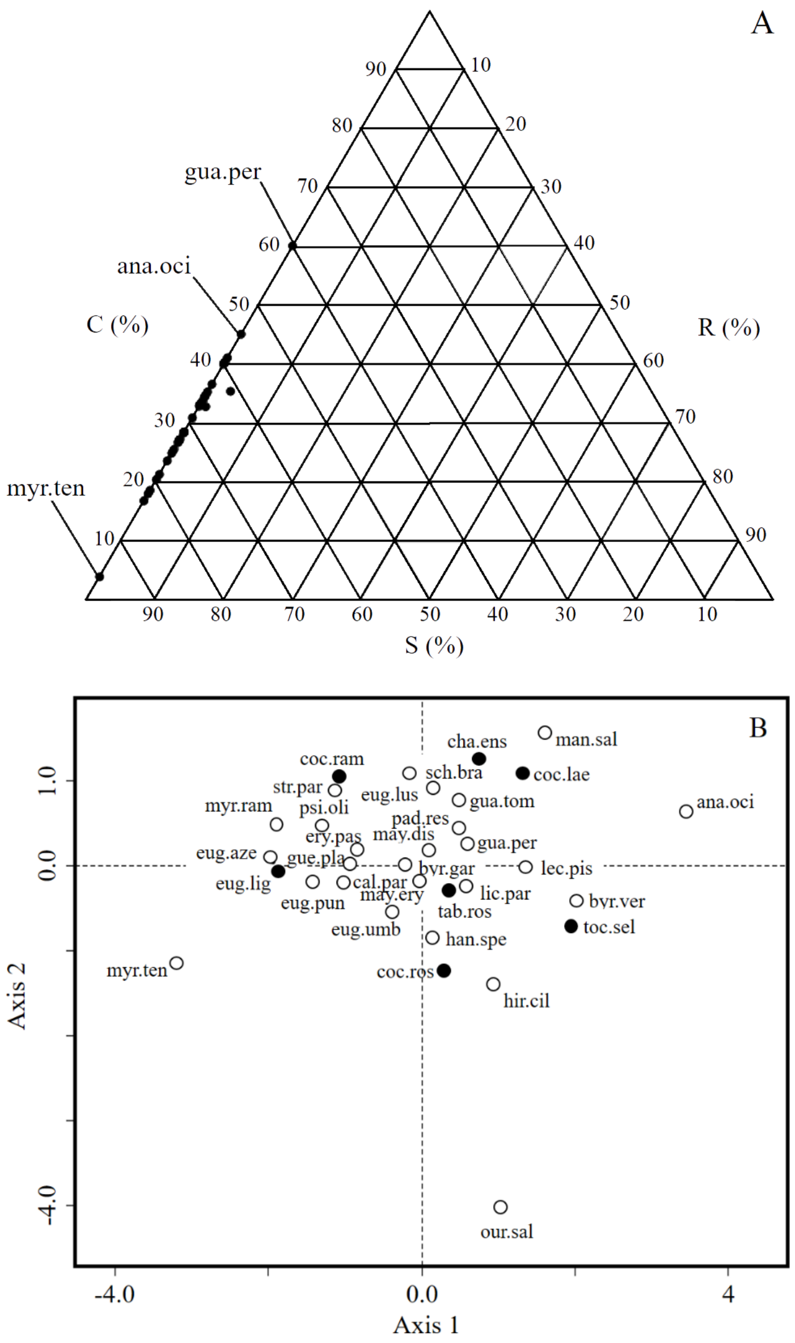

Figure 2. Two representations of the functional space occupied by species of the Restinga heath ecosystem in CSR ternary and multiple factor analysis (MFA) plots. The ternary plot (A) is characterized by the leaf area (C-strategy), leaf dry mass (S-strategy) and specific leaf area (R-strategy) according to the CSR classification, while the MFA plot (B) is characterized by multiple co-variation of 14 traits. In B, white dots represent evergreen species, while black dots represent semi- or deciduous species. Species' acronyms are as in Table S1.

Discussion

A single axis of trait coordination has been shown to explain from 25% to 60% of the whole-plant functioning in local communities, landscapes, and even globally (Li et al. 2015; Diaz et al. 2016; Méndez-Alonzo et al. 2016). We found that leaf traits showed substantial covariation even though their relationships with stem traits was not so strong. Variation of plant form and function was split into two weak and mostly independent economic spectra, as suggested by the small explained variation and similar eigenvalues of the multiple factor analysis' axes (Dwyer & Laughlin 2017b). This result places the Restinga vegetation among the communities with the lowest whole-plant trait coordination (Li et al. 2015; Diaz et al. 2016; Méndez-Alonzo et al. 2016). In addition, results contradicted our expectation that harsh conditions in the coastal sandy plains of Northeastern South America would strengthen the degree of within-community trait coordination by decreasing the viable niche space (Westoby & Wright 2006; Dwyer & Laughlin 2017a; b).

Trait independence seems to allow species to better optimize their survival and growth by investing differently in their form and function than strong coordination of traits would (Baraloto et al. 2010; Fortunel et al. 2012). The low trait coordination observed among Restinga species might reflect the fact that climate conditions in coastal sandy plains in Northeastern South America are not as harsh as other environments in which trait coordination has been tested. Dwyer & Laughlin (2017a) tested the strenght of trait coordination in herbaceous communities along a gradient of environmental harshness from savannas to deserts in Western Australia, which presented more severe abiotic conditions than the coastal plain we studied. Although Restinga vegetation faces high soil salinity and acidity and poor nutrition, the annual precipitation in the study region averages 1746 mm, and it may act as an important driver of leaf and stem independence. South American coastal plains have been colonized by species from diverse neighboring vegetation types, such as the semi-arid Caatinga, the Cerrado savanna, and the Amazon and Atlantic rainforests (Scarano 2002). Species groups with distinct biogeographic origins might show a higher trait diversity to deal with harsh conditions than a community assembled with phylogenetically related species, such as Australian savannas and deserts. Lack of root traits for this functional axis could also explain part of the trait independence seen in our data, as leaf, stem, and root traits are jointly the basis for species strategies (Fortunel et al. 2012). However, homogeneity of soil nutrients distribution in the study area (Silva et al. 2015) makes strong root trait coordination unlikely.

Despite weak trait coordination, the pattern of trait correlations on the MFA’s main axis fit well with the global plant economic spectrum, which supports small-leaved species with dense stems facilitating slower strategies and opposes large-leaved species with soft stems facilitating faster ecological strategies (Reich 2014; Diaz et al. 2016). This axis corresponded to the competitor-stress tolerant side of Grime's (1977) CSR triangle. Woody shrubs and trees are often positioned between the C-S extremities in the CSR triangle, but the stronger S orientation we found for Restinga species implies that dune fields and sandy plains greatly favor tolerance to poor soil conditions (low nutrients, high salinity, and low water retention) coupled with high radiation exposure and long dry seasons (Grime 1997; Pierce et al. 2013). This result also implies that Restinga is likely to lack species categorized near the competitor end of the CSR triangle, such as species from mesic vegetation types (i.e. Amazon and Atlantic rainforests) but present more drought-prone semi-arid species from the Caatinga and Cerrado savannas.

Some degree of trait coordination characterizing a stress tolerant strategy is likely an ecophysiological requirement for plants to colonize Restinga heath vegetation and deal with low soil nutrients and marked drought seasonality. After accounting for phylogenetic relatedness, we found that leaf area was negatively correlated to vessel density, while positively correlated to vessel diameter, and bark dry mass; and that stem vulnerability index was correlated to the cuticle layer of leaves. Furthermore, leaf area was negatively correlated to stem density in the multiple factor analysis. These trait relationships reflect trade-offs related to water movement from stems to leaves (Chave et al. 2009; Méndez-Alonzo et al. 2016). Regulation of water movement between plant organs is a key functional requirement for plants to maintain hydraulic safety in seasonally dry vegetation, where they have to deal with long periods of water shortage combined with high radiation and heat loads (Markesteijn et al. 2007, 2011; Pivovaroff et al. 2014; Méndez-Alonzo et al. 2016). Hydraulic safety requirements would explain these relationships as well as the prevalence of species with small thick leaves and dense stems in the study region, which is consistent with previous findings in the literature (Jacobsen et al. 2007; Pivovaroff et al. 2014). Small leaves dissipate more heat and, consequently, have lower transpiration costs than large leaves (Wright et al. 2006). Additionally, dense stems have lower hydraulic efficiency and higher resistance to drought-induced embolism by air seeding than softer stems (Chave et al. 2009; Scholz et al. 2013).

According to the leaf economic spectrum, higher leaf area is related to cheap resource-acquisitive leaves that are more efficient in carbon uptake, and have lower water economy (Wright et al. 2004). Acquisitive leaves are characterized by high photosynthetic and transpiration rates, low carbon investment, high C:N ratios, and high nutrient turnover (Reich 2014; Ishida et al. 2008). High concentrations of Rubisco enzyme (reflected in leaf N), biosynthetic precursors (reflected in leaf P), and cellular fuels as sucrose and starch (reflected in leaf C) are also characteristics of acquisitive leaves (Reich et al. 2003). In turn, the high transpiration costs required by large leaves to maintain leaf cooling might decrease their lifespans and induce leaf-shedding behavior at the first water shortage event (Reich et al. 2003; Méndez-Alonzo et al. 2016). Although leaf lifespan has been shown to correlate with some phenological traits, it is still debated whether leaf lifespan or other leaf traits are correlated with leaf litterfall production (Li et al. 2016). However, the correlation between SLA and deciduousness (Méndez-Alonzo et al. 2016), as well as between SLA and the ecosystem productivity (Reich 2014) have suggested that litterfall production might also be correlated with the leaf economic spectrum. Acquisitive leaves also investment more in productivity tissues (e.g., palisade parenchyma) than in protective tissues (e.g., epidermis), with the palisade layer containing a greater portion of leaf nitrogen (Markesteijn et al. 2007; Somavilla et al. 2014; Li et al. 2015). Our results partially corroborate these expectations. We found that large leaves (1) had higher synthesis of biosynthetic precursors and cellular fuels (indicative of high photosynthetic activity; Reich et al. 2003), and (2) were more often deciduous than small leaves (indicative of short leaf lifespan; Fu et al. 2012; Méndez-Alonzo et al. 2016). Large-leaved species showed less litterfall mass than small-leaved species, although the strength of this spectrum was weak within the Restinga community. However, (3) large leaves were not richer in acquisitive anatomical traits, as suggested by the MFA analysis. Further investigations in systems under distinct degrees of stress will contribute to understand the generality of whole-plant trait coordination within local communities in stressful environments.

References

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., & Sparovek, G. 2013. Koppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728.

Baraloto, C., Paine, C.E.T., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.M., Hérault, B., Patiño, S., Roggy, J.C., & Chave, J. 2010. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* 13: 1338–1347.

Bradford, M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry* 72: 248–254.

Brancalion, P.H.S., Vidal, E., Lavorenti, N.A., Batista, J.L.F., & Rodrigues, R.R. 2012. Soil-mediated effects on potential Euterpe edulis (Arecaceae) fruit and palm heart sustainable management in the Brazilian Atlantic Forest. *Forest Ecology and Management* 284: 78–85.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., & Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., & Ni, J. 2001. Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11: 356–370.

Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., (…) & Gorne, L.D. 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.

Dray, S., & Josse, J. 2015. Principal component analysis with missing values: a comparative survey of methods. *Plant Ecology* 216: 657-667.

Dwyer, J.M., & Laughlin, D.C. 2017a. Constraints on trait combinations explain climatic drivers of biodiversity: the importance of trait covariance in community assembly. *Ecology Letters* 20: 872–882.

Dwyer, J.M., & Laughlin, D.C. 2017b. Selection on trait combinations along environmental gradients. *Journal of Vegetation Science* 28: 672–673.

Felsenstein, J. 1985. Phylogenies and the comparative method. *The American naturalist* 1: 1–15.

Fortunel, C., Fine, P.V.A., & Baraloto, C. 2012. Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology* 26: 1153–1161.

Fu, P.L., Jiang, Y.J., Wang, A.Y., Brodribb, T.J., Zhang, J.L., Zhu, S.D., & Cao, K.F. 2012. Stem hydraulic traits and leaf water-stress tolerance are co-ordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. *Annals of Botany* 110: 189–199.

Grime, J.P. 1997. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American naturalist* 111: 1169–1194.

Ishida, A., Nakano, T., Yazaki, K., Matsuki, S., Koike, N., Lauenstein, D.L., Shimizu, M., & Yamashita, N. 2008. Coordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant angiosperms. *Oecologia* 156: 193–202.

Jacobsen, A.L., Pratt, R.B., Ewers, F.W., & Davis, S.D. 2007. Cavitation resistance among 26 chaparral species of Southern California. *Ecological Monographs* 77: 99–115.

Kleyer, M., & Minden, V. 2015. Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic and Applied Ecology* 16: 1–9.

Lê, S., Josse, J., & Husson, F. 2008. FactoMineR: An R Package for Multivariate Analysis. *J. of Statistical Software* 25: 1–18.

Li, L., McCormack, M.L., Ma, C., Kong, D., Zhang, Q., Chen, X., Zeng, H., Niinemets, Ü., & Guo, D. 2015. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecology Letters* 18: 899–906.

Li, F.L., Liu, X., & Bao, W. 2016. Leaf lifespan is positively correlated with periods of leaf production and reproduction in 49 herb and shrub species. *Ecology and Evolutionvolution* 6: 3822–3831.

Markesteijn, L., Poorter, L., & Bongers, F. 2007. Light-dependent leaf trait variation in 43 tropical dry forest tree species. *American Journal of Botany* 94: 515–525.

Markesteijn, L., Poorter, L., Bongers, F., Paz, H., & Sack, L. 2011. Hydraulics and life history of tropical dry forest tree species : coordination of species' drought and shade tolerance. *New Phytologist* 191 480–495.

McCready, R.M., Guggolz, J., Siliviera, V., & Owens, H.S. 1950. Determination of starch and amylose in vegetables. *Analytical Chemistry* 22: 1156–1158.

Méndez-Alonzo, R., Paz, H., Cruz, R., Rosell, J.A., & Olson, M.E. 2016. Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93: 2397–2406.

Muehe, D., Lima, C.F., & Lins-de-Barros, F.M. 2006. Erosão e propagação do litoral Brasileiro. *Ministério do Meio Ambiente, Brasília, Brazil.*

Pagès, J. 2004. Multiple factor analysis: Main features and application to sensory data. *Revista Colombiana de Estadistica* 27: 1–26.

Paradis, E., Claude, J., & Strimmer, K. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289–290.

Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S.S., Cornwell, W.K.K., Craine, J.M.M., Gurvich, D.E.E., & Cornelissen, J.H.C. 2013. New Handbook for standardized measurment of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.

Pierce, S., Brusa, G., Vagge, I., & Cerabolini, B.E.L. 2013. Allocating CSR plant functional types: The use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology* 27: 1002–1010.

Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright, S.J., Soudzilovskaia, N.A., Onipchenko, V.G., & Tampucci, D. 2016. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology* 31: 444–457.

Pires, L.A., Britez, R.M. De, Martel, G., & Pagano, S.N. 2006. Produção, acúmulo e decomposição da serapilheira em uma restinga da Ilha do Mel, Paranaguá, PR, Brasil. *Acta Botanica Brasilica* 20: 173–184.

Pivovaroff, A.L., Sack, L., & Santiago, L.S. 2014. Coordination of stem and leaf hydraulic conductance in southern California shrubs: a test of the hydraulic segmentation hypothesis. *New phytologist* 203: 842–850.

R Core Team. 2013. R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna*.

Reich, P.B. 2014. The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology* 102: 275–301.

Reich, P.B., Wright, I.J., Cavender-bares, J., Craine, J.M., Oleksyn, J., Westoby, M., Walters, M.B., Cavender-Bares, J., & Walters, M.B. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* 1643: 143–164.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Annals of Botany* 90: 517–524.

Scholz, A., Klepsch, M., Karimi, Z., & Jansen, S. 2013. How to quantify conduits in wood? *Frontiers in plant science* 4: 56.

Silva, J.L.A., Souza, A.F., Jardim, J.G., & Goto, B.T. 2015. Community assembly in harsh environments: the prevalence of ecological drift in the heath vegetation of South America. *Ecosphere* 6: 18.

Silva, A.C., Silva, J.L.A., & Souza, A.F. 2016. Determinants of variation in heath vegetation structure on coastal dune fields in northeastern South America. *Revista Brasileira de Botanica* 39: 605–612.

Somavilla, N.S., Kolb, R.M., & Rossatto, D.R. 2014. Leaf anatomical traits corroborate the leaf economic spectrum: a case study with deciduous forest tree species. *Revista Brasileira de Botanica* 37: 69–82.

Van Buuren, S., & Groothuis-Oudshoorn, K. 2011. Multivariate Imputation by Chained Equations. *Journal Of Statistical Software* 45: 1–67.

Van Handel, E. 1968. Direct microdetermination of sucrose. *Analytical Biochemistry* 22: 280–283.

Vinya, R., Malhi, Y., Brown, N., & Fisher, J.B. 2012. Functional coordination between branch hydraulic properties and leaf functional traits in miombo woodlands: Implications for water stress management and species habitat preference. *Acta Physiologiae Plantarum* 34: 1701–1710.

Waite, T. A., & Campbell, L.G. 2006. Controlling the false discovery rate and increasing statistical power in ecological studies. *Ecoscience* 13: 439–442.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., & Wright, I.J. 2002. Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics* 33: 125–159.

Westoby, M., & Wright, I.J. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21.

Wikstrom, N., Savolainen, V., & Chase, M.W. 2001. Evolution of angiosperms: Calibrating the family tree. *Proceedings of the Royal Society B* 268: 2211–2220.

Wright, I.J., Falster, D.S., Pickup, M., & Westoby, M. 2006. Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics. *Physiologia Plantarum* 127: 445–456.

Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornellissen, J.H.C., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Supplemental Material

Table S1. Studied species, botanical names and acronyms.

Family	Species	Code
Anacardiaceae	*Anacardium occidentale*	ana.oci
Malpighiaceae	*Byrsonima gardneriana*	byr.gar
Malpighiaceae	*Byrsonima verbascifolia*	byr.ver
Fabaceae	*Calliandra parvifolia*	cal.par
Fabaceae	*Chamaecrista ensiformis*	cha.ens
Polygonaceae	*Coccoloba laevis*	coc.lae
Polygonaceae	*Coccoloba ramosissima*	coc.ram
Polygonaceae	*Coccoloba rosea*	coc.ros
Erythroxylaceae	*Erythroxylum passerinum*	ery.pas
Myrtaceae	*Eugenia azeda*	eug.aze
Myrtaceae	*Eugenia ligustrina*	eug.lig
Myrtaceae	*Eugenia luschnathiana*	eug.lus
Myrtaceae	*Eugenia punicifolia*	eug.pun
Myrtaceae	*Eugenia umbelliflora*	eug.umb
Nyctaginaceae	*Guapira pernambusensis*	gua.per
Nyctaginaceae	*Guapira tomentosa*	gua.tom
Rubiaceae	*Guettarda platypoda*	gue.pla
Apocynaceae	*Hancornia speciosa*	han.spe
Chrysobalanaceae	*Hirtella ciliata*	hir.cil
Lecythidaceae	*Lecythis pisonis*	lec.pis
Chrysobalanaceae	*Licania parvifolia*	lic.par
Sapotaceae	*Manilkara salzmannii*	man.sal
Celastraceae	*Maytenus distichophylla*	may.dis
Celastraceae	*Maytenus erythroxylon*	may.ery
Myrtaceae	*Myrcia ramuliflora*	myr.ram
Myrtaceae	*Myrciaria tenella*	myr.ten
Ochnaceae	*Ouratea salicifolia*	our.sal
Sapotaceae	*Padrosia restingae*	pad.res
Myrtaceae	*Psidium oligospermum*	psi.oli
Schoepfiaceae	*Schoepfia brasiliensis*	sch.bra
Loganiaceae	*Strychnos parvifolia*	str.par
Bignoniaceae	*Tabebuia roseoalba*	tab.ros
Rubiaceae	*Tocoyena sellowiana*	toc.sel

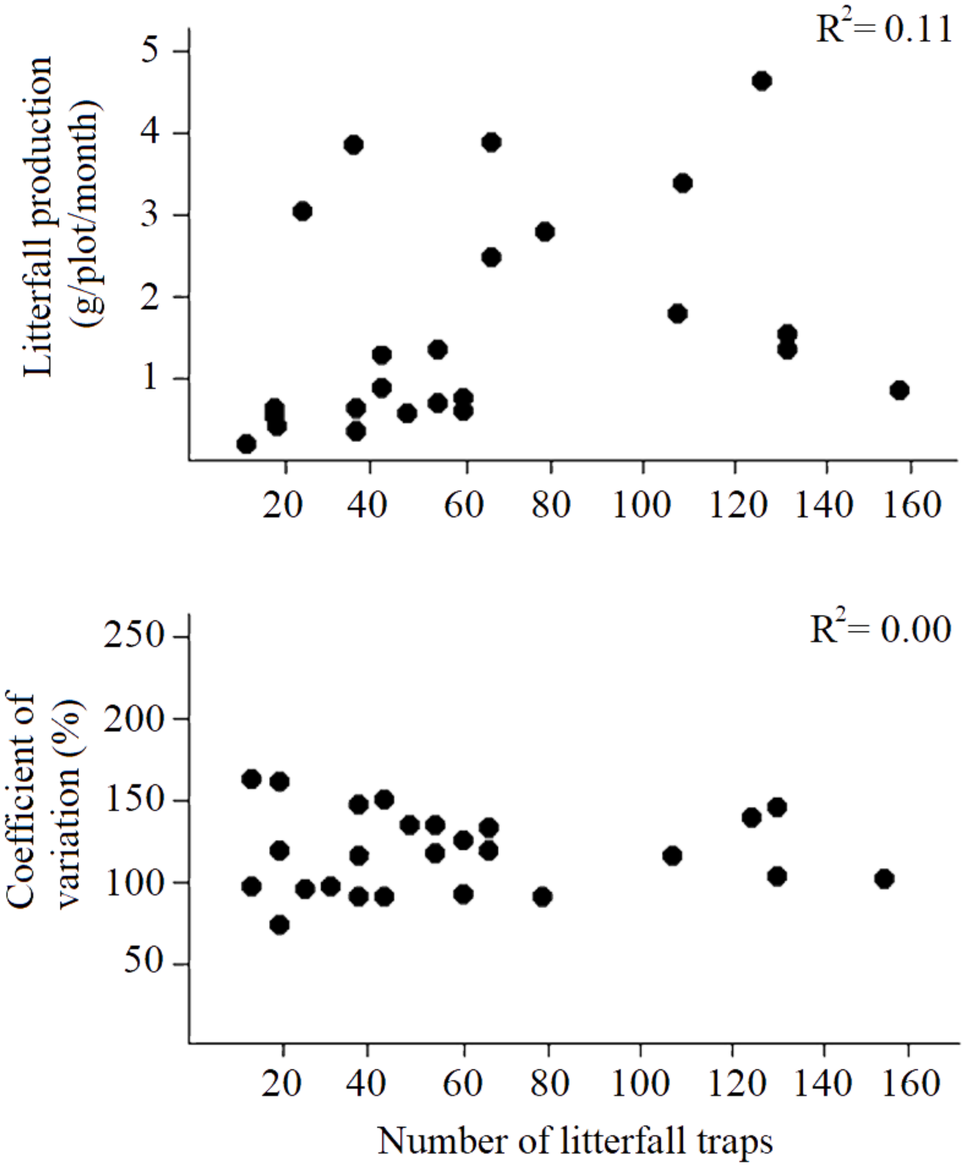

Figure S1. The correlation between the mean and the coefficient of variation of litterfall production, and the number of litterfall traps in which *Restinga* species were found. Species-specific mean litter traits are represented by black dots.

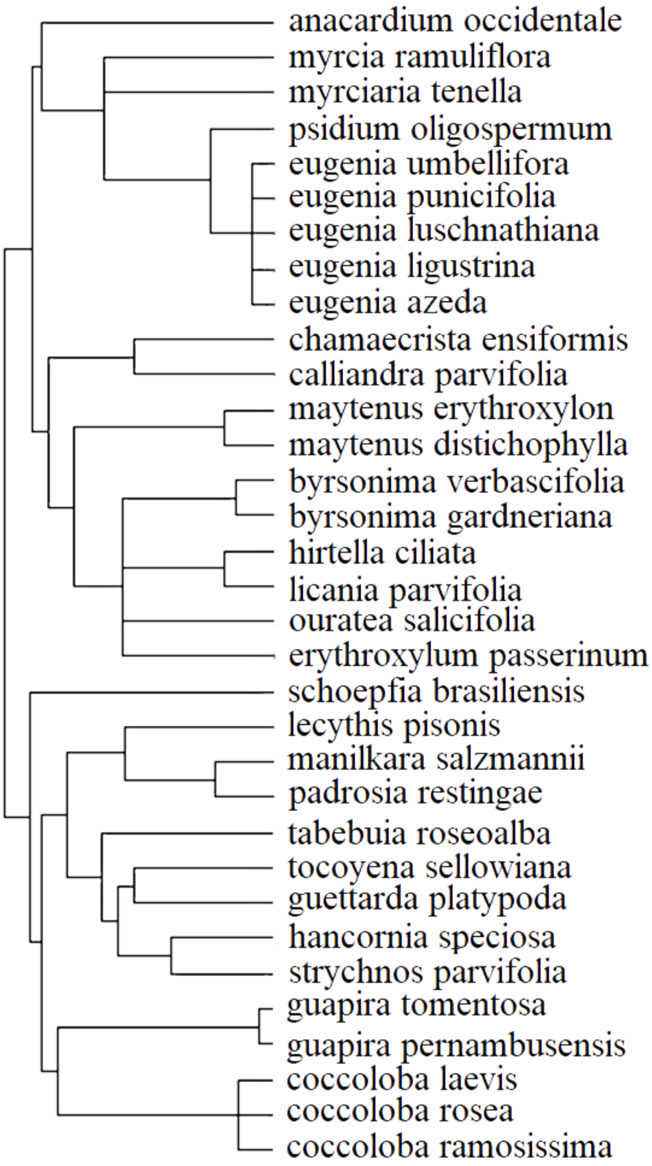

Figure S2. Phylogenetic tree of 33 native woody species from the *Restinga* heath vegetation, Northeastern Brazil.

Table S2. Mean trait values for leaf morphology, litterfall productivity, stem morphology, stem anatomy and the CSR ecological strategies of 33 *Restinga* species at Parnamirim, Northeastern Brazil. The minimum, maximum, as well as the order of magnitude of trait variation are also shown bellow.

	Leaf morphology				Litterfall productivity			Stem morphology					Stem anatomy			Strategy
Species	Ldmass	Larea	SLA	Lmois	Litter	Vlitter	Lshed	Smois	Bark	Sdens	Slength	Sdiam	Vdiam	Vdens	Vindex	CSR
	g	cm^2	$cm^2.g^{-1}$	%	g.ind. month^{-1}	%		%	%	$g.cm^{-3}$	m	mm	µm	vessel .mm^{-2}		
ana.oci	1.08	83.07	78.33	54	-	-	E	0.5	0.44	0.5	7.32	88.16	161.3	7.15	25.23	SC
byr.gar	0.1	8.23	83.14	49.87	1.48	98.4	E	0.38	0.26	0.68	3.43	47.23	98.71	33.67	2.98	S/SC
byr.ver	1.16	73.63	67.37	61	-	-	E	0.51	0.5	0.49	-	-	79.28	30.18	2.62	SC
cal.par	0.13	24.1	137.8	30	0.51	132.2	E	0.36	0.18	0.71	4.13	38.53	53.66	57.19	0.97	S/SC
cha.ens	0.3	43.03	148.3	50.87	3.91	128.7	D	0.26	0.23	0.87	4.65	65.36	82.7	37.42	2.3	S/SC
coc.lae	1.35	99.14	79.44	57	3.87	88.7	SD	0.34	0.36	0.74	4.62	46.65	84.19	50.4	1.81	SC
coc.ram	0.13	10.24	79.75	51.09	4.64	136.0	D	0.3	0.11	0.81	4.23	46.01	47.65	120.5	0.4	S/SC
coc.ros	1.03	79.96	75.49	55	-	200.0	SD	0.31	0.27	0.8	3.39	42.74	55	50.25	1.11	S/SC
ery.pas	0.12	10.3	86.76	47.63	0.66	113.3	E	0.33	0.25	0.75	3.85	43.82	54.11	121.5	0.45	S/SC
eug.aze	0.08	3.49	42.37	46.43	2.48	116.5	E	0.3	0.1	0.81	3.03	48.26	40.86	110.5	0.42	S
eug.lig	0.08	4.52	56.54	44.77	1.31	133.0	E	0.24	0.18	0.86	3.11	48.97	41.63	101.4	0.42	S/SC
eug.lus	0.12	9.8	100.6	56	0.84	87.6	E	0.33	0.11	0.81	4.55	64.91	44.92	53.25	0.94	S/SC
eug.pun	0.06	3.06	58.83	48	0.43	159.5	E	0.28	0.23	0.78	4	62.6	40.41	138.3	0.31	S
eug.umb	0.16	9.58	59.44	55.62	-	-	E	0.37	0.19	0.68	2.65	54.71	73.52	50.19	1.52	S/SC
gua.per	0.11	11.33	105.8	80.76	0.54	70.6	E	0.51	0.06	0.51	2.97	55.4	61.89	19.7	3.21	C/SC
gua.tom	0.3	25.74	82.17	56.57	3.39	113.1	E	0.32	0.09	0.74	4.2	55.08	46.94	10.49	4.7	S/SC
gue.pla	0.17	12.18	67.69	54.52	1.32	141.5	SD	0.3	0.17	0.8	3.65	47.77	47.62	103.1	0.49	S/SC
han.spe	0.08	6.5	85.68	57	0.58	145.7	E	0.48	0.26	0.52	3.15	64.6	52.93	20.7	1.93	S/SC
hir.cil	0.2	12.17	57.86	50.81	0.33	112.7	E	0.43	0.3	0.57	3.08	58	124.6	6.84	18.6	S/SC
lec.pis	0.35	30.96	91.34	55	0.47	116.3	E	0.31	0.42	0.76	4.39	65.6	119.0	14.43	8.64	S/SC

lic.par	0.26	17.25	67.53	42	0.18	95.0	E	0.3	0.21	0.84	4.16	60.43	115.0	20.45	6.05	S/SC
man.sal	0.36	23.23	64.6	52.2	9.98	94.9	E	0.36	0.31	0.7	5.5	78.83	114.6	18.97	6.59	S/SC
may.dis	0.54	28.92	56.37	53.63	-	-	E	0.29	0.24	0.81	3.74	38.85	-	-	-	S/SC
may.ery	0.46	23.49	52.21	52.92	0.81	97.6	E	0.29	0.24	0.81	3.39	43	73.09	38.29	2.02	S/SC
myr.ram	0.06	3.72	58.31	43.74	1.76	113.5	E	0.24	0.08	0.87	3.31	52.91	39.19	60.94	0.65	S
myr.ten	0.01	0.99	83.63	44	0.24		E	0.3	0.04	0.79	2.1	58.6	39.86	131.0	0.32	S
our.sal	0.62	34.2	54.58	48.05	-	-	E	0.48	0.65	0.38	1.56	50.19	166.3	11.84	14.62	S/SC
pad.res	0.35	23.86	66.84	46.99	0.68	88.0	E	0.34	0.19	0.76	4.27	63.8	61.83	35.29	1.82	S/SC
psi.oli	0.1	7.63	75.63	48	1.23	148.6	E	0.28	0.05	0.84	3.83	57.23	47.23	96.94	0.49	S/SC
sch.bra	0.16	11.02	69.04	60.88	2.78	86.9	E	0.35	0.2	0.64	3.88	56.04	46.49	29.52	1.7	S/SC
str.par	0.05	4.99	102.1	52	3.03	92.6	E	0.3	0.12	0.73	3.77	46.78	65.08	71.59	0.95	S/SC
tab.ros	0.47	42.85	88.64	53.46	0.59	122.8	D	0.36	0.22	0.65	4.2	49.51	68.51	54.16	1.29	S/SC
toc.sel	0.88	85.43	91.05	65	-	-	D	0.37	0.25	0.69	-	-	76.06	37.08	2.13	SC
Min	0.01	0.99	42.37	30	0.18	70.61	-	0.24	0.04	0.38	1.56	38.53	39.19	6.84	0.31	-
Max	1.35	99.14	148.3	80.76	9.99	200.0	-	0.51	0.65	0.87	7.32	88.16	166.3	138.3	25.23	-
Magnitude	135	100.1	3.5	2.69	9.81	2.84	-	2.12	16.2	2.28	4.69	2.28	4.24	20.22	81.38	-

Notes: Traits and abbreviations: Leaf dry mass (Ldmass), leaf area (Larea), specific leaf area (SLA), leaf moisture (Lmois), stem moisture (Smois), bark (Bark), stem density (Sdens), vessel diameter (Vdiam), vessel density (Vdens), vulnerability index (Vindex), stem length (Slength), stem diameter (Sdiam), litter production (Litter), variability in litter production (Vlitter), leaf-shedding behavior (Lshed) [E=evergreen, SD= semi-deciduous, D=deciduous], and the CSR plant strategy according to Pierce *et al.*(2013). Species acronyms are as in Table S1.

Table S3. Mean trait values of leaf anatomy and biochemistry from 21 *Restinga* species. Minimum, maximum and the order of magnitude of trait variation are shown below.

	Leaf anatomy				Leaf biochemistry		
	Meso	Cut	P/S	M/T	Starch	Sucrose	TSP
Species	µm	µm	%	%	mg.g DM^{-1}	mg.g DM^{-1}	mg.g DM^{-1}
byr.gar	183.93	5.68	0.65	0.72	34.53	14.85	12.08
cal.par	-	-	-	-	55.19	11.9	3.84
cha.ens	129.93	5.64	0.66	0.72	26.88	25.66	6.11
coc.ram	237.59	3.61	0.87	0.73	17.82	6.54	8.81
ery.pas	208.18	4.65	0.58	0.76	36.34	10.3	5.41
eug.aze	418.76	9.61	0.17	0.89	21.67	26	5.84
eug.lig	376.43	9.02	0.23	0.88	21.93	26.4	16.9
eug.umb	427.17	6.74	0.49	0.92	13.78	12.08	9.56
gua.per	368.53	6.26	0.45	0.59	60.69	7.7	6.98
gua.tom	238.24	8.52	0.82	0.84	14.67	6.81	6.03
gue.pla	118.08	5.38	2.00	0.64	11.65	22.4	1.97
han.spe	285.04	5.68	0.65	0.87	21.53	27.35	9.9
hir.cil	182.47	6.84	0.89	0.57	32.68	22.25	10.55
man.sal	289.21	4.62	0.75	0.81	13.74	17.24	7.46
may.dis	291.09	-	0.42	0.71	14.76	15	9.01
may.ery	316.23	7.3	0.4	0.72	33.41	15.32	10
myr.ram	298.48	2.8	0.64	0.89	20.51	7.38	6.99
our.sal	285.28	9.48	0.4	0.76	15.24	20.74	7.34
pad.res	178.17	6.18	0.69	0.79	23.58	29.02	8.72
sch.bra	366.86	6.49	0.67	0.88	20.22	20.34	14.16
tab.ros	168	4.99	0.86	0.8	50.81	17.09	2.71
Min	118.08	2.8	0.17	0.57	11.65	6.54	1.97
Max	427.17	9.61	2.00	0.92	60.69	29.02	16.9
Magnitude	3.62	3.43	11.76	1.61	5.21	4.44	8.57

Notes: Traits and abbreviations: Mesophyll thickness (Meso), cuticle thickness (Cut), palisade layer per spongy parenchyma layer (P/S), mesophyll layer per total leaf thickness (M/T), starch content (Starch), sucrose content (Sucrose), and total soluble protein (TSP). Species acronyms are as in Table S1.

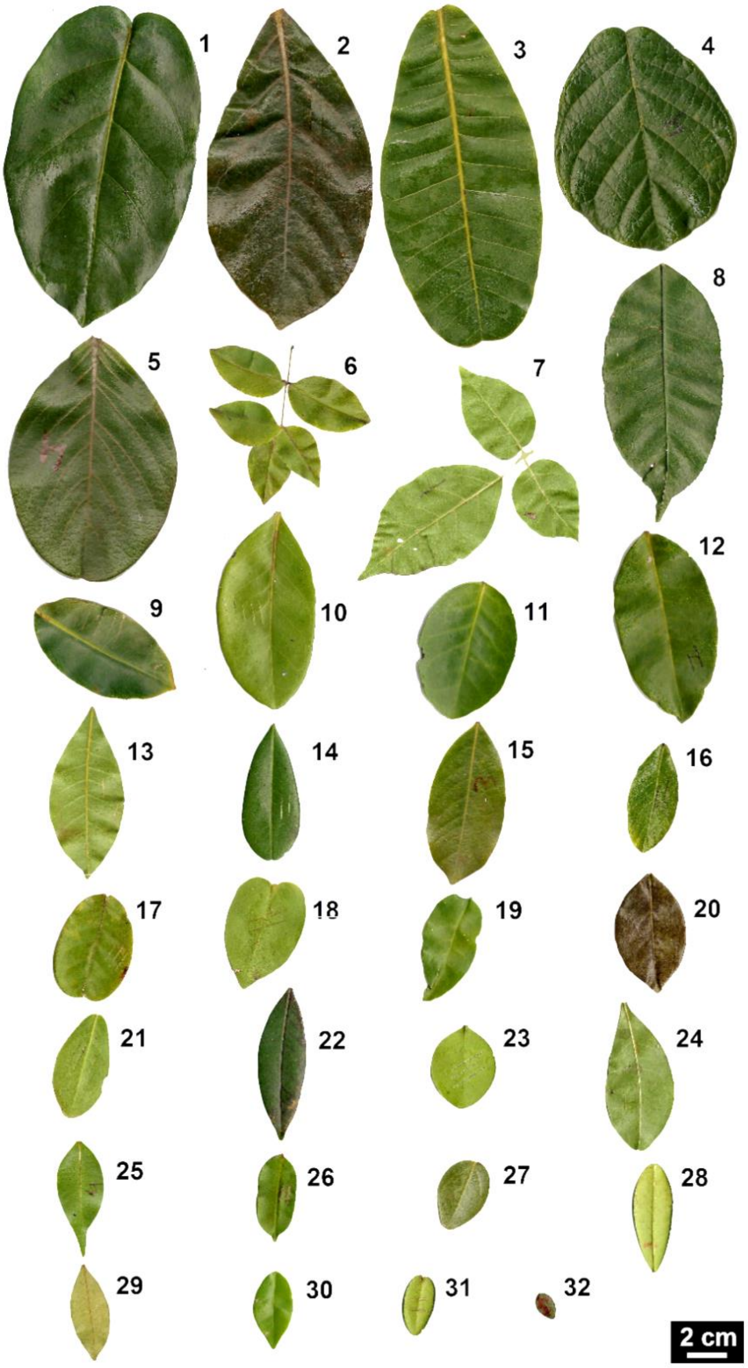

Figure S3. Leaves from the studied species. Species are ordered from the largest to the smallest leaf area: 1-*Coccoloba laevis,* 2-*Tocoyena sellowiana,* 3-*Anacardium occidentale,* 4-*Coccoloba rosea,* 5-*Byrsonima verbascifolia,* 6-*Chamaecrista ensiformis,* 7-*Tabebuia roseoalba*, 8-*Lecythis pisonis,* 9-*Ouratea salicifolia,* 10-*Maytenus distichophylla,* 11-*Maytenus erythroxylon,* 12-*Guapira tomentosa,* 13-*Padrosia restingae,* 14-*Manilkara salzmannii,* 15-*Licania parvifolia,* 16-*Guettarda platypoda,* 17-*Hirtella ciliata*, 18-*Guapira pernambusensis,* 19-*Schoepfia brasiliensis,* 20-*Erythroxylum passerinum,* 21-*Coccoloba ramosissima,* 22-*Eugenia luschnathiana,* 23-*Eugenia umbelliflora*, 24-*Byrsonima gardneriana*, 25-*Psidium oligospermum*, 26-*Hancornia speciosa*, 27-*Strychnosparvifolia*, 28-*Eugenia ligustrina*, 29-*Eugenia punicifolia,* 30-*Myrcia ramuliflora,* 31-*Eugenia azeda, and* 32-*Myrciaria tenella.*

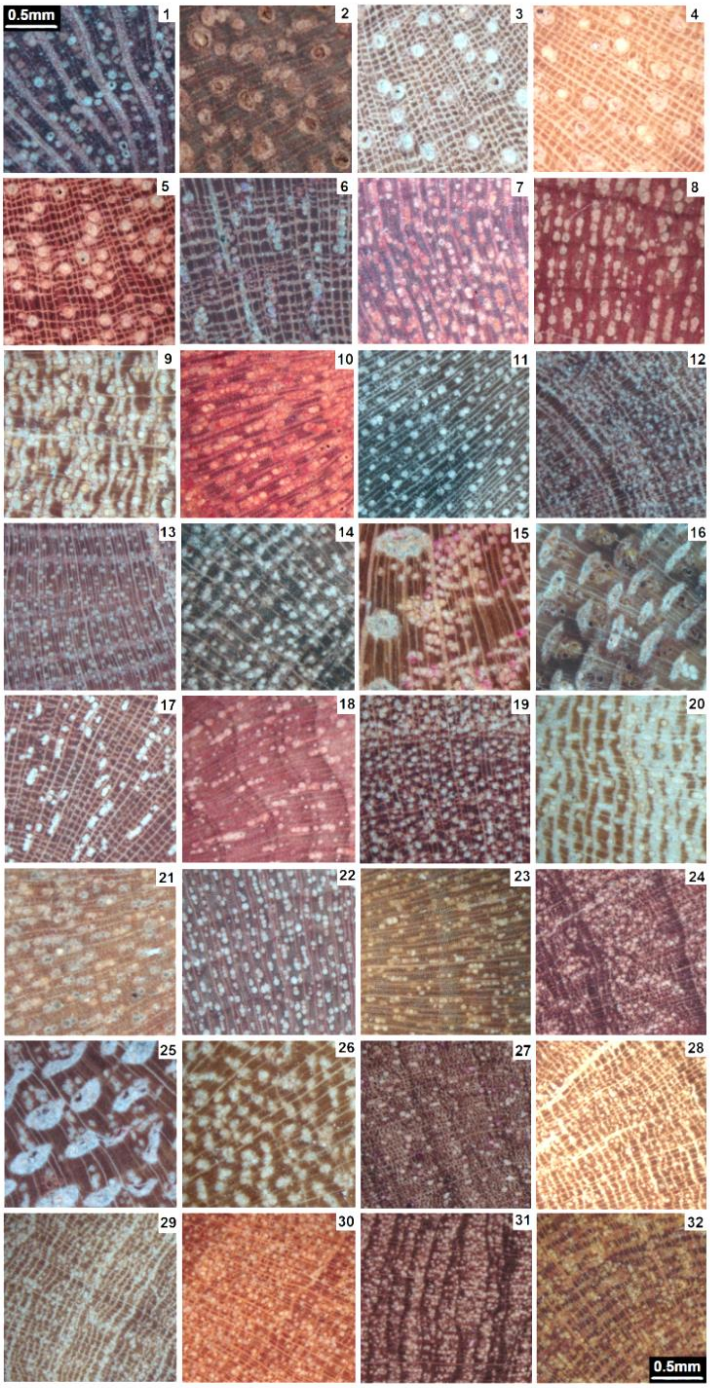

Figure S4. Panel of cross-anatomical stem sections from *Restinga* species. Species are ordered from the widest to the narrowest xylem vessel diameter: 1-*Ouratea salicifolia*, 2-*Anacardium occidentale*, 3-*Hirtella ciliata*, 4-*Lecythis pisonis*, 5-*Licania parvifolia*, 6-*Manilkara salzmannii*, 7-*Byrsonima gardneriana*, 8-*Coccoloba laevis*, 9-*Chamaecrista ensiformis*, 10-*Byrsonima verbascifolia*, 11-*Tocoyena sellowiana*, 12-*Eugenia umbelliflora*, 13-*Maytenus distichophylla/erythroxylon*, 14-*Tabebuia roseoalba*, 15-*Strychnosparvifolia*, 16-*Guapira pernambusensis*, 17-*Padrosia restingae*, 18-*Coccoloba rosea*, 19-*Erythroxylum passerinum*, 20-*Calliandra parvifolia*, 21-*Hancornia speciosa*, 22-*Coccoloba ramosissima*, 23-*Guettarda platypoda*, 24-*Psidium oligospermum*, 25-*Guapira tomentosa*, 26-*Schoepfia brasiliensis*, 27-*Eugenia luschnathiana*, 28-*Eugenia ligustrina*, 29-*Eugenia azeda*, 30-*Eugenia punicifolia*, 31- *Myrciaria tenella, and* 32-*Myrcia ramuliflora*.

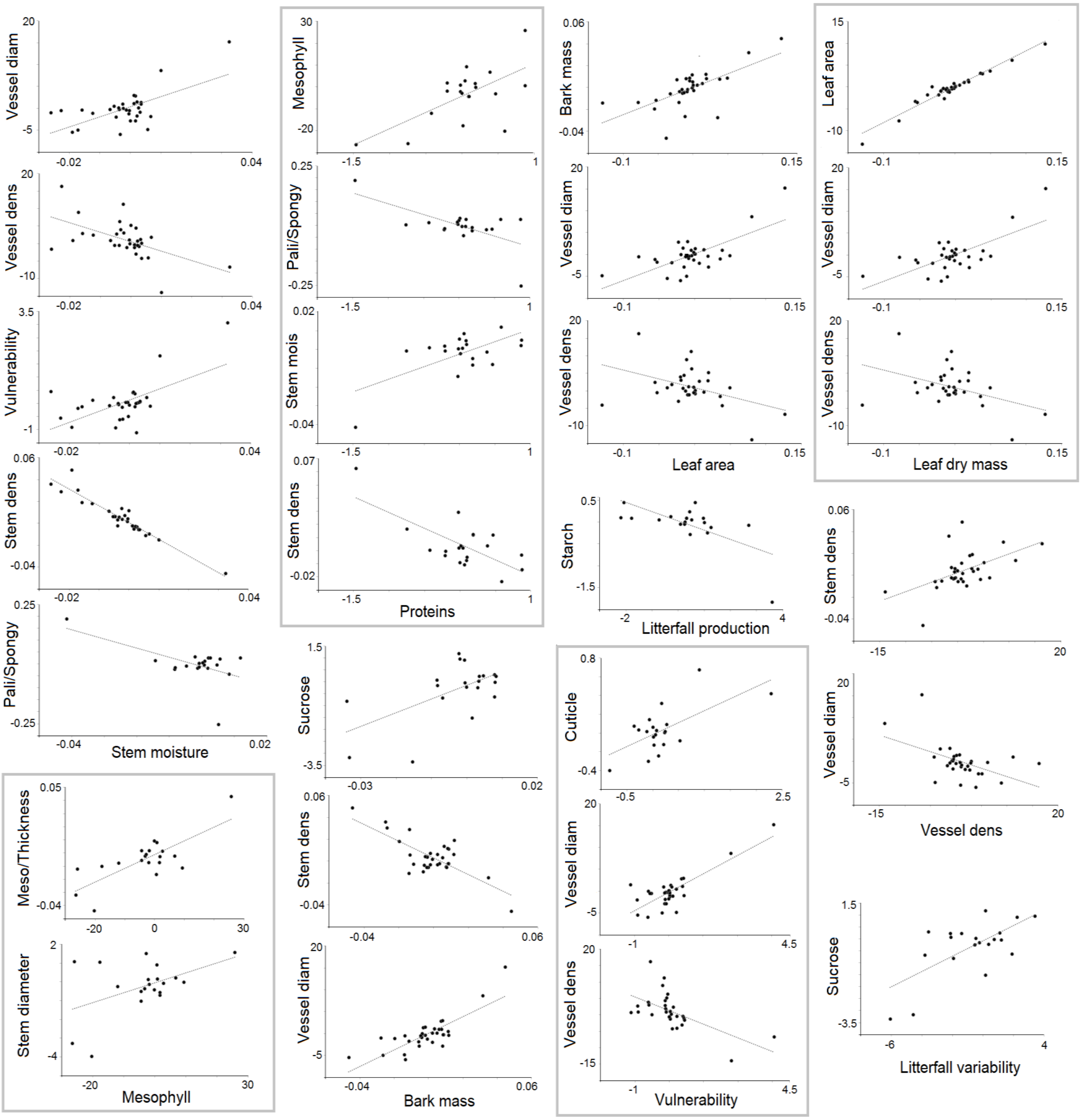

Figure S5. Significant pairwise correlations (P ≤ 0.05) between leaf and stem traits using phylogenetic independent contrasts values.

Table S4. Multiple Factor Analysis (MFA) based on raw data and phylogenetically independent contrasts (PICs) for sets of leaf and stem traits of 33 *Restinga* species.

	MFA 1 (raw data)	MFA 1 (PICs)
Eigenvalue	1.80	2.26
% of var.	33	43
Leaf		
Ldmass	**0.80**	**0.90**
Lmois	**0.45**	**0.60**
Larea	**0.80**	**0.89**
SLA	0.07	0.05
Litter	0.28	0.11
Vlitter	0.06	-0.17
Stem		
Smois	**0.62**	**0.62**
Sdens	**-0.57**	**-0.56**
Bark	**0.69**	**0.71**
Vdiam	**0.69**	**0.81**
Vdens	**-0.67**	**-0.62**
Vindex	**0.58**	**0.75**
Slength	**0.64**	**0.78**
Sdiam	**0.63**	**0.84**

CAPÍTULO II

Phenotypic plasticity and niche overlap as the basis of weak neutrality in Restinga heath vegetation in South America

Foto: Morvan França (*in memoriam*)

Abstract

Understanding how communities are organized is a central theme in community ecology. To contribute to the debate, we asked if plant communities established on stressful habitats are influenced by weak neutral effects on functional trait distribution, even in the presence of completely stochastic species distribution. We evaluated 19 traits of 21 tree and shrub species, as well as 13 abiotic variables in 72-25 m² plots in dune tops, valleys, flats and steep microenvironments of a coastal area, Northeastern Brazil. We evaluated environmental filtering and niche overlap indices based on species and individual trait variability relative to null models, regressions between species richness and niche overlap, and regressions between community-weighted mean (CWM) traits and abiotic variables. We compared results from trait-based approaches to previous evidence that species occurrence, phylogenetic relatedness, and environmental heterogeneity across plots in this coastal region are barely related. The environmental filtering index did not deviate from null expectations for any trait. Models that included individual variability performed similarly to models that used mean traits. We only found non-significant flat relationships between species richness and niche overlap. However, explicit consideration of environmental gradients by CWM analysis revealed functional patterns that would remain undetected if only trait distributions were analyzed. CWM traits were not driven by species turnover because β-diversity in the study area is low. Therefore, regression results suggested phenotypic plastic responses to environmental heterogeneity. We conclude that analyses of species occurrence or phylogenetic relatedness may be insufficient for a full understanding of community processes and should be complemented with analyses of functional traits to correctly reveal processes underpinning community assembly. Variation in community structure is based on phenotypic plasticity, with variation in species traits rather than changes in species identity and phylogenetic structure. In this regard, we accept that Restinga plant communities established in stressful habitats of Northeastern South America are influenced by weak neutral effects on functional trait distributions.

Keywords: Restinga, Heath vegetation, Seasonally dry forest, Harsh environment, Stress-tolerant species, Plant functioning, Niche-based processes, Neutral processes.

Introduction

Understanding how species from a regional pool colonize and interact to form local communities is a central theme in ecology, although it is still hotly debated. The debate revolves around whether processes underpinning community assembly are dependent on species phylogenetic relatedness, species occurrence, and functional traits (Guo et al. 2015; Conti et al. 2017). Niche-based theory asserts that filters produced by stress, productivity, or disturbance gradients sort species and functional traits within a given region (Götzenberger et al. 2012). At smaller spatial scales, these filters tend to be overshadowed by the role of species interactions, due to reduced environmental heterogeneity (Götzenberger et al. 2012). Conversely, neutral theory proposes that communities result essentially from the interplay between dispersal limitation and stochastic drifts in the abundance of trophically equivalent species (Bell 2001; Hubbell 2001).

Much progress has been made to reconcile niche and neutral theory (Tilman 2004; Gravel et al. 2006). Weak neutrality theory has been proposed as a conceptual basis that does not require strict equivalence in species performance (Bell 2001; Zobel 2001; Holt

2006; Munoz & Huneman 2016). A community would show a weak neutral pattern if abiotic gradients and/or species interactions impose sorting on functional traits and species performances, but not on species occurrence, since occurrence tends to be largely offset by autocorrelated environmental factors, drift, and dispersal limitation (Tilman 2004; Gravel et al. 2006; Holt 2006; Pinto & MacDougall 2010; Beckage et al. 2012). Dispersal limitation, for example, can prevent species from reaching optimal habitats where they would have better performance, or concentrate propagules in sub-optimal habitats, thereby creating a mismatch between environmental heterogeneity, species occurrence, and phylogenetic relatedness (Pinto & MacDougall 2010; Souza et al. 2016).

Community assembly theories suggest distinct patterns for species phylogenetic relatedness, species occurrence, and trait distributions (Cavender-Bares et al. 2009; Cornwell & Ackerly 2009; Pinto & MacDougall 2010). They also generate distinct expectations for the relationship between species richness and niche overlap (i.e. how species share the niche, Violle et al. 2012). The detection of phylogenetic structure as clustered or overdispersed communities, the departure of species and trait distributions from null expectations, and the decrease in species richness with increasing niche overlap would support the signature of niche-based processes (Fig. 1; see Götzenberger et al. 2012 for review concepts). If meaningful niche dimensions are used in a similar way by species with high overlap, then less species can co-occur (Violle et al. 2012). Conversely, random patterns of phylogenetic relatedness, species occurrence and trait distributions, as well as no relationship between species richness and niche overlap would support the signature of neutrality. The detection of functional organization in the community despite random patterns of other components would provide evidence of weak neutrality (Munoz & Huneman 2016). Differences among individuals in phenotypical plasticity could enable both environmental filtering and species interactions to alter species distributions and interactions in several complex ways (Miner et al. 2005; Jung et al. 2010). This can happen if individuals respond to fluctuating environments through phenotypic plasticity, even if the populations to which they belong do not. Thus, it has been recommended that intraspecific variability be considered in community analyses (Violle et al. 2012).

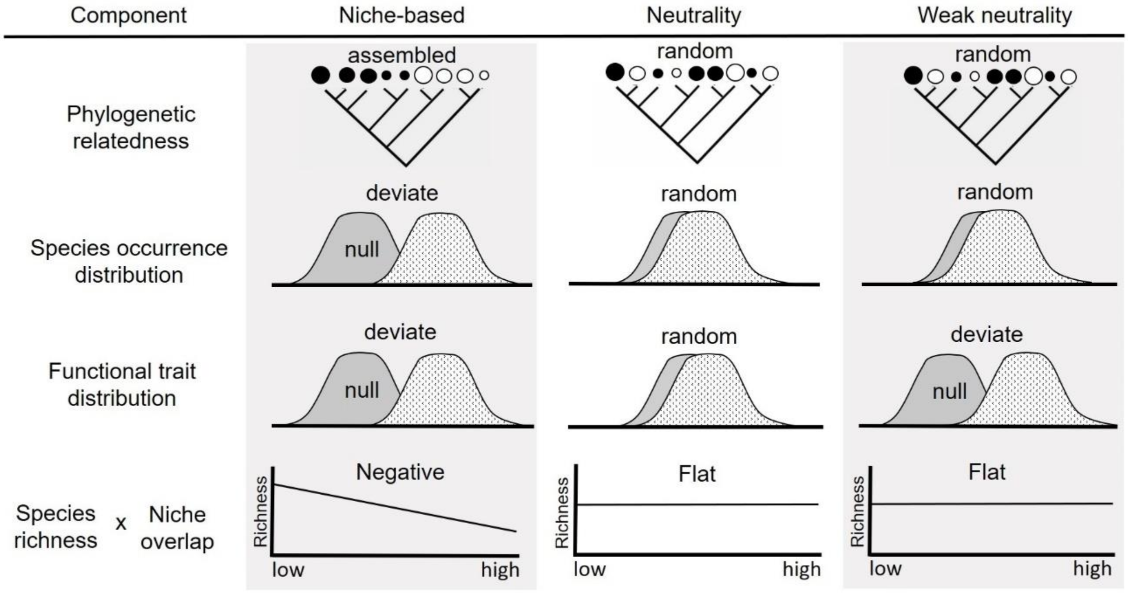

Figure 1. Theoretical diagram summarizing three alternative scenarios of community assembly for species phylogenetic relatedness, species occurrence, functional traits, and the relationship between species richness and niche overlap.

Despite the theoretical and analytical advantages of integrating traits, species occurrence, and phylogenetic approaches to detect and quantify processes, most studies in natural systems have not covered these aspects simultaneously. There are examples from Mediterranean forests (De la Riva et al. 2016), mixed subtropical rainforests (Souza et al. 2016), and saltmarshes (Guo et al. 2015), but many other vegetation types remain unstudied, such as Restinga heath vegetation on coastal sandplains. Coastal areas are characterized by strong spatial and temporal gradients of water availability that impose the major physiological selective pressure favoring stress tolerant species (De la Riva et al. 2016). These gradients are often intensified or attenuated by dunes, rocks and marine effects that result in high habitat heterogeneity from meters to a few kilometers (Cornwell & Ackerly 2009; Moeslund et al. 2013; Jager et al. 2015; Conti et al. 2017). Costal dunes, for example, create wind-protected habitats on their leeward slopes and stressful wind-eroded habitats on windward slopes (Moeslund et al. 2013). Leeward dune sides usually have lower evaporation rates and dry out slower than windward sides. Therefore, coastal areas are ideal systems to test community assembly hypotheses at fine scales due to their high environmental complexity (Cornwell & Ackerly 2009; Brunbjerg et al. 2014; Moeslund et al. 2013; de Oliveira et al. 2014; Jager et al. 2015; Conti et al. 2017).

Coastal plant communities may show a phylogenetically clustered structure at the regional scale, which is often related to the sea-inland abiotic gradient (Brunbjerg et al. 2014). However, stochastic processes such as populational drift and dispersal limitation seem to produce random phylogenetic patterns in many cases (de Oliveira et al. 2014; Silva et al. 2015). In Northeastern South America, even the occurrence of species seems to be the outcome of neutral processes (Silva et al. 2015). This result is consistent with recent findings at continental spatial scales, which suggest that groups of common species show extensive overlap in their distribution and weak environmental affinities (Silva et al. 2018). Here we ask whether Restinga plant communities established on stressful habitats could be influenced by weak neutral effects on functional trait distribution, even in the presence of completely stochastic species and phylogenetic distribution. We expected that environmental filters would create patterns in leaf and stem traits, despite the random species distribution and phylogenetic relatedness, which would support the weak neutrality hypothesis (Fig. 1).

Although our data cannot predict which type of species interaction could be involved in the assembly process of Restinga heath vegetation communities, we expected that species interactions would affect niche overlap and trait organization. Species in harsh environments tend to interfere intensely in the establishment of others either by competition of limited resources or by ameliorating local condition through facilitation (Castanho et al. 2015; Conti et al. 2017). For example, nurse species may ameliorate locally stressful conditions and benefit the establishment of less stress-tolerant species with different trait values (Castanho et al. 2015; Conti et al. 2017). However, under the canopy of nurse plants, species may compete for the limited water supply, sometimes just after an initial phase of facilitation (Maestre et al. 2005, 2009). In other cases, species even compete with the nurse plant after an initial phase of facilitation. Facilitation can also be replaced by competition or neutral interactions if plants experience severely stress conditions (Castanho et al. 2015).

Material and Methods

Study area

The study was carried out in the Barreira do Inferno Launch Center, Rio Grande do Norte state, Northeastern Brazil (Fig. 2). The Launch Center is a 1,900 ha coastal area containing tall dunes near the sea (ca. 80 m a.s.l.), and relatively flat areas (ca. 40 m a.s.l.) punctuated by short palaeodunes further inland (Muehe et al. 2006). The climate is tropical with a severe dry season (6 - 9 months), with mean annual temperature of 26 ºC, and mean annual precipitation of 1,746 mm (INMET 2017; http://www.inmet.gov.br/portal/).

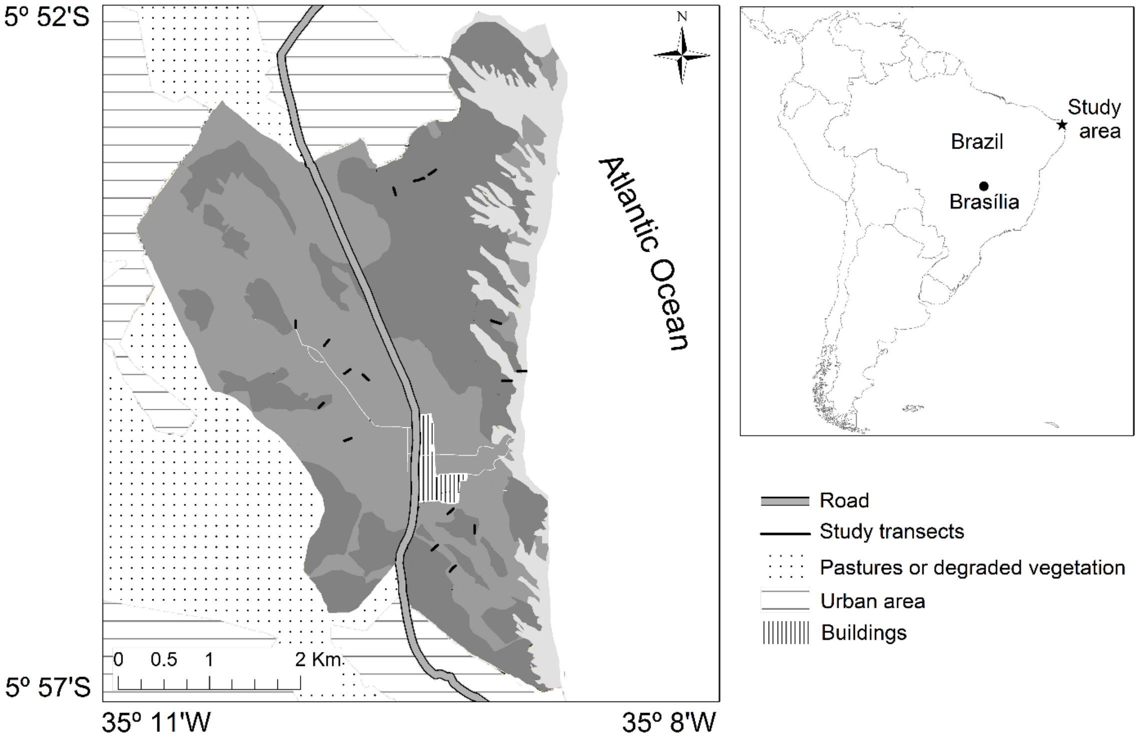

Figure 2. The spatial distribution of transects in the study area, Northeastern Brazil. Shades of gray correspond to mobile dunes (light grey), shrub (medium grey) and coastal forest (dark grey).

Data collection

This study benefited from previous ones that collected information on species composition, abiotic variables, and functional traits of these species (Silva et al. 2015, 2017). Compositional data was collected using the sampling designed made by Silva et al. (2015). Originally, they established 85 plots of 25 m² along 17-100 m long transects (five plots randomly placed on each transect) placed perpendicularly to pre-existing and accessible trails. The use of transects allowed coverage of different parts of the study area in a variety of vegetation types like scrub and forest physiognomies. In this study, we retained only the plots with at least five individuals (total of 72 plots). Each plot was characterized as exposed, consisting of flat areas and the windward sides of foredunes, or sheltered, consisting of valleys, windward and leeward sides of interdunes, as well as by elevation, dune steepness, and eleven other edaphic attributes (pH, Na, K, P, total N, Ca + Mg, H + Al, cation exchange capacity, organic matter, soil density, and the sum of silt and clay content).

Most of the functional trait data was obtained from Silva et al. (2018), who provided mean values of leaf dry mass, leaf area, specific leaf area, starch content, soluble sugars, total soluble proteins, mesophyll thickness, cuticle thickness, palisade to spongy thickness ratio, mesophyll to leaf thickness ratio, stem density, stem moisture, bark dry mass, xylem vessel diameter, xylem vessel density, and the vulnerability to xylem cavitation index of the 21 most abundant species in the area. Leaves and stems were collected from the same individual whenever possible following standardized protocols (Pérez-Harguindeguy et al. 2013). Individuals were often hundreds of meters to a few kilometers apart to encompass as much phenotypic variability as possible. In addition, we included stem length, stem diameter, and species basal area in the analyses, since these traits were sampled for almost all individuals within and among plots.

Data analyses

Three complementary approaches were used to test whether environmental filtering and species interactions create functional organization despite the random species occurrence and phylogenetic relatedness detected by Silva et al. (2015) at the plot level. The first approach was based on three multi-level indices (individual - I, population - P, community - C, and region - R) proposed by Violle et al. (2012), which compute trait variance at each level. The indices can be named as the index of environmental filtering based on interspecific variability [$T_{PC/PR}$], the index of environmental filtering based on inter- and intraspecific variability [$T_{IC/IR}$], and the index of niche overlap based on interand intraspecific variability reflecting species interactions [$T_{IP/IC}$], where “T” stands for traits. The two first indices allowed us to test whether local abiotic heterogeneity affect trait spatial organization. Support for it would arise if the trait variance of species belonging to a given community (plot) differed from the total trait variance over all species in the regional pool (Violle et al. 2012). The regional pool referred to the total sampling area, comprising 72 plots. The index of niche overlap allowed us to test whether interactions affected trait spatial organization. Differences between the trait variance between a given species and the total variance over all species in the same community is interpreted as support for species interactions (Violle et al. 2012). Violle et al. also attributed low niche overlap at local scales to microenvironmental heterogeneity, and then advocated that results must be carefully interpreted for each case. We believe that micro-heterogeneity might not affect woody species at the scale of 25 m^2, although it could affect other functional groups such as herbaceous or cactus even at small scales of 1 m^2 (Conti et al. 2017).

In order to evaluate whether the studied processes changed between spatial scales, and to check for potential nesting effects, we computed the indices considering each plot as a different community, and then recalculated them considering each transect as a different community. We were able to compute all the three Violle et al.’s indices for traits with information at the individual level such as stem diameter and length, and basal area. Missing values of these traits (diameter - 10% of the total, basal area - 10%, and length - 17%) were replaced by the mean values of species; otherwise, indices could not be computed using the ‘Tstats’ function of Cati package (Taudiere & Violle 2012) in R 3.1.2 (R Core Team 2017). For the other traits, however, we were only able to compute the environmental filtering index based on species means ($T_{PC/PR}$), and we had to assign a single value of the mean trait wherever a species occurred.

The choice of the null model is determined with respect to the mechanisms considered (Götzenberger et al. 2016). The observed values of each of the indices were compared with the ones generated under specific null models. Randomization procedures depended on the type of index (Taudiere & Violle 2016). Null models were created by: (1) assigning the species-mean value for each individual before randomizing them within the regional pool without replacement, and keeping the number of individuals in each community constant (specifically for $T_{PC/PR}$); or (2) randomizing individual trait values within the regional pool without replacement, and keeping the number of individuals in each community constant ($T_{IC/IR}$); or (3) randomizing individual trait values within communities ($T_{IP/IC}$). Null and observed values of indices were calculated using the 'Tstats' function of the Cati package (Taudiere & Violle 2016). The standardized effect size (SES) quantified the magnitude of deviation of each community from the null model for traits with different units. SES = (observed value – mean of null values) / standard deviation of null values (Taudiere & Violle 2016). We analyzed their deviation from the null model, and whether or not values were < or > than zero.

Second, we adjusted linear regressions between species richness and the index of niche overlap reflecting species interactions ($T_{IP/IC}$; Violle et al. 2012) for plot and transect scales. Niche-based theory predicts a negative relationship between niche overlap and species richness, because the number of co-occurring species is constrained by how they share resources, with high similarity and thus high niche overlap leading to fewer species (Fig. 1). Conversely, neutral theory predicts non-significant flat relationships. The niche overlap index $T_{IP/IC}$ was normalized (0 - 1) to allow for comparisons among traits.

Finally, we adjusted linear regressions between environmental variables and Community-Weighted Mean Traits (CWM, Pillar & Duarte 2010). Mean traits were weighted by the relative species abundance in each plot to obtain CWM (Lavorel et al.

2008). All 19 CWM and 13 environmental variables were log-transformed before analysis. Due to the high number of comparisons (total of 247), we only adjusted regressions for the 22 pairs of variables with coefficients of correlation ≥ 0.40 (Tab. 1). The categorical abiotic variable that described plots as exposed or sheltered was used to distinguish plots in these relationships to increase the characterization of the abiotic conditions of plots. Kruskal-Wallis analyses were run to detect differences between wind-exposed versus sheltered habitats.

Results

Trait distribution

The index that reflects environmental filtering based on interspecific variability (Violle et al. 2012) did not deviate from the null expectation for any traits at either the plot scale or the transect scale of study (Fig. 3). The index of environmental filtering that considered intraspecific variability (Violle et al. 2012) did not modify the results provided by interspecific variability only (Fig. 3). This suggested that nesting effects of plots within transects were not relevant. These results also suggested that the trait variance of species belonging to a given community was not different from the total trait variance over all species in the regional pool. The index of niche overlap reflecting species interactions (Violle et al. 2012) did not deviate from null expectations at the community scale, which means that the trait variance of a given species was not different from the total variance over all species in the same community (Fig. 3).

Table 1. Coefficient of correlation between 19 community-weighted mean traits and 13 abiotic variables.

	Slope	Elevation	pH	Na	K	Ca+Mg	H+Al	P	N	Cation capacity	Soil Density	Organic Matter	Silt +Clay
Trait (unit)	º	M	none	cmol c	cmol c	cmol c	cmol c	mg.Kg^{-1}	g.dm^{-3}	none	Kg. dm^{-3}	g.Kg^{-1}	g.Kg^{-1}
Basal area (m^2)	0.40	0.25	-0.10	-0.43	0.09	0.04	0.30	0.11	-0.36	0.30	-0.41	0.16	-0.22
Stem diameter (mm)	0.12	0.08	-0.04	-0.34	0.17	-0.01	0.19	-0.09	-0.23	0.20	-0.33	0.09	0.05
Stem length (m)	0.59	0.31	-0.18	-0.32	-0.04	0.20	0.48	0.30	-0.39	0.49	-0.47	0.33	-0.38
Stem density (g.cm^{-3})	0.23	0.12	-0.14	0.06	0.00	0.12	0.18	0.01	-0.30	0.20	-0.26	0.31	-0.17
Stem moisture (%)	-0.02	-0.12	0.12	-0.16	-0.11	-0.10	-0.12	0.12	0.26	-0.15	0.21	-0.25	-0.02
Bark dry mass (%)	0.00	0.07	0.08	-0.13	-0.02	-0.10	0.17	0.21	0.06	0.13	0.03	-0.11	0.00
Vulnerability index (none)	-0.28	-0.03	-0.01	-0.07	0.16	-0.19	-0.05	-0.08	0.10	-0.08	0.09	-0.16	0.17
Vessel density (vessel.mm^{-2})	0.07	-0.01	-0.10	0.26	-0.15	0.01	-0.04	0.03	-0.01	-0.04	-0.01	0.08	-0.03
Vessel diameter (µm)	0.10	0.00	0.03	-0.23	-0.05	-0.12	0.17	0.21	0.05	0.13	0.02	-0.14	-0.09
Specific leaf area (cm^2.g^{-1})	0.50	0.23	-0.05	-0.40	-0.04	0.23	0.52	0.34	-0.14	0.53	-0.10	0.13	-0.42
Leaf area (cm^2)	0.49	0.29	0.03	-0.46	-0.05	0.20	0.56	0.47	-0.23	0.55	-0.24	0.14	-0.36
Leaf dry mass (mg.g^{-1})	-0.42	0.24	-0.08	0.37	0.23	-0.13	-0.10	-0.22	-0.05	-0.11	-0.05	0.11	0.27
Sucrose (mg.g DM^{-1})	0.21	0.33	0.12	-0.24	-0.02	0.12	0.39	0.26	-0.11	0.37	-0.10	0.13	-0.15
Starch (mg.g DM^{-1})	0.24	-0.09	0.09	-0.11	-0.33	0.12	0.06	0.31	0.07	0.05	0.13	-0.02	-0.26
Protein (mg.g DM^{-1})	0.02	-0.08	-0.01	-0.05	0.11	-0.10	-0.08	0.10	0.16	-0.10	0.26	-0.02	-0.26
Mesophyll (µm)	-0.33	-0.51	0.08	0.16	0.00	-0.16	-0.52	-0.31	0.17	-0.50	0.14	-0.19	0.29
Mesophyll/Thickness (%)	-0.29	-0.14	0.04	0.22	0.18	-0.07	-0.30	-0.41	0.00	-0.27	-0.02	0.02	0.31
Palisade/Spongy (%)	0.14	0.23	-0.11	0.05	-0.01	0.05	0.20	0.01	-0.04	0.20	-0.16	0.11	0.02
Cuticle layer (µm)	0.13	0.04	0.13	-0.15	-0.05	0.11	0.15	0.20	0.14	0.14	0.18	-0.07	-0.20

Notes: Significant correlations ($P \leq 0.05$) are shown in boldface. Correlations ≥ 0.40 are shown in grey.

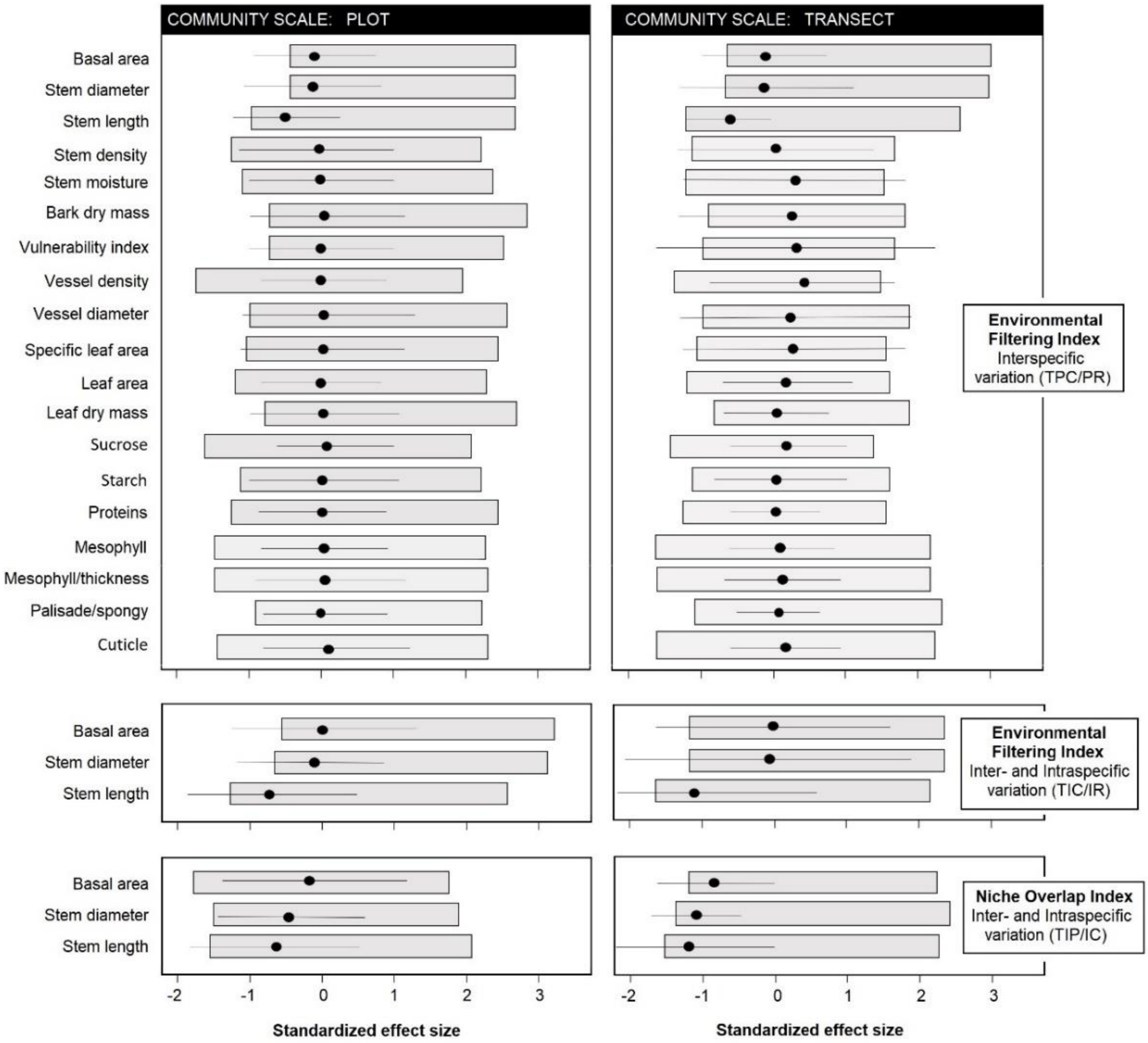

Figure 3. Standardized effect size of Violle et al.' indices for 19 traits at the plot and transect scale. Boxes indicate the confidence interval of the null model, and dots and segments represent, respectively, the mean and the standard deviation of standardized effect size values for a given index.

Richness and niche overlap

We found only non-significant flat relationships ($P > 0.05$) between species richness and the index of niche overlap related to basal area, stem diameter, and stem length (Fig. 4). This suggested that species interactions did not influence the number of species in plots or transects.

Traits and environmental gradients

Community-weighted mean basal area, mesophyll thickness, specific leaf area, leaf area, and stem length were significantly related to environmental gradients. We found that basal area decreased in soils with high concentration of sodium (Fig. 5A). The increase in elevation and cation exchange capacity in the soil were associated with decreases in mesophyll thickness of leaves (Fig. 5B-C). The increase in dune steepness and cation exchange capacity increased specific leaf area (Fig. 5D-E), leaf area (Fig. 5F-G), and stem length (Fig. 5H-I). Results for soil aluminum concentration were very similar to cation exchange capacity (not shown). Sheltered and exposed habitats did not differ in mean trait values.

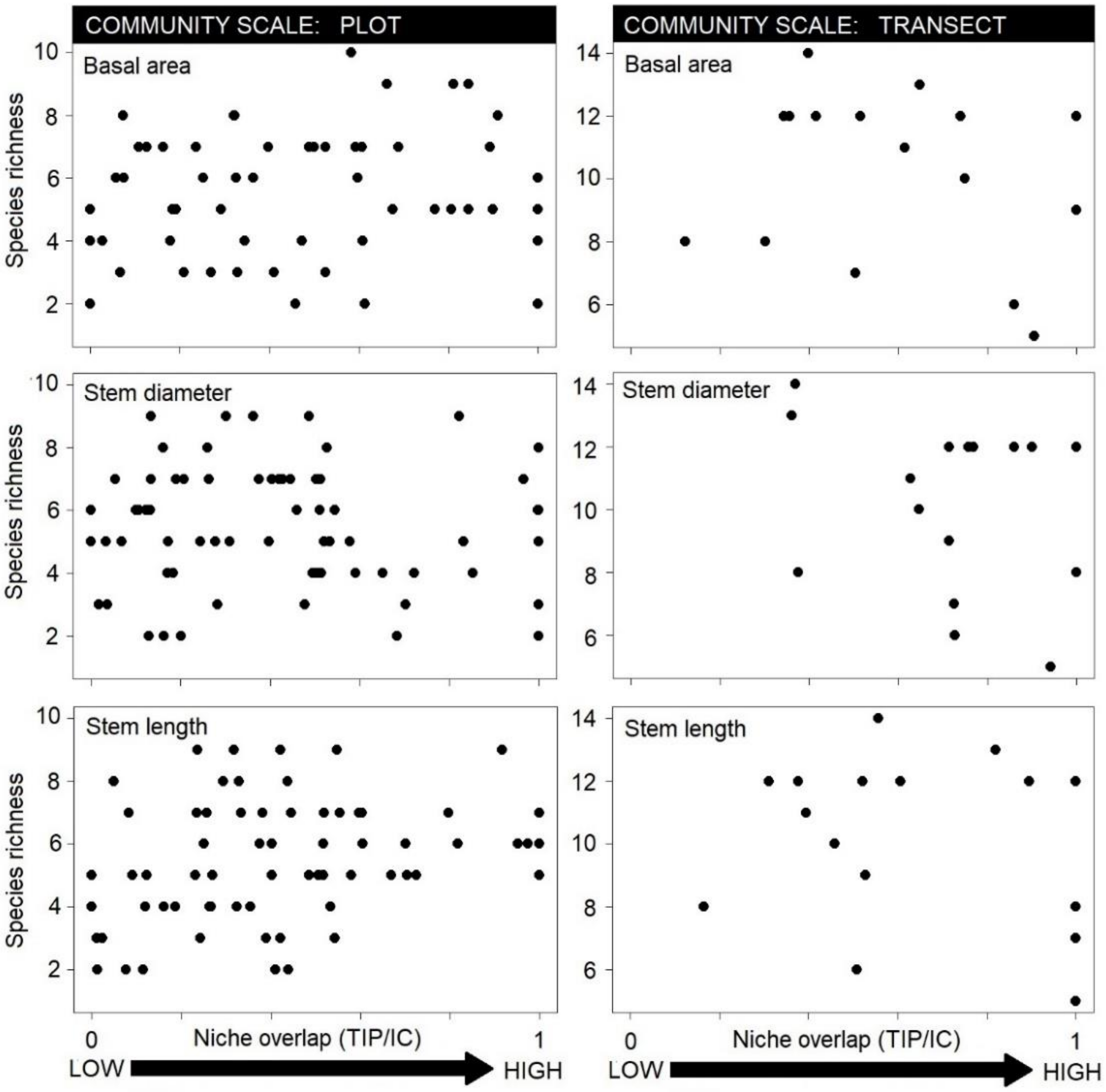

Figure 4. Relationship between species richness and the index of niche overlap for communities with spatial scales of plots and transects.

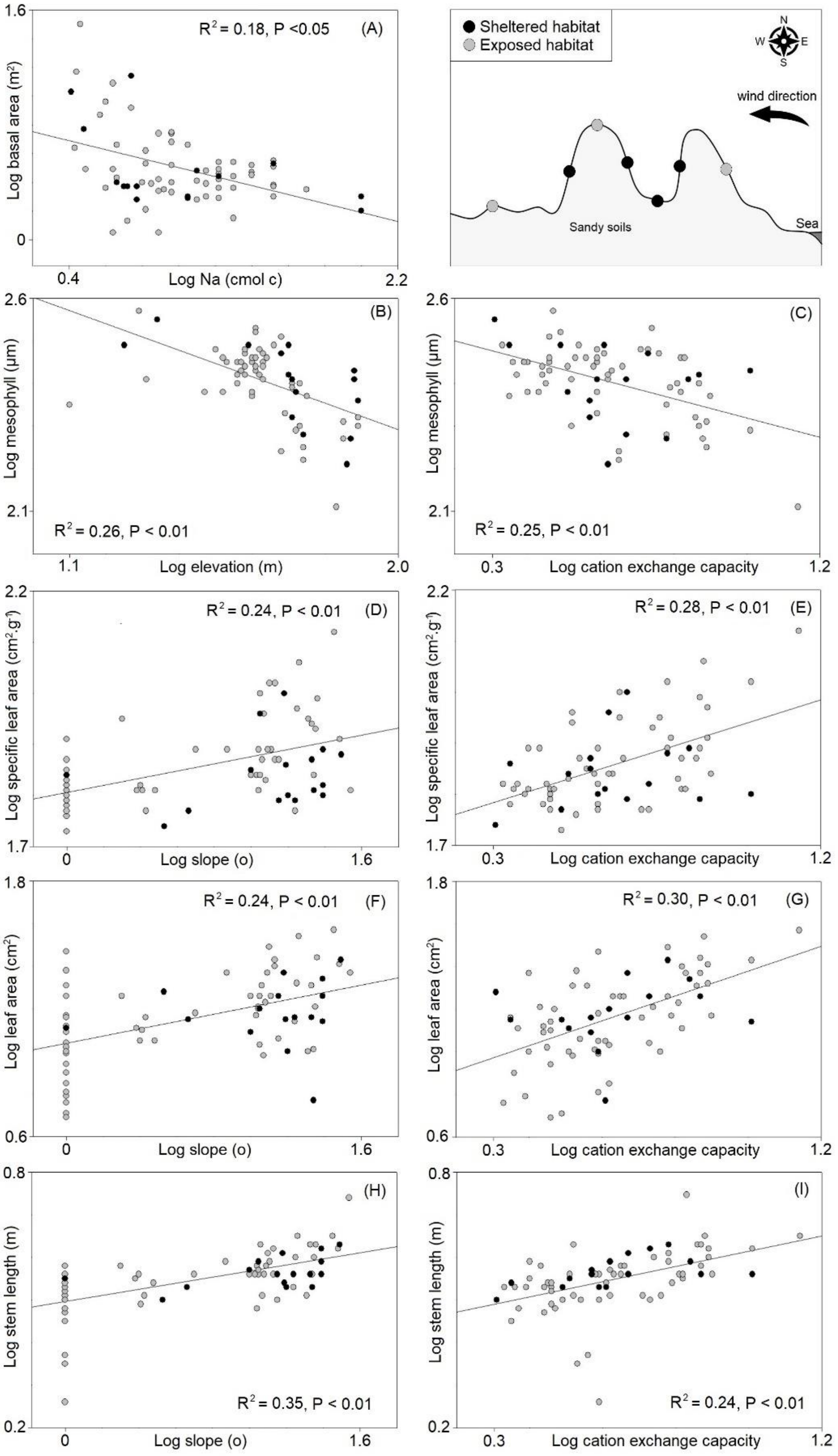

Figure 5. Relationship between community-weighted mean traits and environmental gradients at sheltered and wind-exposed habitats of 25m².

Discussion

We asked whether Restinga plant communities established on stressful habitats in Northeastern South America could be influenced by weak neutral effects on functional trait distribution using three complementary approaches. We did not find evidence for effects of species interactions or environmental filtering based on the distribution of traits at the spatial scales of study. Additionally, it should be noted that the few community trait-environment relationships we found were overall modest and with much unexplained variation. The combination of these results would corroborate the previous interpretation of the prevalence of neutrality in the study coastal area (Silva et al. 2015). However, environmental variation did affect mean trait shifts among localities, confirming support for the weak neutral hypothesis (Fig. 1). The plant community would follow a weak neutral pattern if abiotic gradients and/or species interactions imposed sorting on functional traits and species performance, but not on species occurrence, since occurrence tends to be largely offset by autocorrelated environmental factors, drift, and dispersal limitation (Zobel 2001; Tilman 2004; Gravel et al. 2006; Holt 2006; Pinto & MacDougall 2010; Beckage et al. 2012).

A study on perennial herbaceous communities in Mediterranean rangeland shows that the explicit consideration of environmental gradients in community analysis can reveal functional patterns that would remain undetected when just trait distribution alone was analyzed (Bernard-Verdier et al. 2012). Our results agree with those of Bernard-Verdier et al. (2012) since traits themselves were randomly distributed among the study plots and transects. Models that included individual variability performed similarly to models that used mean traits. Overall, this means that species belonging to a given plot or transect did not share more similar trait values than species drawn randomly from the regional pool, and that the environmental variation between local communities does not filter particular trait values (Violle et al. 2012; Taudiere & Violle 2016). However, the overall outcome of co-occurring species at the community level responded to abiotic changes faced by the community as shown by the relationships that explicitly considered the abiotic gradients.

Community trait responses to environmental gradients were not driven by species turnover since β-diversity has been shown to be very low in the study area (Silva et al. 2015). In fact, all localities can experience harsh conditions, and environmental variation from one locale to another does not filter different sets of species within the region. Several studies have shown reduced levels of both α- and β-diversity among localities that experience harsh environmental conditions (Chase 2010). If trait-environmental relationships do not result from the turnover of species, then it must result from phenotypical plasticity of individuals (Lepš et al. 2011). We hypothesize that, in South American Restinga heath vegetation, environmental conditions only filter species at the biogeographical scale. This would result from a selection of species from the species pool of neighboring ecosystems like the Cerrado savannahs, the Atlantic and Amazon forests, and the Caatinga dry woodlands. Colonizing species at this scale should be selected based on adaptations to withstand water and nutrient restrictions. After the colonization of coastal sandplains, however, species positions along local environmental filters seem to be offset by the role of local neutral processes (de Oliveira et al. 2014; Silva et al. 2015). Our results agree with others showing that functional traits are sorted by environmental filters at biogeographical and local spatial scales independently from species sorting (Cornwell & Ackerly 2009; de Oliveira et al. 2014; Souza et al. 2016).

The plastic responses of size (basal area), specific leaf area, leaf size, mesophyll thickness, and stem length relative to other traits probably enabled species to occur in a wide range of microhabitats (Miner et al. 2005; Jung et al. 2010). Two well-described types of stress in coastal areas are salinity and wind disturbance (Marques et al. 2015). The salinification of soils and water in the soil can constrain the development of roots, and consequently reduce the access of plants to resources, as well as the development of above-ground biomass, which in our case was expressed in terms of basal area of individuals (Parida & Das 2005). Topography in its turn creates micro-habitats in the windward and leeward slopes with high and low wind disturbance, respectively (Moeslund et al. 2013). Several lines of evidences show that the development of high stem biomass is confined to sheltered habitats, such as steep leeward slopes, otherwise individuals become short regardless of soil fertility and the leaf traits displayed by them (Coutand et al. 2008). In this case, the carbon gain by leaves is probably allocated towards other parts of the plant such as roots (Coutand et al. 2008). Leeward or windward slopes were not different from each other regarding the mean of response traits, which is probably due to restricted sample size on foredunes, and surely deserves to be addressed in further studies. In the case of stem length, the difference between slope faces was not apparent, probably because stem length does not necessarily express vertical plant growth. In fact, plants on windward dune slopes may display long but prostate stems (Marques et al. 2015; Silva et al. 2016). The variation in basal area and stem length are famous for creating complex physiognomic structure in South America coastal plains from sparse to closed shrub lands, as well as from low to tall Restinga forests, which alternate in relatively short distances (Marques et al. 2015; Silva et al. 2016). Our study indicates that this physiognomic variation is much more a result of phenotypic plasticity than species turnover due to fine-scale adaptations to different points along environmental gradients.

The combination of low salinity, high elevation, high steepness, and high capacity to store micronutrients creates microhabitats for phenotypes with more acquisitive traits, whereas phenotypes with more conservative traits tend to occur in stressed microhabitats with opposite conditions. The increase in soil capacity to store micronutrients is known to be associated with more productive individuals with thinner and more photosynthetically active leaves (Jager et al. 2015). This result agrees with studies in inland tropical forests (Asefa et al. 2017) and coastal tropical forests (de Oliveira et al. 2014), which report similar effects of resource-rich versus resource-poor habitats on the organization of local communities.

As species in harsh environments tend to interfere intensely in the establishment of others either by competition or facilitation (Castanho et al. 2015; Conti et al. 2017), we expected that interactions would affect niche overlap and determine the local species richness of communities. However, trait variance of a given species was not different from the total variance over all species in the same community, and the number of co-occurring species was not constrained by how species share resources (Violle et al. 2012). At least the first result is consistent with the point made by Ricklefs (2008) that species interactions often occur over wide gradients rather than at local plot scales.

Understanding which processes are relevant to community organization in the Restinga ecosystem has practical implications since conservation planning, management plans, and restoration projects need accurate knowledge on species distribution, habitat dependencies, and functional responses to environmental variation. We conclude that analyses of species occurrence or phylogenetic relatedness may be insufficient for a full understanding of community processes, and should be complemented with analyses of functional traits to correctly reveal the processes underpinning community assembly. To ignore functional traits may lead to underestimations of niche-based processes (Souza et al. 2016). As highlighted by Souza et al. (2016), the analyzes of different aspects of the same community such as its phylogenetic structure, species, and trait distribution at different scales may reveal patterns that would not be evident from the analysis of each aspect separately. Moreover, it shows why more than one approach is commonly adopted by community ecologists to strength the support of a conclusion. We advocate that further studies explicitly investigate the role of phenotypical plasticity in the community process of harsh environments, as environmental filtering can influence the traits themselves, through phenotypic responses of all species and individuals in the community rather than particular sets of species or individuals.

References

Asefa, M., Cao, M., Zhang, G., Ci, X., Li, J., & Yang, J. 2017. Environmental filtering structures tree functional traits combination and lineages across space in tropical tree assemblages. *Scientific Reports* doi:10.1038/s41598-017-00166-z.

Beckage, B., Gross, L., Platt, W., Godsoe, W., & Simberloff, D. 2012. Individual variation and weak neutrality as determinants of forest diversity. *Frontiers of Biogeography* 3: 145–155.

Bell, G. 2001. Neutral macroecology. *Science* 293: 2413–2418.

Bernard-Verdier, M., Navas, M., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Functional Ecology* 22: 134–147.

Brunbjerg, A.K., Cavender-Bares, J., Eiserhardt, W.L., Ejrnæs, R., Aarssen, L.W., Buckley, H.L., Forey, E., Jansen, F., Kattge, J., (…) & Svenning, J.C. 2014. Multi-scale phylogenetic structure in coastal dune plant communities across the globe. *Journal of Plant Ecology* 7: 101–114.

Castanho, C.T., Oliveira, A.A., & Prado, P.I.K.L. 2015. Does extreme environmental severity promote plant facilitation? An experimental field test in a subtropical coastal dune. *Oecologia* 3: 855–866.

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

Chase, J.M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328: 1388–1391.

Conti, L., de Bello, F., Lepš, J., Acosta, A.T.R., & Carboni, M. 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. *Journal of Vegetation Science* 28: 762–773.

Cornwell, W.K., & Ackerly, D.D. 2009. Community Assembly and Shifts in Plant Trait Distributions across an Environmental Gradient in Coastal California. *Ecological Monographs* 79: 109–126.

Coutand, C., Dupraz, C., Jaouen, G., Ploquin, S., & Adam, B. 2008. Mechanical stimuli regulate the allocation of biomass in trees: Demonstration with young Prunus avium trees. *Annals of Botany* 101: 1421–1432.

Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. 2012. Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews* 87: 111–127.

Götzenberger, L., Botta-Dukát, Z., Lepš, J., Pärtel, M., Zobel, M. & de Bello, F. 2016. Which randomizations detect convergence and divergence in trait-based community assembly? A test of commonly used null models. *Journal of Vegetation Science* 27: 1275–1287.

Gravel, D., Canham, C.D., Beaudet, M., & Messier, C. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9: 399–409.

Guo, H., Chamberlain, S.A., Elhaik, E., Jalli, I., Lynes, A.R., Marczak, L., Sabath, N., Vargas, A., Więski, K., Zelig, E.M., & Pennings, S.C. 2015. Geographic variation in plant community structure of salt marshes: Species, functional and phylogenetic perspectives. *PLoS ONE* 10: 1–12.

Holt, R. 2006. Emergent neutrality. *Trends in Ecology and Evolution* 21: 531–533.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton, NJ, US.

Jager, M.M., Richardson, S.J., Bellingham, P.J., Clearwater, M.J., & Laughlin, D.C. 2015. Soil fertility induces coordinated responses of multiple independent functional traits. *Journal of Ecology* 103: 374–385.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98: 1134–1140.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., & Bonis, A. 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology* 22: 134–147.

de La Riva, E.G., Pérez-Ramos, I.M., Tosto, A., Navarro-Fernández, C.M., Olmo, M., Marañón, T., & Villar, R. 2016. Disentangling the relative importance of species occurrence, abundance and intraspecific variability in community assembly: A trait-based approach at the whole-plant level in Mediterranean forests. *Oikos* 125: 354–363.

Lepš, J., de Bello, F., Šmilauer, P., & Doležal, J. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* 34: 856–863.

Maestre, F.T., Valladares, F., & Reynolds, J.F. 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* 93: 748–757.

Maestre, F.T., Callaway, R.M., Valladares, F., & Lortie, C.J. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97: 199–205.

Márcia, C.M., Silva, S.M., & Liebsch, D. 2015. Coastal plain forests in southern and southeastern Brazil: ecological drivers, floristic patterns and conservation status. *Brazilian Journal of Botany* 38: 1–18.

Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K., & Relyea, R.A. 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* 20: 685–692.

Moeslund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., & Svenning, J.-C. 2013. Topography as a driver of local terrestrial vascular plant diversity patterns. *Nordic Journal of Botany* 31: 129–144.

Muehe, D., Lima, C.F., & Lins-de-Barros, F.M. 2006. Erosão e propagação do litoral Brasileiro. In *Ministério do Meio Ambiente*, Brasília, Brazil.

Munoz, F., & Huneman, P. 2016. From the neutral theory to a comprehensive and multiscale theory of ecological equivalence. *The Quarterly Review of Biology* 91: 321–342.

de Oliveira, A.A., Vicentini, A., Chave, J., Castanho, C.D.T., Davies, S.J., Martini, A. M.Z., Lima, R.A.F., Ribeiro, R.R., Iribar, A., & Souza, V.C. 2014. Habitat specialization and phylogenetic structure of tree species in a coastal Brazilian white-sand forest. *Journal of Plant Ecology* 7: 134–144.

Parida, A.K., & Das, AB. 2005. Salt tolerance and salinity effects on plants: a review. *Ecotoxicology and Environmental Safety* 3: 324–49.

Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S.S., Cornwell, W.K.K., Craine, J.M.M. (…) & Cornelissen, J.H.C. 2013. New Handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.

Pillar V.D., & Duarte, L.D.S. 2010. A framework for metacommunity analysis of phylogenetic structure. *Ecology Letters* 13: 587–96.

Pinto, S.M., & MacDougall, A.S. 2010. Dispersal Limitation and Environmental Structure Interact to Restrict the Occupation of Optimal Habitat. *The American Naturalist* 175: 675–686.

R Core Team. 2017. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, AT.

Ricklefs, R.E. 2008. Disintegration of the ecological community. *The American Naturalist* 172: 741–50.

Silva, J.L.A., Souza, A.F., Jardim, J.G., & Goto, B.T. 2015. Community assembly in harsh environments: the prevalence of ecological drift in the heath vegetation of South America. *Ecosphere* 6: 18.

Silva, A.C., Silva, J.L.A., & Souza, A.F. 2016. Determinants of variation in heath vegetation structure on coastal dune fields in northeastern South America. *Revista Brasileira de Botanica* 39: 605–612.

Silva, J.L.A., Souza, A.F., Caliman, A., Voigt, E.L., & Lichston, J.E. 2018. Weak whole-plant trait coordination in a seasonally dry South American stressful environment. *Ecology and Evolution* 8: 4–12.

Silva, K.J.P., & Souza, A.F. 2018. Common species distribution and environmental determinants in South American coastal plains. *Ecosphere* 00: e02224.10.1002/ecs2.2224

Souza, A.F., Bezerra, A.D., & Longhi, S.J. 2016. Quasi-neutral community assembly: Evidence from niche overlap, phylogenetic, and trait distribution analyses of a subtropical forest in South America. *Perspectives in Plant Ecology, Evolution and Systematics* 23: 1–10.

Taudiere, A., & Violle, C. 2016. Cati: an R package using functional traits to detect and quantify multi-level community assembly processes. *Ecography* 39: 699–708.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* 101: 10854–10861.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., & Messier, J. 2012. The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology and Evolution* 27: 244–252.

Zobel, K. 2001. On the species-pool hypothesis and on the quasi-neutral concept of plant community diversity. *Folia Geobotanica* 36: 3–8.

CAPÍTULO III

Quantifying effects of biodiversity and environmental aspects on components of primary productivity of a semideciduous heath vegetation

Foto: Morvan França (*in memoriam*)

Abstract

Biodiversity is a key driver of ecosystem functioning and often leads positive cause-effect relationships. Support, however, comes mostly from experimental studies conducted in low-diversity systems in the temperate region. To help filling this knowledge gap for South American tropical forests, we investigated a hypothetical model that connects biodiversity facets (functional and phylogenetic diversities, species richness, and vegetation structure) and environmental aspects (topography and soil resources) to the annual rate of litterfall production and the stand basal area across 41 25-m^2 permanent plots in a semideciduous vegetation, where niche mechanisms are not the main drivers of community organization. We addressed three other points to this debate by asking (1) if the temporal dynamic process of litterfall production can be regulated by spatial patterns of plant diversity and natural levels of environmental conditions, (2) if biodiversity effects will exist in a community that shows a weak niche-based organization, and (3) if the role of rare-species diversity can be compared to the role of common-species diversity. We found that species and traits diversities had only very weak influence on either the most dynamic and the most stable component of primary productivity (litterfall and wood biomass storage, respectively). The inclusion of high-yielding species (or traits) with the increase of species richness regulated biodiversity-Ecosystem relationships regardless of the degree of niche overlap and complementarity. Groups of rare versus common species had different influence on litterfall production, but not on basal area. We conclude that components of primary productivity of a semideciduous vegetation can respond mainly to abiotic environmental aspects and just secondarily to species richness and few CWM traits, but not to other facets of biodiversity.

Key-words: Primary productivity, effect traits, coastal area, stressful environment, *Restinga*.

Introduction

Several empirical studies and meta-analyses have shown that plant biodiversity has a positive effect on ecosystem processes such as primary productivity and decomposition, which places the biodiversity as a key driver of ecosystem functioning (Cardinale et al. 2006, 2013; Caliman et al. 2010; Hooper et al. 2005; Reich et al. 2014; Duffy, Godwin & Cardinale 2017). Most studies supporting this cause-effect relationship were conducted in short-term and small-scale experiments in the temperate region (Caliman et al. 2010; Clark et al. 2017). Although a growing body of research has helped to fill the knowledge gap on tropical ecosystems (Lohbeck et al. 2015; Pooter et al. 2015, 2017; Sakschewski et al. 2016; Sullivan et al. 2017; Jucker et al. 2018; van der Sande et al. 2018), the tropics are still much less unrepresented in the Biodiversity-Ecosystem Functioning (or BEF) research, despite their importance for local, regional and global biodiversity and biogeochemical cycles, and despite high species-loss rates faced by them (Lohbeck et al. 2015; Clark et al. 2017). Perhaps more critical is the lack of studies in seasonally dry forests, sites where processes that vary seasonally such as litterfall production may or not be regulated by biodiversity.

Litterfall production is one of the best predictors of the overall forest functioning when all main components of net primary productivity cannot be measured, especially if the increment of aboveground wood biomass is slow and demands some decades to be noticed such as in stressful environments; or if the wood increment is limited to short length-growth periods like in rainy seasons (Malhi, Doughty & Galbraith 2011). In these cases, litterfall is the main flux of biomass and nutrients from the vegetation to the soil and is important to other ecosystem processes such as decomposition and nutrient returns (Scherer-Lorenzen, Bonilla & Potvin 2007; Huang et al. 2017). In addition, as much of the primary production is not consumed by herbivores and, consequently, enters the debris pool (Cebrian 1999), then litterfall production is strongly correlated with primary productivity (Clark 2001). However, effects of biodiversity on litterfall production can be weaker than on stand basal area or wood biomass (Paquette & Messier 2011; Lohbeck et al. 2015), which partly reflect the strong dynamic nature of litterfall production that is more affected by regional climatic variations over time than by variations of plant diversity over space. Basal area, on the other hand, may be rather influenced by spatial differences of plant diversity across either short and large distances. Although basal area is not an ecosystem process *per se*, as it does not measure changes of basal area over time (a rate by definition), it was treated in this study as a proxy of wood biomass storage, because sites holding higher values of basal area has accumulated more wood biomass than sites with lower basal area in the same interval of vegetation development, even though their actual productivity rate are lower (Clark 2001).

A hot debate promoted by the BEF research revolves around two main, not mutually exclusive, mechanisms that underlie the positive BEF relationship – *Niche complementarity* and *Sampling effects* (Huston 1997; Loreau & Hector 2001). *Niche complementarity* refers to the alternative ways species explore the total available resources and conditions by partitioning niches, which may stabilize species coexistence and enhance ecosystem productivity (Loreau & Hector 2001; Cardinale, Palmer & Collins 2002). In its turn, *Sampling effects* refer to the inclusion of high-yielding or dominant species in the community composition just by chance with the increase of species richness (Huston 1997; Cardinale et al. 2013). These mechanisms can be more easily measured in experimental studies using metrics that compare species performance in mixtures versus monocultures (Loreau & Hector 2001; Isbell et al. 2018). However, it has been quite difficult to measure them by observational approaches (Clark et al. 2017).

Wojdak & Mittelbach (2007) proposed an approach to identify either *Niche complementarity* or *Sampling effects* is the major underlying mechanism behind the BEF relationship that can be used by observational studies. According to them, *Niche complementarity* is the prevailing mechanism if there is a positive relationship between species richness and the ecosystem process, in combination with a negative relationship between the degree of niche overlap among species and the same process. *Sampling effects* may shape the BEF relationship if niche overlap and the ecosystem process are not related despite species richness effects (Wojdak & Mittelbach 2007). Complementarily, Community Weighted Mean (CWM) traits of species can help to test for *Sampling effects*, as a given site or community can be heavily influenced by dominant functional traits that promote high-yielding species or have any other disproportional effects on them (Hooper et al. 2005; Finegan et al. 2015; Lohbeck et al. 2015). CWM traits also fit in the Grime's (1998) mass-ratio theory that predicts that ecosystem processes are driven by characteristics of the most dominant species in the community. Despite a clear connection between BEF and community research fields, most of the BEF studies were conducted without a prior understanding of underlying processes that govern species distribution in their natural ecosystems. To help filling the two above-mentioned knowledge gaps for South American tropical forests (firstly, the region unrepresentativeness, and secondly, the lack of studies in which community processes are well known), we investigated a hypothetical model (Fig. 1) that connects biodiversity facets (functional and phylogenetic diversities, species richness, and vegetation structure) and environmental aspects (topography and soil resources) to the annual rate of leaf litterfall production and the stand basal area across permanent plots in one semideciduous *Restinga* vegetation.

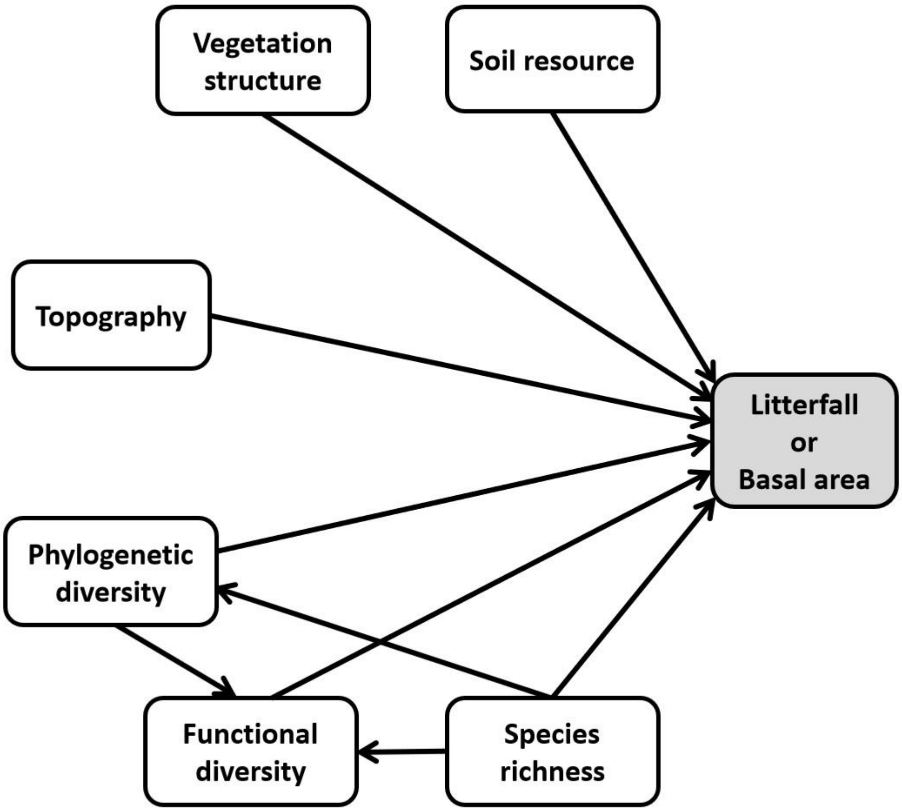

Figure 1. Theoretical model illustrating causal links between facets of biodiversity, environment aspects, vegetation structure, litterfall production and stand basal area.

Restinga refers to the coastal heath vegetation that grows on sandy plains produced by marine transgressions and regressions in the late Quaternary (Scarano 2002; Marques, Swaine & Liebsch 2011). In South America, Southeast Asia and parts of Africa, heath vegetations develop as edaphic climax communities, because their growth is more limited by well-drained and nutrient-poor sandy soils than climatic conditions (Miyamoto et al. 2003; Brunbjerg, Ejrnæs & Svenning 2012; van Wilgen 2013; Silva & Souza 2018). The study *Restinga* vegetation, located in the Northeastern Brazil, does not show clusters of phylogenetically-related species across local sites (plots of 25 m^2), or neither gradients of species occurrence that respond to local environmental heterogeneity, which means that species have high niche overlap over space and respond more to neutral dynamics than to niche-based mechanisms for the community organization (Silva et al. 2015). We expected that if species' niches overlap significantly and the community is not governed by niche-based mechanisms, then litterfall production and stand basal area may respond only to variations in species richness and few key CWM traits, but not to functional and phylogenetic diversities (*Sampling Effect* hypothesis, hereafter). In other words, we asked for two alternative hypotheses as follow: (1) significant effect of biodiversity will not occur or will be very weak on litterfall production due to its effect be masked by temporal controls (e.g. temperature and precipitation) despite its potential effects on basal area; and (2) if any effects of biodiversity on litterfall production and basal area exist, these will not be determined by *Niche complementarity*.

In addition to the underlying mechanisms driving the possible effects of biodiversity on the ecosystem productivity, we were also interested in evaluating the role of common- versus rare-species diversities. In the literature, the contribution of biodiversity to ecosystem processes is very limited to species that have large impacts on ecosystem processes, because of their higher relative abundance and biomass (Hooper et al. 2005; Jain et al. 2014). Common species may have a key impact on the processes (Smith & Knapp 2003), but in many cases it can be equivalent to the contribution of rare species when those are considered in aggregation (Lyons et al. 2005). For example, few rare species had dominant effects on the resistance to invasions of exotic species (Lyons & Schwartz 2001). It brings into question if the maintenance of an entire suite of species is necessary to maintain ecosystem processes (Lyons et al. 2005; Jain et al. 2014). Thus, we also asked if the combined contribution of many rare species could be equivalent to the combined contribution of few common species.

Material and Methods

Study area and data collection

This study benefited from a previous one that established 85 25-m² plots along 17 100-m transects in the Barreira do Inferno Launch Center, Rio Grande do Norte state, Northeastern Brazil (Silva et al. 2015). It is a 1,900-ha coastal area containing tall dunes near the sea (ca. 80 m a.s.l.), and relatively flat areas (ca. 40 m a.s.l.) punctuated by short palaeodunes further inland. The climate is tropical with a severe dry season (6 - 9 months), with mean annual temperature of 26 ºC, and mean annual precipitation of 1,464 mm. Each plot was characterized by elevation, dune steepness, and eleven other edaphic attributes (pH, Na, K, P, total N, Ca + Mg, H + Al, cation exchange capacity, organic matter, soil density, and the sum of silt and clay content).

All individuals in each plot with a stem diameter at soil level ≥ 3 cm were identified by species, counted and had the stem diameter and the main stem length measured to characterize the vegetation structure (Silva et a. 2015; Silva, Silva & Souza 2016). In addition, canopy cover was estimated through three nonoverlapping wide-angle digital photographs in each plot, taken by using a 16-mm lens and a digital camera during uniformly overcast sky conditions. For the 33 most abundant species in the area, Silva et al. (2018) provided species-specific mean values of leaf dry mass content, leaf area, specific leaf area, starch content, soluble sugars, total soluble proteins, mesophyll thickness, cuticle thickness, the ratio of palisade to spongy parenchyma thickness, the ratio of mesophyll to leaf thickness, stem density, stem moisture, bark dry mass, xylem vessel diameter, xylem vessel density, and the index of vulnerability to xylem cavitation. Leaves and stems were collected following standardized protocols (Pérez-Harguindeguy et al. 2013) in the same individuals, whenever possible, as described by Silva et al. (2018).

Here we conducted a 1-year (2015 - 2016) field study to collect litterfall production of species as part of a long-term plant phenology project that takes place in 41 plots with the tallest vegetations (3 – 7 m on average). Six 0.12-m² traps were established in each plot (total of 246). Leaf litterfall was collected once a month, then oven dried at 70 ºC for 72 hours, and finally sorted by species. Leachate mass loss is known to reduce litterfall mass inside traps if sampling intervals exceeds two weeks, although this effect is more relevant in humid forests than in semideciduous forests (Clark 2001; Taylor et al. 2017). We took it into account by installing litterbags with three grams of leaf debris inside several traps, and then measure species-specific decomposition rates in the dry and rainy seasons. After one month, the litterbags were removed, and oven dried at 70 ºC for 72 hours. Decomposition rate was estimated by the decay constant, and the values were used to correct mass losses. This estimative considered either the decomposition rate and the time in which debris stayed in traps. This time was unknown and assumed to be half of the period used to calculate monthly production. For six species, we only had the decay constant of the dry season. Then, we estimated missing values by multiplying the decay constant of the dry season (known value) by a value estimated from the regression between decay rates of all species in the dry and rainy seasons. It showed a very good fit ($R^2 = 0.75$) and was accepted for account decomposition rates in the rainy season.

Data analysis

To evaluate the extent the plant biodiversity and environmental variability influenced basal area and litterfall production (Question 1, Fig. 1), we first calculated species richness and some phylogenetic and functional α-diversity metrics (i.e. diversity within plots) for each plot. It is worth noting that richness and other metrics were not based on the total number of species inside plots, but only on focal species that met the following criteria: (1) species must have had trait information (available for 33 species, Silva et al. 2018), which was necessary to calculate functional diversities; (2) species must have had at least five individuals; and (3) they could not have had a very low litterfall production. These criteria were considered to avoid errors regarding sampling collection of litterfall. Therefore, the number of focal species was expected to be lower than the total richness, which is around 55 species across plots (Silva et al. 2015).

Among commonly used phylogenetic metrics, we considered the phylogenetic diversity (PD, Faith 1992), phylogenetic species richness (PSR), phylogenetic species evenness (PSE), and phylogenetic species variability (PSV), and adopted the metric less correlated with species richness (Qian & Jin 2016; Tucker et al. 2016). The phylogenetic tree used to calculate the evolutionary links among species was created by the S.PhyloMaker function of Phytools package with the PhytoPhylo megatree (see details in Qian & Jin 2016) in the R 3.1.2 (R Core Team 2017). All phylogenetic metrics were calculated using the pd function of the Picante package (Kembel et al. 2010) without including the root node. By pruning the root node, the metric values corresponded to α-diversity values (Cadotte, Cardinale, & Oakley 2008).

To represent functional diversity in the plots, we chose between functional dispersion (FDis, Laliberté & Legendre 2010) and functional diversity (FD, Petchey & Gaston 2002) the metric less correlated with species richness (Cadotte, Carscadden & Mirotchnick 2011; Paquette & Messier 2011). The calculation of FD works similarly to PD as it converts the trait matrix into a distance matrix, and then produces a dendrogram to calculate the total branch length (Petchey & Gaston 2002). In its turn, FDdis computes the average distance of species in a PCoA space relative to the centroid for a set of communities (Laliberté & Legendre 2010). FD was created using the pd function without including the root node, whereas FDips was calculated with the fdisp function of FD package (Laliberté & Legendre 2010). To compute FDips and FD, we only considered functional traits that showed significant relationships between species-specific mean traits or CWM traits and response variables (see selected traits in the Results section). As basal area and litterfall production may be related to distinct set of traits, we calculated twice each functional metric based on traits correlated to them. Species-specific mean traits were standardized prior computation of metrics (Cadotte, Cardinale & Oakley 2008; Cadotte, Carscadden & Mirotchnick 2011).

Topography, soil resources and vegetation structure were represented by the variables mostly correlated with litterfall production and basal area. All variables were log-transformed to achieve parametric assumptions. We used the selected variables as described above in two alternative path models in the Amos 22.0 program (SPSS 2013), by using maximum likelihood estimation procedures (Grace 2006). We tested each component of productivity in separate models, instead of all together, because our sampling size was limited to 41 plots. The standard error estimates of the models were obtained through standard maximum likelihood bootstrapping techniques by using 5000 bootstrap iterations. We assess the model fit using the following measurements: (1) Qui square divided by degrees of freedom (χ^2/DF, target value < 3), Root Mean Square Error of Approximation (RMSEA, target value <0.10), Comparative Fit Index (CFI, target value > 0.90), and AIC values (Grace 2006). Pathways were regarded whenever $P \leq 0.05$. An advantage of using Amos program was the possibility of adding new paths with an index of modification (SPSS 2013).

To assess the influence of *Niche complementarity* and *Sampling effects*, we compared the significance of functional and phylogenetic diversities, and species richness in the path model (Fig. 1), based on the interpretation proposed by Wojdak & Mittelbach (2007). Functional and phylogenetic diversities were taken as a proxy of niche overlap, as local communities with higher diversities may show a higher number of ecological strategies and species with niches that overlap little than local communities with lower functional and phylogenetic diversities. In addition, we analyzed CWM traits' effects on litterfall and basal area using Pearson correlations.

Finally, to evaluate if the combined contribution of many rare species is equivalent to the combined contribution of few common species (Question 2), first we classified species by dominance through the relationship between frequency of occurrence and relative abundance of species. Then, we discounted the combined contribution of groups of common versus rare species to the overall litterfall production and basal area of plots, separately, and compared relative contributions with Wilcoxon or t-test.

Results

The study semideciduous forest had a peak of litterfall production in the dry season (Fig. 2). Litterfall was obtained from 22 focal species (Fig. 3a), but the amount of litterfall found in the traps was higher than the produced by these 22 species, because it included inputs from the surroundings as well as from non-focal species rooted inside plots. It was not a problem to represent species composition of plots as the "used" species number was highly correlated with the "real" species number ($r = 0.86$, $P < 0.01$), as well as most of the non-focal species had less than 5 individuals and, therefore, low influence on this process.

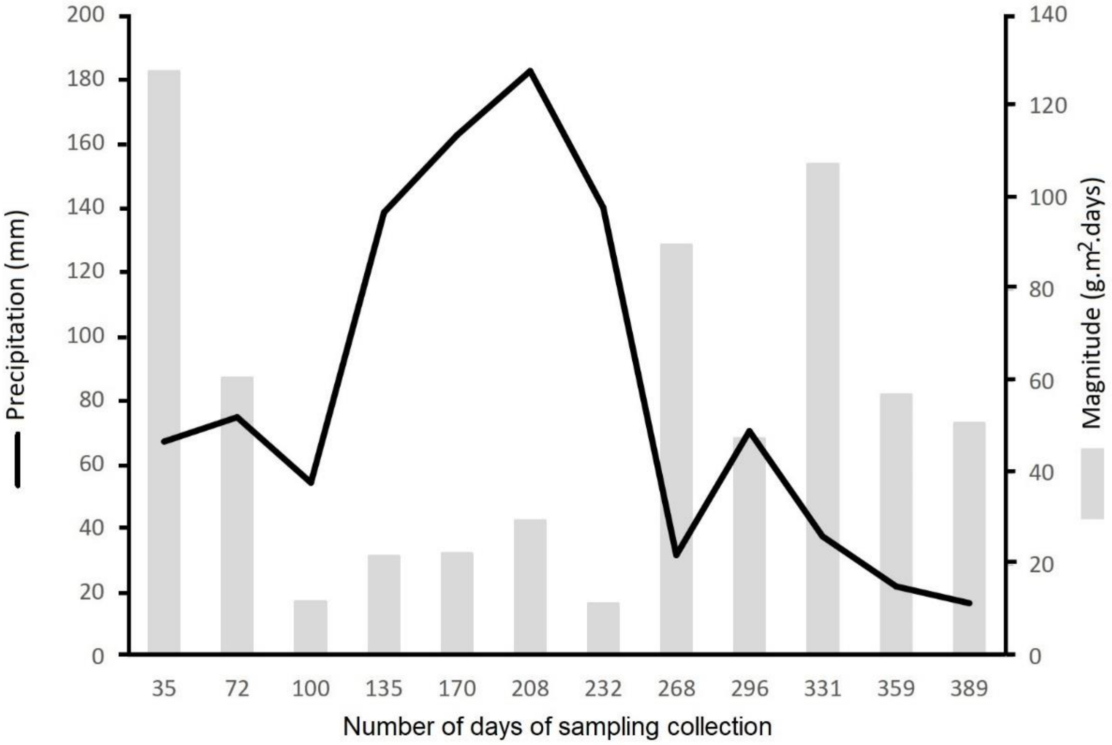

Figure 2. Ecosystem productivity (g.m^2.days) and precipitation (mm) from December 2015 to November 2016. Since collecting periods had unequal numbers of days, monthly magnitude of litterfall production was normalized using ±30 days for analyses.

Functional metrics were computed by using stem density and leaf starch content when comparing them to litterfall production. Species with higher production had higher stem density (Fig. 3b), and lower leaf starch content (Fig. 3c). Despite these relationships, CWM stem density and starch content were not correlated with litterfall production (both R coefficients < 0.10). In fact, there were no correlations between litterfall and any other CWM trait. When comparing functional metrics to basal area, we used specific leaf area, starch content, stem diameter, and xylem vessel density. Species with higher basal area had either lower specific leaf area (Fig. 3d) and starch content (Fig. 3e). In addition, basal area increased with CWM stem diameter ($R = 0.47$, $P < 0.01$), and decreased with CWM xylem vessel density ($R = -0.36$, $P = 0.02$).

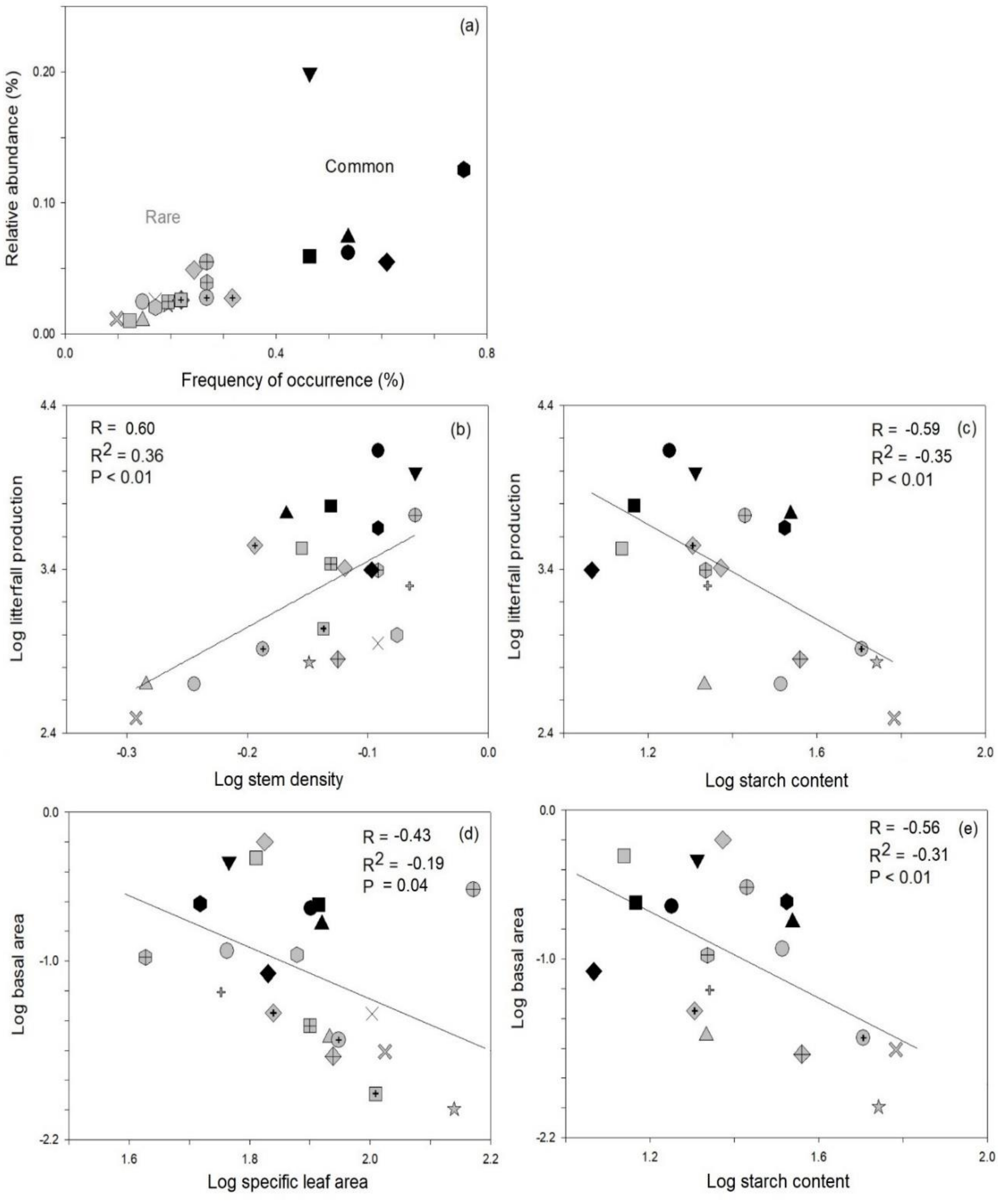

Figure 3. Classification of rare and common species (a), and their position in the relationships between stem density and litterfall production (b), starch content and litterfall (c), specific leaf area and basal area (d), and starch content and basal (e).

Functional dispersion (FDis) and Phylogenetic species evenness (PSE) were the metrics less correlated with species richness (PSE: R < 0.20; FDis: R < 0.65), and then adopted in the path model. Nitrogen, elevation and canopy cover were used due to the best correlations with litterfall production (0.28, 0.28, and 0.36, respectively) and basal area (0.47, 0.25, and 0.28, respectively) among all variables. The increase in species richness and canopy cover led to similar increases in litterfall production (Fig. 4a). Species richness influenced other facets of biodiversity, such as functional and phylogenetic diversities, but neither of them affected litterfall production, directly nor indirectly. CWM traits were not correlated to litterfall. Elevation had indirect effects on litterfall (0.19) via canopy cover. In addition, elevation and nitrogen affected, respectively, phylogenetic evenness and functional dispersion, but they did not have direct influences on litterfall. These predictors accounted for 30% of the total explained variance (Fig. 4a and Tab. 1). Conversely, environmental variation had stronger influence on basal area than facets of biodiversity (Fig. 4b), with direct effects of nitrogen as well as direct and indirect effects (0.08) of elevation. Basal area was directly influenced by species richness, and just indirectly by canopy cover via nitrogen (0.16). Functional dispersion was the only variable to not have casual relationships with the others. Basal area was also correlated with CWM stem diameter (R = 0.47, P < 0.01) and CWM vessel density (R = -0.36, P = 0.02). The model of basal area had better goodness-of-fit statistics than the model of litterfall, accounting for 45% of total explained variance.

Six common species occurred from 46% to 76% of the plots and accounted for 57% of the total number of individuals (Fig. 3a). This group of common species contributed with 59% of the overall litterfall production, and 41% of the overall basal area. At the plot level, their relative contribution for litterfall was of 61% on average (± 0.25 SD), and for basal area of 52% on average (± 0.31 SD). On the other hand, sixteen rare species occurred in only 10% to 32% of the plots. The combined contribution of rare-species diversity to the plot-level production was significantly lower than the combined contribution of common-species diversity, but there was no difference between these two species groups to local basal area (Fig. 5).

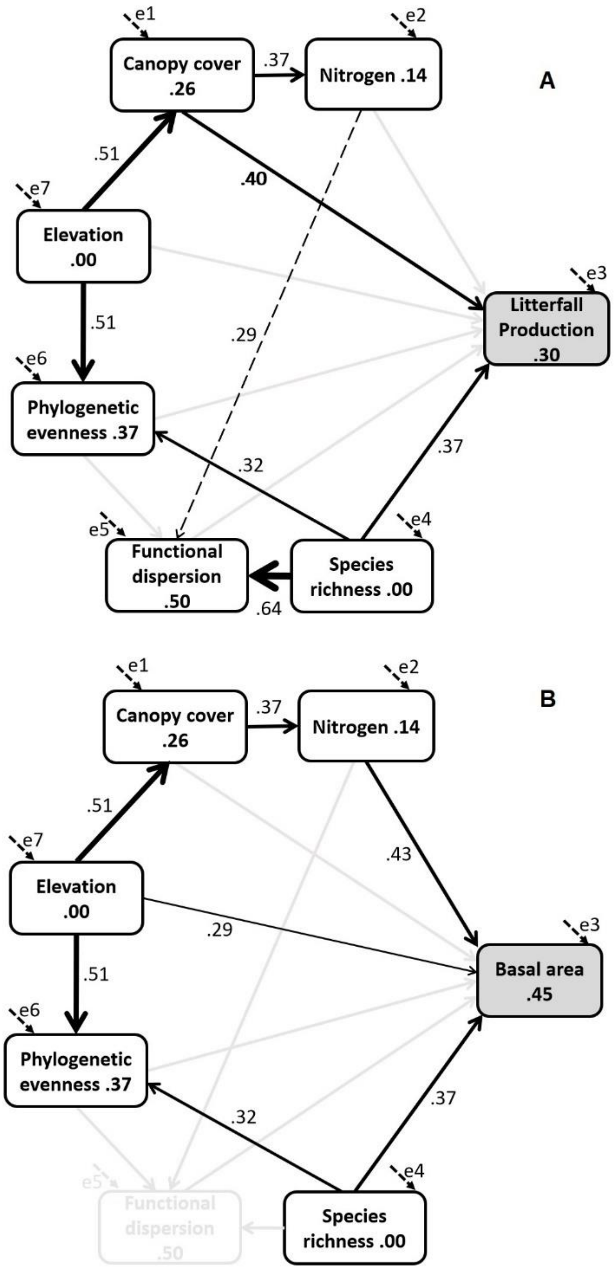

Figure 4. Final models of litterfall production (a) and basal area (b) summarizing standardized coefficients of significant causal paths (numbers beside arrows), and the individual and total explained variances (numbers inside white and grey boxes,

respectively). The width of arrows is proportional to the strength of the causal relationship. Dashed-lines represent negative coefficients. Light-grey boxes and paths represent predictors that were initially tested, but further removed as they had non-significant effects.

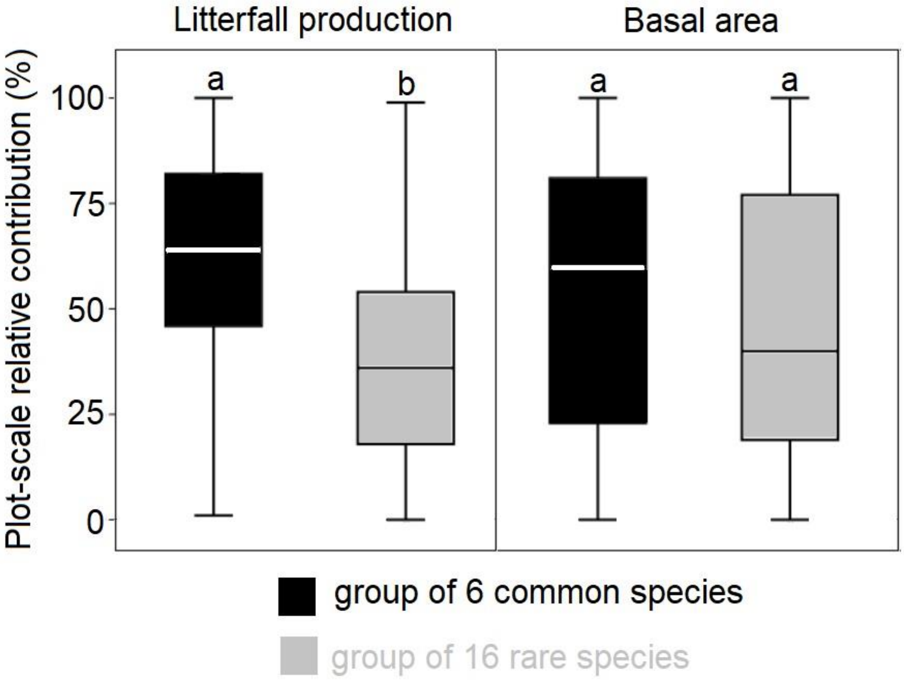

Figure 5. Combined contributions of groups of common versus rare species relative to the overall litterfall production and basal area at the plot scale.

Discussion

Recent studies have brought into question if positive effects of biodiversity on ecosystem processes detected in the temperate region can be extrapolated to diverse tropical forests (Caliman et al. 2010; Lohbeck et al. 2015; Clark et al. 2017; Duffy, Godwin & Cardinale 2017). We addressed three other points to this debate by asking (1) if the temporal dynamic process of litterfall production in a semideciduous tropical forest can be regulated by spatial patterns of plant diversity and natural levels of environmental conditions, (2) if biodiversity effects will exist in a community that shows a weak niche-based organization, and (3) if the role of rare-species diversity can be compared to the role of common-species diversity. Contrarily to our Hypothesis 1, the variety and diversity of species and traits had only very weak influence on both the most dynamic component (litterfall production) and the most stable component (basal area or wood biomass storage) of the ecosystem productivity. In addition, BEF relationships were not mediated by *Niche complementarity* (Hypothesis 2). In fact, environmental conditions were better predictors than biodiversity facets to at least wood biomass storage. Group of rare species had less influence on litterfall production than group of common species, whereas there was no difference between groups when comparing basal area. These findings are in line with others that suggest that facets of biodiversity related to quality and variety are of limited importance for certain components of productivity relative to those related to vegetation quantity, or even to environmental aspects (Finegan et al. 2015; Lohbeck et al. 2015; van der Sande et al. 2018).

Basal area was more influenced by environmental conditions than by facets of biodiversity. The study area is composed by a mature *Restinga* vegetation that grows on sandy soils with poor nutritional conditions, and that faces strong wind effects, such as the degree of wind disturbance and soil dryness exposure, which are strongly mediated by dune elevation and position (Marques, Swaine & Liebsch 2011; Silva et al. 2015; Silva & Souza 2018). Both nitrogen and elevation led to increases in standing biomass storage, as have been widely reported among studies (see review in Moeslund et al. 2013; Silva, Silva & Souza 2016; Jucker et al. 2018). Despite weaker effects of species richness and CWM traits, they were the only facets of biodiversity associated with basal area, which support the hypothesis that the inclusion of high-yielding or dominant species (or traits) in the community, with the increase of species richness, would lead to increases in productivity (*Sampling Effect* hypothesis, Huston 1997; Grime 1998; Hooper et al. 2005; Wojdak & Mittelbach 2007; Cardinale et al. 2006, 2013; Finegan et al. 2015; Lohbeck et al. 2015).

In its turn, the flow of matter via litterfall production was driven by canopy cover and species richness without effects of environmental covariates, probably because temporal abiotic variations weaken effects of abiotic variations over the space. Although canopy cover fails to quantify all three dimensions of the canopy, by not taken the vertical dimension of biomass availability, it still reflects a quantitative status of standing biomass. In a functional perspective, this status can be understood as an integrative property that result from linkage among several functional traits, or alternatively, from few individual traits with disproportional influences on the construction and maintenance of the canopy. One way or another, this result is another evidence that *Sampling effects* regulate BEF relationships in the study ecosystem and not *Niche complementarity* (Hypothesis 2).

Although functional diversity has improved models of ecosystem process in global analyses (Duffy, Godwin & Cardinale 2017), the inclusion of functional diversity as well as individual CWM traits not always imply in better prediction of productivity (Paquette & Messier 2011; Lohbeck et al. 2015), which suggest context dependence. Our results are in line with others that did not detect significant functional influences on ecosystem processes, despite our efforts to cover many aspects of the plant functioning through the inclusion of anatomical, biochemical and morphological leaf and stem traits. It is always possible that belowground traits such as root depth drive the analyzed components of productivity instead of aboveground traits, due to direct links with nutrient and water uptakes (Bardgett, Mommer & Vries 2014). The main reason we accounted for phylogenetic diversity was to capture unmeasured functional traits and ecological differences among species (Cadotte, Cardinale & Oakley 2008). However, the fact that we did not find influences of phylogenetic species evenness is an indication, but not a conclusion, that root traits may not guarantee a better explanation of these productivity components. It would occur if any effects of biodiversity on litterfall production and basal area were determined by *Niche complementarity*, which is not the case.

Niche complementarity has not been supported in a wide range of dry to moist tropical forests across Bolivia, Brazil and Costa Rica (Finegan et al. 2015). It is not surprising that primary productivity was not mediated by *Niche complementarity* in the study ecosystem, as some evidences has shown that this type of plant community has weak niche-based organization, with environmental and biotic filters do not acting on species niches (Silva et al. 2015; Silva & Souza 2018). The study *Restinga* vegetation, for example, does not show gradients of species occurrence or clusters of phylogenetically-related species across plots, with species displaying high niche overlap over space (Silva et al. 2015).

To gain insights into an often-unexplored aspect of biodiversity, we asked if the combined contribution of many rare species could be equivalent to the combined contribution of few common species (Lyons & Schwartz 2001; Smith & Knapp 2003; Hooper et al. 2005; Lyons et al. 2005). Our result of litterfall production suggests that on average common-species diversity determine this ecosystem process and not the whole species diversity. On the other hand, it diverges from the wood biomass storage, which was significantly impacted by rare-species diversity, and led to the conclusion that the maintenance of the whole community composition is necessary to maintain the ecosystem functioning, including many other rare species not studied yet (Lyons et al. 2005; Jain et al. 2014). Moreover, it is possible that rare species are important to other processes such as decomposition and nutrient cycling, because the quality of their leaves may differ from common species, which potentially interferes in the local dynamic of plots (Lyons et al. 2005; Hooper et al. 2005). The study area is considered a transitional environment that group several rare species from neighboring ecosystems, including Caatinga semiarid forest, Cerrado savanna, Amazon and Atlantic rain forests (Scarano 2002; Marques, Swaine & Liebsch 2011; Silva & Souza 2018). Such species are at the border of their distributions and face harsh environmental conditions such as aridity and drought seasonality. It configures an unfavorable environment for most species to express an optimal performance and productivity (Scarano et al. 2001; Farias, Fernandes, & Reise 2006). If rarity is a synonym of species having non-optimal performance, then it is not surprising that even in aggregation their contribution was lower than the combined contribution of common species for litterfall production. Our results do not reduce the role of rare species but address the need for further investigations assess other process they may influence most.

We conclude that components of primary productivity depended mainly on the abiotic environmental and secondarily on species richness and few CWM traits, but not to other facets of biodiversity. Although observational studies capture more realistic conditions than experiments, a caveat of using the first approach is that effects cannot be inferred with certainty (Oehri et al. 2017). We agree with this limitation and in addition we address that the explicability power of the model may depend on the nature of the ecosystem process rather than a lack of functional traits, with observed weaker cause-effect links if the response variable has a strong temporal dynamic. In this case, a dry seasonal dynamic can be considered a confounding characteristic that mask plant diversity effects over space. Non-seasonal tropical forests have shown opposing effects of biodiversity on litterfall production which support this line of reasoning (Lohback et

2015). Further studies should contrast differences in litterfall production between dry and rainy seasons in longer time scales than the one covered by our study to better separate effects of spatial environmental heterogeneity from annual temporal dynamics.

References

Bardgett, R.D., Mommer, L., & Vries, F. T. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* 29: 692–699.

Brunbjerg, A.K., Ejrnæs, R., & Svenning, J.C. 2012. Species sorting dominates plant metacommunity structure in coastal dunes. *Acta Oecologica* 39: 33–42.

Cadotte, M.W., Cardinale, B.J., & Oakley, T.H. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the United States of America* 105: 17012–17017.

Cadotte, M.W., Carscadden, K., & Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48: 1079–1087.

Caliman, A., Pires, A.F., Esteves, F.A., Bozelli, R.L., & Farjalla, V.F. 2010. The prominence of and biases in biodiversity and ecosystem functioning research. *Biodiversity and Conservation* 19: 651–664.

Cardinale, B.J., Palmer, M.A., & Collins, S.L. 2002. Species diversity enhances ecosystem functioning through interspecies facilitation. *Nature* 415: 426–429.

Cardinale, B. J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., & Jouseau, C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989–992.

Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., Ruijven, J.V, Reich, P.B., Scherer-Lorenzen, M., & Wilsey, B.J. 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94: 1697–1707.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. *The American Naturalist* 154: 449–468.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., & Ni, J. 2001. Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11: 356–370.

Clark, D.A., York, P.H., Rasheed, M.A., & Northfield, T.D. 2017. Does biodiversity–ecosystem function literature neglect tropical ecosystems? *Trends in Ecology and Evolution* 32: 320–323.

Duffy, J.E., Godwin, C.M., & Cardinale, B.J. 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* 549: 261–264.

Faith, D.P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61: 1–10.

Farias, A.S.C., Fernandes, M.E.B., & Reise, A. 2006. Comparison of litterfall yield of two mangrove stands with different structural features on the Bragança peninsula, Pará. *Ciências Naturais* 1: 53– 60.

Finegan, B., Pena-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M.S., Carreno-Rocabado, G., Casanoves, F., Diaz, S., Velepucha, P.E., Fernandez, F., (...) & Poorter, L. 2015. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology* 103: 191–201.

Grace, J.B. 2006. *Structural Equation Modeling and Natural Systems.* Cambridge University Press, Cambridge, UK.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3–35.

Huang, Y., Ma, Y., Zhao, K., Niklaus, P.A., Schmid, B., & He, J-S. 2017. Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest. *Journal of Plant Ecology* 1: 28–35.

Huston, M.A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449–460.

Isbell, F., Cowles, J., Dee, L.E., Loreau, M., Reich, P.B., Gonzalez, A., Hector, A., & Schmid, B. 2018. Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecology Letters* 21: 763–778.

Jain, M., Flynn, D.F.B., Prager, C.M., Hart, G.M., DeVan, C.M., Ahrestani, F.S., Palmer, M. I., Bunker, D.E., Knops, J.M.H., Jouseau, C.F., & Naeem, S. 2014. The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution* 4: 104–112.

Jucker, T., Bongalov, B., Burslem, D.F.R.P, Nilus, R., Dalponte, M., Lewis, S.L., Phillips, O.L., Qie, L., & Coomes, D.A. 2018. Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters* 21: 989–1000.

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

Laliberté, E., & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.

Lohbeck, M. Poorter, L., Martinez-Ramos, M., & Bongers, F. 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecological Society of America* 96: 1242–1252.

Loreau, M., & Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.

Lyons, K.G., & Schwartz, M.W. 2001. Rare species loss alters ecosystem function: invasion resistance. *Ecology Letters* 4: 358–365.

Lyons, K.G., Brigham, C.A., Traut, B.H., & Schwartz, M.W. 2005. Rare species and ecosystem functioning. *Conservation Biology* 19: 1019–1024.

Malhi, Y., Doughty, C., & Galbraith, D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society of London B* 366: 3225–3245.

Marques, M.C.M., Swaine, M.D., & Liebsch, D. 2011. Diversity distribution and floristic differentiation of the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest. *Biodiversity and Conservation* 20: 153–168.

Miyamoto, K., Suzuki, E., Kohyama, T., Seino, T., Mirmanto, E., & Simbolon, H. 2003. Habitat differentiation among tree species with small-scale variation of humus depth and topography in a tropical heath forest of Central Kalimantan, Indonesia. *Journal of Tropical Ecology* 19: 43–54.

Moeslund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., & Svenning, J-C. 2013. Topography as a driver of local terrestrial vascular plant diversity patterns. *Nordic Journal of Botany* 31: 129–144.

Oehria, J., Schmida, B., Schaepman-Struba, G., & Niklaus, P.A. 2017. Biodiversity promotes primary productivity and growing season lengthening at the landscape scale. *Proceedings of the National Academy of Sciences* 38: 10160–10165.

Paquette, A., & Messier, C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20: 170–180.

Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S.S., Cornwell, W.K.K., Craine, J.M.M., (…) & Cornelissen, J.H.C. 2013. New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.

Petchey, O.L., & Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5: 402–411.

Poorter, L., Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., (…) & Pena-Claros, M. 2015. Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography* 24: 1314–1328.

Poorter, L., Sande, M.T., Arets, E., Ascarrunz, N., Enquist, B., Finegan, B., Licona, J.C., Martinez-Ramos, M., Mazzei, L., Meave, J.A., (...) & Pena-Claros, M. 2017.

Biodiversity and climate determine the functioning of Neotropical forests. *Global Ecology and Biogeography* 26: 1423–1434.

Qian, H., & Jin, Y. 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology* 9: 233–239.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, AT.

Reich, P.B. 2014. The world-wide “fast-slow” plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

van der Sande, M.T., Arets, E.J.M.M., Pena-Claros, M., Hoosbeek, M.R., Cáceres-Siani, Y., van der Hout, P., & Poorter, L. 2018. Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. *Functional Ecology* 32: 461–474.

Sakschewski, B., von Bloh, W., Boit, A., Poorter, L., Pena-Claros, M., Heinke, J., Joshi, J., & Thonicke, K. 2016. Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change* 6: 1032–1036.

Scarano, F.R., Duarte, H.M., Ribeiro, K.T., Rodrigues, P.J.F.P., & Barcellos, E.M.B. 2001. Four sites with contrasting environmental stress in Southeastern Brazil: relations of species, life form diversity, and geographic distribution to ecophysiological parameters. *Botanical Journal of the Linnean Society* 136: 345–364.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Annals of Botany* 90: 517–524.

Scherer-Lorenzen, M., Bonilla, J.L., & Potvin, C. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos* 116: 2108–2124.

Silva, J.L.A., Souza, A.F., Jardim, J.G., & Goto, B.T. 2015. Community assembly in harsh environments: the prevalence of ecological drift in the heath vegetation of South America. *Ecosphere* 6: 111.

Silva, A.C., Silva, J.L.A., & Souza, A.F. 2016. Determinants of variation in heath vegetation structure on coastal dune fields in northeastern South America. *Revista Brasileira de Botanica* 39: 605–612.

Silva, J.L.A., Souza, A.F., Caliman, A., Voigt, E.L., & Lichston, J.E. 2018. Weak whole-plant trait coordination in a seasonally dry South American stressful environment. *Ecology and Evolution* 8: 4–12.

Silva, K.J.P., & Souza, A.F. 2018. Common species distribution and environmental determinants in South American coastal plains. *Ecosphere* 9: e02224.

Smith, M.D., & Knapp, A.K. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* 6: 509–517.

SPSS (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.)

Sullivan, M.J.P., Talbot, J., Lewis, S.L., Philips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., (…) & Zemagho, L. 2017. Diversity and carbon storage across the tropical forest biome. *Scientific Reports* 7: 39102.

Taylor, P.G., Cleveland, C.C., Wieder, W.R., Sullivan, B.W., Doughty, C.E., Dobrowski, S.Z., & Townsend, A.R. 2017. Temperature and rainfall interact to control carbon cycling in tropical forests. *Ecology Letters* 20: 779–788.

van Wilgen, B.W. 2013. Fire management in species-rich Cape fynbos shrublands. *Frontiers in Ecology and the Environment* 11: 35–44.

Wojdak, J.M., & Mittelbach, G.G. 2007. Consequences of niche overlap for ecosystem functioning: an experimental test with pond grazers. *Ecology* 88: 2072–2083.

CONCLUSÃO GERAL DA TESE

O uso de atributos funcionais para entender a estrutura da comunidade vegetal e do funcionamento do ecossistema Restinga revelou que a resposta das espécies às variações do ambiente abiótico e o impacto da biodiversidade sobre a produtividade dependem fracamente das diferenças de nicho entre elas. Estas espécies de plantas não estão condicionadas a terem uma forte coordenação entre os atributos funcionais para lidar com o estresse hídrico e de escassez nutricional do solo, tornando difícil prever variações de atributos de folha baseados nas variações de atributos de lenho, e vice-versa. Qualquer definição ou modelagem da comunidade pode falhar caso pressuponha que a Restinga é formada por espécies que se agrupam em uma mesma categoria de tolerância ao estresse. É muito provável que hajam subgrupos de estratégias funcionais representados por espécies que se distinguem, por exemplo, em função da sua origem biogeográfica.

Embora a identidade das espécies nas comunidades locais seja difícil de ser predita, pelo fato de que a composição de espécies depende predominantemente de processos estocásticos (dispersão e deriva) e não de variações do ambiente abiótico, ainda assim foi possível identificar que os atributos funcionais das espécies são sensíveis às mudanças espaciais do ambiente. Isto significa, por exemplo, que a composição florística de comunidades locais em topos de dunas não se diferencia completamente da composição florística de comunidades locais em vales de dunas, embora o mesmo não aconteça para a média de alguns atributos funcionais. Este resultado sugere que ignorar os atributos funcionais pode levar a subestimação de processos que estruturam as comunidades de Restinga baseados nos nichos das espécies, mesmo que seus efeitos não sejam fortes.

Por outro lado, considerar ou não os atributos funcionais, bem como a diversidade funcional das comunidades locais, parecem não ser tão decisivo para o entendimento do impacto da biodiversidade sobre o componente mais dinâmico e mais estável da produtividade primária (produção de serapilheira e estoque de biomassa lenhosa, respectivamente). Estes componentes de produtividade primária responderam principalmente a aspectos ambientais abióticos e apenas secundariamente à riqueza de espécies e a média de poucos atributos, mas não a outras facetas da biodiversidade. Além disto, as relações entre biodiversidade e componentes de produtividade existem independentemente do grau de sobreposição e complementaridade do nicho das espécies. A diversidade de espécies raras versus a diversidade de espécies comuns teve influência diferente na produção de serapilheira, mas não na área basal. Estes resultados reforçam a interpretação de que as diferenças de nicho entre espécies promovem efeitos apenas modestos na estrutura e ainda menores no funcionamento da Restinga.