UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE BIOCIÊNCIAS
DEPARTAMENTO DE BOTÂNICA
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA VEGETAL

LUCAS ERICKSON NASCIMENTO DA COSTA

O PAPEL DAS VARIAÇÕES AMBIENTAIS LOCAIS SOBRE A ESTRUTURA FUNCIONAL DA ASSEMBLÉIA DE SAMAMBAIAS NA FLORESTA ATLANTICA NO NORDESTE DO BRASIL

Recife
2020

LUCAS ERICKSON NASCIMENTO DA COSTA

O PAPEL DAS VARIAÇÕES AMBIENTAIS LOCAIS SOBRE A ESTRUTURA FUNCIONAL DA ASSEMBLÉIA DE SAMAMBAIAS NA FLORESTA ATLANTICA NO NORDESTE DO BRASIL

Tese apresentada ao Programa de Pós- Graduação em Biologia Vegetal da Universidade Federal de Pernambuco como um dos requisitos necessários para a obtanção do título de Doutor em Biologia Vegetal.

Área de concentração: Ecologia e Conservação

Orientador: Dra. Iva Carneiro Leão Barros

Coorientador: Dr. Michael Kessler

Recife

2020

Catalogação na fonte:
Bibliotecária Claudina Queiroz, CRB4/1752

Costa, Lucas Erickson Nascimento da
O papel das variações ambientais locais sobre a estrutura funcional da assembléia de samambaias na Floresta Atlântica no nordeste do Brasil / Lucas Erickson Nascimento da Costa - 2020.
201 folhas: il., fig., tab.

Orientadora: Iva Carneiro Leão Barros
Coorientador: Michael Kessler
Tese (doutorado) – Universidade Federal de Pernambuco. Centro de Biociências. Programa de Pós-Graduação em Biologia Vegetal. Recife, 2020.

Inclui referências e anexos.

1. Samambaias 2. Floresta Atlântica 3. Diversidade funcional I. Barros, Iva Carneiro Leão (Orientadora) II. Kessler, Michael (Coorientador) III. Título

587.3 CDD (22.ed.) UFPE/CB-2020-122

LUCAS ERICKSON NASCIMENTO DA COSTA

O PAPEL DAS VARIAÇÕES AMBIENTAIS LOCAIS SOBRE A ESTRUTURA FUNCIONAL DA ASSEMBLÉIA DE SAMAMBAIAS NA FLORESTA ATLANTICA NO NORDESTE DO BRASIL

Tese apresentada ao Programa de Pós- Graduação em Biologia Vegetal da Universidade Federal de Pernambuco como um dos requisitos necessários para a obtanção do título de Doutor em Biologia Vegetal.

Aprovada em: 19/02/2020

BANCA EXAMINADORA

Dra. Iva Carneiro Leão Barros (Orientadora)
Universidade Federal de Pernambuco

Dra. Fernanda Maria P. de Oliveira (Examinadora Externa)
Universidade Federal de Pernambuco

Dr. Klaus Mehltreter (Examinador Externo)
Institute of Ecology (INECOL) - México

Dr. Bruno Karol Cordeiro Filgueiras (Examinador Externo)
Universidade Federal de Pernambuco

Dr. Augusto César Pessoa Santiago (Examinador Externo)
Universidade Federal de Pernambuco

À minha mãe, Joseane Barreto Sales,
à Irmã Margarida Galindo,
e à minha professora de língua portuguesa
do ensino médio, Ivanilda,
Dedico.

AGRADECIMENTOS

Esse trabalho é fruto da colaboração direta e indireta de diversas pessoas. Agradeço aos meus familiares especialmente à minha mãe. A todos os meus amigos do Alto do Pascoal. À Amanda, Belinha e Adriana por estarem sempre comigo;

Aos amigos da Universidade e a Pós-Graduação: Fernando, Lígia, Bruno, Camila, Silvia Caroline, Laís e Silvia Santos. À Robinho meu grande amigo. À Eline e Madson pelas conversas aleatórias e discussões cientificas, bem como pelos momentos de descontração.

Aos amigos do Laboratório de Pteridófitas, Augusto, Mayara e Milena. Aos amigos da Universidade de Zurique e do Instituto de Botânica Sistemática e Evolutiva.

À Rafael Farias, que tem colaborado comigo desde o início de minha vida acadêmica e que hoje é um amigo e parceiro de muitos estudos que ainda estão por vir.

À minha querida orientadora, Iva Carneiro Leão Barros, por acreditar em mim e sempre me incentivar a desenvolver pesquisas científicas, sempre contribuindo para o meu crescimento pessoal e profissional. Ao meu coorientador Michael Kessler por me receber e compartilhar seus conhecimentos comigo.

Aos membros da Banca, pela disponibilidade e futuras contribuições para melhoria deste trabalho.

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pela concessão da bolsa de doutorado. À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), pela concessão da bolsas sanduiche.

“Eu encontrei um viajante de uma terra antiga
Que disse:—Duas gigantescas pernas de pedra sem torso
Erguem-se no deserto. Perto delasna areia,
Meio afundada, jaz um rosto partido, cuja expressão
E lábios franzidos e escárnio de frieza no comando
Dizem que seu escultor bem aquelas paixões leram
Que ainda sobrevivem, estampadas nessas partes sem vida,
A mão que os zombava e o coração que os alimentava.
E no pedestal estas palavras aparecem:
"Meu nome é Ozymandias, rei dos reis:
Contemplem minhas obras, ó poderosos, e desesperai-vos!"
Nada resta: junto à decadência
Das ruínas colossais, ilimitadas e nuas
As areias solitárias e inacabáveis estendem-se à distância.”
Ozymandias (SHELLEY, 1818)

RESUMO

O estudo da estrutura funcional das comunidades ao longo das variações ambientais tem sido utilizado como ferramenta para investigar os mecanismos regulando a coexistência de espécies. Assim, o objetivo deste estudo foi analisar a estrutura funcional da assembleia de samambaias em remanescentes de Floresta, visando identificar o papel dos atributos funcionais na partição de nicho das espécies, como determinaram as estratégias ecológicas das espécies. Além disso, foi analisada a convergência e divergência de atributos entre as espécies de samambaias co-ocorrentes. Foi verificado quão propensa a compartilhar atributos semelhantes as espécies estreitamente relacionadas eram (denotando restrições filogenéticas). A relação entre os componentes funcional e taxonômico das assembleias de samambaias também foi analisada, bem como o papel das condições ambientais locais nos padrões de diversidade alpha e beta funcionais das assembleias. As assembleias de samambaias foram amostradas em 22 parcelas ($200m^2$) em remanescentes de Floresta Atlântica no nordeste do Brasil. Condições ambientais locais foram coletadas em cada parcela. Atributos foliares e do rizoma foram avaliadas de acordo com cada objetivo. Os resultados demonstraram que a segregação de nicho foi relacionada com os atributos funcionais das espécies. Ainda, esses atributos denotaram que as samambaias estavam organizadas em torno de estratégias ruderais. A competitividade e ruderalidade das assembleias foram afetadas pelo pH do solo e pelo potássio do solo, com associações negativas e positivas, respectivamente. As espécies co-ocorrentes apresentaram convergente funcional, sem sinal filogenético aparente (exceto para o teor de matéria seca das folhas). As estruturas funcional e taxonômica estavam relacionadas de forma complexa e a riqueza, diversidade e composição de espécies tiveram efeitos notáveis nos padrões funcionais. O pH do solo e a disponibilidade de nutrientes foram as variáveis mais importantes, afetando a riqueza, redundância e divergência funcional das assembleias. Enquanto o pH do solo e a temperatura afetaram a diversidade beta funcional, de forma positiva e negativa, respectivamente. Finalmente, a filtragem ambiental afetou significativamente os padrões funcionais das assembleias de samambaias de forma coordenada desde a segregação do nicho, estratégias ecológicas das assembleias e a diversidade funcional em ambos os componentes (alpha e beta).

Palavras-Chave: Atributos foliares. Diversidade funcional. Escala local. Estratégias CSR. Nicho.

ABSTRACT

Understanding the processes structuring the distribution of species across environmental gradients have been challenging ecologists. The study of the functional structure of the communities along environmental variations has been applied as an important tool to investigate the mechanisms regulating species coexistence. In this sense, this study aimed to identify the role of functional traits on species niche partitioning, and how these traits determine species ecological strategies (using Grime's CSR strategies). Further, we analyzed trait convergence and divergence patterns among co-occurring species. It was analyzed whether closely related species were prone to share similar traits (denoting phylogenetic constraints). The relationship between the functional and taxonomic components of the assemblages was also analyzed, as well as, the role of environmental conditions on alpha and beta functional patterns. Assemblages were sampled from 22 plots (200m^2) among Atlantic forest remnants in northeastern Brazil. Local environmental conditions (e.g., number of trees, rock coverage, edaphic conditions) were collected in each plot. Leaf and rhizome traits were analyzed according to specific aims. The results denoted that niche segregation was related to shifts in species' functional traits. Yet, these traits demonstrated that ferns were organized around ruderal strategies. The competitivity and ruderality of the assemblages were affected by soil pH and K content, with negative and positive effects, respectively. Co-occurring species exhibited a convergent pattern that was not phylogenetically constrained (except to leaf dry matter content). Functional and taxonomic structures of assemblages were complexly related and species richness, diversity and identity affected substantially functional patterns. Soil pH and nutrient availability were the most important variables driving ferns functional richness, redundancy and divergence, while soil pH and temperature affected beta functional patterns. Finally, the environmental filtering affected the functional patterns of fern assemblages with a coordinated effect from niche segregation, towards ecological strategies and functional diversity (alpha and beta components).

Keywords: CSR strategies. Functional convergence. Functional diversity. Leaf traits. Local scale. Niche.

SUMÁRIO

1 INTRODUÇÃO

Compreender como as comunidades se organizam e afetam o funcionamento dos ecossistemas ao longo dos ambientes tem sido uma questão central na ecologia (RICKLEFS, 2008; HECTOR et al., 2010). As variações ambientais, via filtragem ambiental e processos de nicho, bem como os limites de similaridade tem sido reportados como importantes estruturadores das comunidades, embora processos espaciais (vi limites de dispersão) também envolvidos nos padrões gerados (CORNWELL et al., 2006; GÖTZENBERGER et al., 2011; DE BELLO et al., 2012). Uma vez que esses processos atuam simultaneamente sobre as comunidades ao longo de diferentes escalas, a contribuição relativa de cada processo pode variar de acordo com o grupo biológico, o ambiente envolvido (MÜNKEMÜLLER et al., 2011; PAVOINE; BONSALL, 2011).

Embora a maioria dos estudos tenham focado no componente taxonômico das comunidades (i.e., riqueza, diversidade e identidade das espécies), este componente reflete apenas uma das facetas das comunidades (MCGILL et al., 2006; PAVOINE; BONSALL, 2011). Ainda, a interpretação a partir de um único componente pode levas a interpretações equivocadas ou incompletas, sendo necessário a análise de forma complementar ao longo de diferentes escalas (PAVOINE; BONSALL, 2011). De fato, a análise de gradientes ambientais a partir do componente taxonômico é pouco informativo quando comparado com o componente funcional, visto que este esta diretamente relacionado ao papel do ambiente moldando as estratégias ecológicas das espécies, e como essas estratégias estruturam as comunidades e afetam o funcionamento dos ecossistemas (VIOLLE et al., 2007; REICH, 2014).

A estrutura funcional está baseada na análise dos atributos funcionais das comunidades, que podem ser entendidos como quaisquer, características morfofisiológicas ou fenológicas que afetam a aptidão do organismo, estando muitas vezes relacionada com funções ecossistêmicas desempenhadas pelas espécies (VIOLLE et al., 2007; CIANCIARUSO et al., 2009), podem determinar a ocorrência das espécies, a forma como elas interagem entre si, bem como suas respostas às variações a ambientais (LAVOREL et al., 1997; POORTER; BONGERS, 2006; REICH, 2014). Os atributos funcionais estão inseridos em demandas conflitantes, como no caso de alguns atributos foliares. Dentro os quais podemos destacar o espectro econômico foliar (EEF) (e.g., WRIGHT et al., 2004; DÍAZ et al., 2016). De acordo com o EEF, os atributos estariam inseridos numa demanda conflitante entre aquisição de recursos, onde em um dos extremos do gradiente encontramos atributos relacionados a aquisição de recursos, enquanto atributos associados a estratégias conservativas representariam o lado oposto (REICH, 2014; DÍAZ et al., 2016).

Os padrões de EEF podem ser utilizados para analisar as estratégias ecológicas das espécies, bem como para avaliar os mecanismos relacionados com a coexistência (e.g., GRIME et al., 2006; PIERCE et al., 2013). Assim como a maioria dos processos ecológicos, os atributos funcionais estão envolvidos em diversas demandas conflitantes que variam de acordo com a escala de observação, assim como seus mecanismos estruturadores (MASON et al., 2007; CAVIERES et al., 2014). Especificamente na escala local, as demandas conflitantes relacionadas a aquisição de recursos, competição e tolerância ao estresse ambiental são proeminentes (CORNELL; LAWTON, 1992; CAVENDER-BARES et al., 2004; LALIBERTÉ et al., 2009).

A compreensão dos mecanismos atuantes em escala local são cruciais para o entendimento dos processos regulando a coexistência de espécies, provendo informações relevantes para a conservação e previsão do impacto das espécies sobre o funcionamento do ecossistema (HOOPER et al., 2005; MCGILL et al., 2006; TERBORGH et al., 2002). Embora os estudos desse cunho tenham avançado exponencialmente nas últimas décadas (LAVOREL; GARNIER, 2002), muitos grupos e sistemas naturais permanecem pouco explorados (NAEEM, 2002; BRUELHEIDE et al., 2018).

Esse é o caso das samambaias na Floresta Atlântica do Brasil. Esses vegetais compreendem um componente importante do sub-bosque da Floresta Atlântica, apresentando diversas espécies ameaçadas pelas ações antrópicas (WINDISCH, 2002). Devido a degradação intensa (EISENLOHR et al., 2015), especialmente no Nordeste, os remanescentes da Floresta Atlântica nordestina (FAN) são altamente fragmentos e isolados, imersos numa matriz, geralmente, de baixa complexidade estrutural, como monoculturas, áreas de pasto e áreas não florestadas (RIBEIRO et al., 2009). Os estudos desenvolvidos com samambaia nesses ambientes apresentaram cunho florístico (e.g., XAVIER; BARROS, 2003; PEREIRA et al., 2011; SANTIAGO et al., 2004), ou focaram nos impactos da fragmentação sobre as assembleias de samambaias (e.g., PEREIRA et al., 2014; SILVA et al., 2014). Esses estudos focaram no componente taxonômico, contudo, atualmente sabe-se que o componente funcional pode ser mais preditivo em relação aos mecanismos estruturando a coexistência, principalmente quando relacionados às variações ambientais (MCGILL et al., 2006).

Neste contexto, esta tese teve como objetivo avaliar como as variações ambientais afetam a estrutura funcional da assembleia de samambaias. Para isso: 1. Particionamos os nichos das samambaias ocorrendo em remanescentes de FAN identificando o papel dos atributos funcionais na segregação de nicho; 2. Analisamos as estratégias ecológicas das samambaias na FAN, via atributos funcionais relacionados ao EEF, ainda, baseado nas estratégias ecológicas das espécies, sumarizamos a assinatura funcional das assembleias e identificamos os fatores ambientais locais relacionados aos padrões observados; 3. Investigamos os processos moldando os padrões funcionais locais das assembleias, bem como o papel das variações ambientais locais, da proximidade filogenética entre as espécies, e do componente taxonômico nos padrões observados; 4. Analisamos o papel das variações ambientais locais e climáticas sobre a substituição de traços funcionais (i.e., diversidade beta funcional) ao longo das assembleias.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 REGRAS DE MONTAGEM NUMA PERSPECTIVA FUNCIONAL

As regras de montagem, descritas por Diamond (1975), evocam dois processos fundamentais: a filtragem ambiental e os limites de similaridade. A partir do estudo de aves ao longo de um arquipélago na Nova Guiné, Diamond trouxe dois importantes paradigmas. O paradigma da ilha indica que espécies com requerimentos similares se evitam devido a sobreposição de seus nichos e por tanto não devem coexistir num mesmo habitat (DIAMOND, 1975). Esse paradigma indica o papel da competição estruturando as comunidades (WEIHER; KEDDY, 1999). Por outro lado, o paradigma das características ligadas ao ambiente, indica que o ambiente seleciona as espécies que podem existir num determinado habitat, indicando que espécie que coexistem possuem atributos semelhantes (DIAMOND, 1975; WEIHER; KEDDY, 1999).

Embora as regras de montagem tenham sido analisadas de um ponto de vista taxonômico, i.e., como a riqueza de espécies ou a composição varia ao longo das comunidades, a análise funcional, tem potencial mais preditivo e generalizável ao longo de diferentes ambientes ou pool de espécies (MCGILL et al., 2006). Neste sentido, a compreensão desses dois mecanismos sobre a diversidade funcional das comunidades indica, assim, o papel das interações via competição e a da filtragem ambiental na seleção dos atributos para possibilitar a coexistência (DIAMOND, 1975; STUBBS; WILSON, 2004; CORNWELL et al., 2006).

Comunidades estruturadas por competição (predizendo uma similaridade limitante) tendem a apresentar uma limitação de similaridade nos atributos das espécies, reduzindo a sobreposição de nicho, consequentemente reduzindo a competição para possibilitar a coexistência (DIAMOND, 1975; STUBBS; WILSON, 2004; KRAFT et al., 2008; ADLER et al., 2010). Contudo, a competição também pode criar um padrão funcional convergente se uma estratégia superior é superior dentro de um dado contexto ambiental (GRIME, 2006; CORNWELL; ACKERLY, 2009).

No caso de comunidades estruturadas majoritariamente por filtros ambientais há padrões funcionais convergentes (CORNWELL et al., 2006; CORNWELL; ACKERLY, 2009; LEBRIJA-TREJOS et al., 2010). Neste sentido, a diversidade de características é limitada pelo nicho local (DÍAZ; CABIDO, 2001). Este processo tende a resultar numa diversidade funcional mais baixa do que o esperado pelo acaso, em um padrão de “clustering” (WEIHER; KEDDY, 1995).

A priori, espera-se que a competição seja mais forte em comunidades ricas em espécies, gerando elevados valores mais elevados de diversidade funcional. Enquanto os filtros ambientais tendem a ser mais prevalentes em comunidade com baixa riqueza sob condições ambientais extremas, resultado numa baixa diversidade funcional. Contudo, comunidades ricas podem conter uma elevada proporção de espécies funcionalmente redundantes, enquanto comunidades pobres podem conter espécies que exploram diferentes nichos (YACHI; LOREAU, 2007). Todavia, processos aleatórios, como a dispersão, a deriva, e fatores históricos parecem ser agentes atuantes na montagem e manutenção das comunidades (VELLEND, 2010). Assim, se as comunidades são compostas por conjuntos aleatórios de espécies, esperasse que os valores de DF não devem ser diferentes do esperado pelo acaso (DE BELLO et al., 2009).

O papel dos processos estocásticos geralmente é evidente, contudo, a completa neutralidade na montagem de comunidades parece pouco provável, dada a associação de estratégias ecológicas (i.e., atributos funcionais) com determinadas situações ambientais e o efeito de interações interespecíficas sobre padrões de distribuição e abundância de espécies (STUBBS; WILSON, 2004; WESTOBY; WRIGHT, 2006).

Os padrões funcionas das comunidades também podem ser afetados por restrições filogenéticas (WEBB et al., 2002). Primeiramente, espécies relacionadas tendem a ser ecologicamente semelhantes (WIENS; GRAHAM, 2005). Adicionalmente, a estrutura do filogenética do atributo também pode afetar os padrões funcionais da comunidade (WEBB et al., 2002). Por exemplo, se um dado atributo com alto valor adaptativo é agrupado na filogenia, espécies relacionadas tendem a compartilhar essa característica promovendo uma convergência funcional na comunidade (CAVENDER-BARES et al., 2004). Por outro lado, se esse atributo é disperso filogeneticamente, espécies diferentes tendem a compartilhar esse atributo, promovendo uma divergência funcional na comunidade (CAVENDER-BARES et al., 2004). Deste modo, que pode haver uma relação entre a proximidade filogenética das espécies, seus atributos funcionais e os processos ecológicos que determinam sua coexistência (KRAFT et al., 2007).

2.1.1 Escalas espaciais e suas demandas conflitantes na montagem das comunidades

Tanto os mecanismos estruturadores, quanto as demandas conflitantes das espécies variam espacialmente, afetando assim a estrutura funcional das comunidades (KNEITEL; CHASE, 2004; MASON et al., 2007). Esses mecanismos não são excludentes e podem ocorrer simultaneamente interagindo ou se substituir ao longo de escalas espaciais (MASON et al., 2007; CAVIERES et al., 2014), levantando incertezas sobre os mecanismos que promovem a coexistência (GRIME et al., 2006). Processos estocásticos tendem a atuar em escalas mais amplas (CORNELL; LAWTON, 1992), enquanto os filtros ambientais podem atuar tanto em escala regional (CORNWELL et al., 2006), quanto em escala local (CORNELL; LAWTON, 1992), juntamente com as interações entre as espécies (e.g. competição) emergindo padrões de montagem na comunidade (CORNELL; LAWTON, 1992; CAVENDER-BARES et al., 2004). Contudo, estudos tem demonstrado processos aleatórios podem atuar mesmo em escala local (VELLEND, 2010), assim, a questao crucial deve ser identificar o mecanismo estruturador mais prevalente, uma vez que todos co-ocorrem (LALIBERTÉ et al., 2009).

Ainda, as demandas conflitantes que afetam os atributos nas comunidades também variam de acordo com a escala (KNEITEL; CHASE, 2004; DE BELLO et al., 2009). Neste contexto, demandas conflitantes relacionas com a tolerância ao ambiente, competição por recursos, bem como resistência a predadores tendem a ser mais preponderantes em escala local (KNEITEL; CHASE, 2004). Por outro lado, demandas conflitantes relacionadas com a capacidade de colonização e habilidades competitivas, bem como, a influência do processo de ocupação de habitats favoráveis tendem a ser mais importantes na escala regional (KNEITEL; CHASE, 2004). Em paisagens heterogêneas, o grau de especialização e a dinâmica de colonização entre habitats favoráveis e desfavoráveis (fonte-dreno) (KNEITEL; CHASE, 2004).

2.2 ATRIBUTOS FUNCIONAIS: CONCEITOS E IMPORTÂNCIA

Os atributos funcionais compreendem quaisquer características morfofisiológicas ou fenológicas que afetam a aptidão do organismo, estando muitas vezes relacionada com funções ecossistêmicas desempenhadas pelas espécies (VIOLLE et al., 2007; CIANCIARUSO et al., 2009). Estudos ecológicos utilizando atributos funcionais aumentaram expressivamente nas últimas décadas (DÍAZ et al., 2007; DÍAZ; CABIDO, 2001; LAVOREL; GARNIER, 2002), sendo empregados para os mais variados propósitos (e.g., PETCHEY; GASTON, 2002; DÍAZ et al., 2004; WRIGHT et al., 2004; POORTER; BONGERS, 2006; GRIME, 2006; STERCK et al., 2011; LOHBECK et al., 2015; ZHANG et al., 2017). Apesar deste "boom" relativamente recente, a importância dos atributos das espécies é reconhecida desde os primórdios da construção do pensamento biológico (CADOTTE et al., 2011). Um exemplo disto é o fato de ainda no período da dinastia Saliana do Império Romano-Germânico (1194-1250), o Imperador Federico II, que era naturalista, rejeitou os esquemas de classificação Aristotélicos em detrimento de uma classificação baseada nas características e hábitos das espécies (CADOTTE et al., 2011).

Sabe-se que diferentes atributos funcionais podem influenciar diferentes processos, afetando de individuos ao ecossistema, bem como, evocar diferentes mecanismos reguladores (LAVOREL et al., 1997). Em suma, os atributos funcionais podem determinar os provaveis habitats de ocorrencia das especies (LAVOREL et al., 1997), a forma como essas especies coexistindem e podem interagir de acordo com a competição, ou mesmo como diferentes especies contribuem para os processos ecossistemicos (VIOLLE et al., 2007; REICH, 2014).

A analise de atributos funcionais apresenta diversas vantagem em relação a outros métodos, como os puramente taxonomicos, como a capacidade de generalização da biodiversidade (McGILL et al., 2006), bem como apresentam uma possibilidade de escalonamento, podendo ser avaliados no nível de individuos e especies, passando por populações e comunidades, até ecossistemas (VIOLLE et al., 2007). Assim, espera-se que abordagens funcionais devem facilitar a sintese entre ecologia de communidade e ecossistemas (McGILL et al., 2006).

Os atributos funcionais podem ser classificados quanto a performance como atributos de efeito ou de resposta (VIOLLE et al., 2007; DÍAZ; CABIDO, 2001). Atributos de efeito são características das espécies podem afetar tanto as condições ambientais, quanto as propriedades do ecossistema (VIOLLE et al., 2007). Por exemplo, a área foliar específica, e o conteúdo de nitrogênio foliar são importantes atributos de efeito sobre a produtividade (PONTES et al., 2007). Por outro lado, alguns atributos podem variar em resposta a alterações ambientais, sendo assim considerados atributos de resposta (VIOLLE et al., 2007). Atributos como taxa de crescimento, produção de folhas e trocas gasosas podem ser importantes atributos resposta a seca (e.g., KURSAR et al., 2009). É importante ressalvar que um atributo pode ser tanto de efeito quanto de resposta (LAVOREL; GARNIER, 2002).

Os atributos funcionais estão hierarquicamente relacionados entre si (LAVOREL; GARNIER, 2002), podendo ser divididos em duas classes que, basicamente, separam os atributos de fácil mensuração mas com baixa precisão em prever processos ou evocar mecanismos estruturadores (i.e., “soft traits”), daqueles que apresentam maior acurácia, sendo também mais difíceis/ e ou custosos de mensurar (i.e., “hard traits”) (HODGSON et al., 2007). Parâmetros ecofisiológicos das plantas, como taxa fotossintética, transpiração, potencial hídrico e condutância estomática configuram “hard traits”, enquanto, a altura da planta, área foliar e espessura foliar são “soft traits” amplamente utilizados (e.g., DÍAZ et al., 2004; WRIGHT et al., 2004; POORTER; BONGERS, 2006; POORTER et al., 2008; LOHBECK et al., 2015). Estudos prévios demonstraram que “soft traits” estão correlacionados com importantes “hard traits” (REICH et al., 2007), sendo assim bons substitutivos em análises funcionais (DÍAZ et al., 2004; WRIGHT et al., 2004; BELLUAU; SHIPLEY, 2018).

2.3 ATRIBUTOS FOLIARES E SUAS DEMANDAS CONFLITANTES

Diversos atributos foliares tem sido utilizados como atributos de resposta e de efeito, tanto “hard traits”, quanto “soft traits”, em diferentes contextos, seja tentando identificar as estratégias das espécies (e.g., GRIME, 1988; POORTER; BONGERS, 2006; PIERCE et al., 2013; LOHBECK et al., 2015), avaliar os mecanismos promovendo a coexistência de espécies (e.g., KRAFT et al., 2008; MASON et al., 2012), ou o efeito das espécies nos processos ecossistêmicos (e.g., DÍAZ; CABIDO, 2001; POORTER; BONGERS, 2006).

Atributos como a área foliar, por exemplo, tem sido identificado como um importante preditor do custo de construção foliar, onde folhas pequenas indicam uma redução na perda de água e um aumento na tolerância a estresses abióticos (CORNELISSEN et al., 2003; NIINEMETS et al., 2007). O conteúdo de massa seca tem sido utilizado para representar estratégias de uso do recurso, de modo que uma elevada massa seca foliar indicaria uma estratégia conservativa, caracterizada por uma baixa taxa de crescimento e uma elevada tolerância ao estresse abiótico, principalmente nutricionais (HODGSON et al., 2011).

Estudos reportaram padrões gerais em relação aos atributos funcionais foliares com respeito a uma marcante demanda conflitante entre aquisição de recursos e a competição, como reportado no espectro econômico foliar (EEF) (e.g., WRIGHT et al., 2004; CAVENDER-BARES et al., 2004; DÍAZ et al., 2016; BRUELHEIDE et al., 2018). Segundo o EEF, as plantas estariam distribuídas ao longo de gradientes de estratégias relacionadas com a aquisição de recursos, de modo que, espécies com características aquisitivas estariam em um lado do gradiente, enquanto espécies conservativas estariam no extremo oposto deste gradiente (REICH, 2014; DÍAZ et al., 2016).

Embora essas relações possam não ser generalizadas para todas as espécies e em todos os sistemas vegetais, utilizar atributos funcionais, a utilização de demandas conflitantes amplamente reconhecidas e estudadas pode ser um bom ponto de partida na seleção de atributos relevantes para responder questões relacionadas a coexistência de espécies, para identificar estratégias ecológicas dominantes, bem como para avaliar o papel das espécies no funcionamento do ecossistema (PIERCE et al., 2013; BELLUAU; SHIPLEY, 2018).

2.4 TIPOS FUNCIONAIS E ESTRATÉGIAS ECOLÓGICAS

Uma análise global incluindo todas as linhagens de plantas vasculares atuais (i.e., samambaias e licófitas, gimnospermas e angiospermas demonstrou que em torno de 74% da variação global de importantes atributos funcionais relacionados com fitness (sobrevivência, crescimento e reprodução) podem ser sumarizados de forma robusta em dois eixos principais (DÍAZ et al., 2016). Essa análise demonstrou que diversa demandas conflitantes entre os atributos limitam a diversidade de estratégias nas plantas vasculares de acordo com um espectro de variação relacionados ao tamanho e a função (DÍAZ et al., 2016).

Assim, apesar da relevância dos atributos funcionais, é necessário ter em mente que o alvo da seleção natural é o fitness do indivíduo e não de atributos individuais (COUGHENOUR, 1985). Dentro dessa premissa métodos alternativos buscaram agrupar as espécies de acordo com a similaridade de atributos ou de funções, bem como segundo o tipo de respostas as condições abióticas (RAUNKIAER, 1934; GRIME, 1974; GRIME, 1977; FUNK et al., 2017). Os estudos de Raunkiaer (1934) foram pioneiros dentro dessa visão funcional de agrupar espécies. Ele classificou as espécies segundo suas formas de vida visando entender as estratégias ecológicas selecionadas em ambientes frios. O esquema folha-altura-semente (do inglês “leaf-height- seed strategy scheme – LHS”) proposto por Westoby (1998) foi uma classificação relativamente recente (meados dos anos 2000) utilizada para tentar entender as respostas das espécies às perturbações, bem como prever a distribuição ao longo de gradientes ambientais (LAURETO; CIANCIARUSO; SAMIA, 2015).

Essa tentativa de agrupar as espécies de acordo com seus tipos funcionais, i.e., grupos de espécies que respondem ao ambiente de forma similar(DÍAZ; CABIDO, 2001), foi impulsionado por uma crescente linha de trabalho (estimulada por Elton e endossada pro Hutchinson) que visualizava as comunidades como um grupo de organismos que usam o recurso de forma similar, que futuramente viria a inspirar o termo guilda (LAURETO; CIANCIARUSO; SAMIA, 2015), embora atualmente o termo grupo funcional seja mais amplamente difundido. Se por um lado as estratégias ecológicas baseadas em atributos funcionais foram importantes para explicar similaridades entre as espécies indicando padrões gerais, por outro lado raramente essas abordagens estão relacionadas a um contexto teórico de estratégias adaptativas (CERABOLINI et al., 2010).

As estratégias CSR propostas por Grime (GRIME, 1977; 2001), estão inseridas num contexto de teoria adaptativa, podendo ser facilmente acessadas a partir de atributos funcionais de fácil mensuração inseridos em importantes demandas conflitantes (PIERCE et al., 2012; PIERCE et al., 2013; REICH, 2014). De acordo com a Teoria CSR, as interações entre as diferentes demandas conflitantes que as plantas experimentam produzem uma variação nas características funcionais em torno de três respostas adaptativas formando um espaço triangular

(GRIME, 1977; 2001; CERABOLINI et al., 2010). A teoria CSR prediz que as espécies estariam distribuídas dentro de espaço triangular segundo suas demandas em relação à capacidade de competitiva em ambientes produtivos (C), tolerar condições de estresse, normalmente associadas a baixa disponibilidade de recursos (S), e tolerar distúrbios ambientas em ambientes produtivos (R), sendo possíveis a ocorrência de situações intermediarias dentro desses três extremos (GRIME, 1977; 2001; CERABOLINI et al., 2010; PIERCE et al., 2013).

Plantas competidoras (C) estão adaptadas a ambientes com variações espaciais na disponibilidade de recursos via baixas taxas metabólicas e conservação de recursos (que inclui a produção de tecidos bem protegidos contra herbívoros e patógenos e duráveis) (GRIME, 2001). As plantas competidoras tendem a ser substituídas por espécies tolerantes ao estresse em ambientes sob estresse ambiental permanente (visto que se espera que uma estratégia de aquisição contínua de recursos tenha baixo valor adaptativo nesses ambientes). Os diferentes mecanismos de tolerância variam de acordo com o tipo de estresse, o que pode explicar a elevada diversidade estratégias em plantas S (GRIME, 2001). Uma das principais formas de estresse que determina a dominância de plantas tolerantes decorre do estresse nutricional do solo (e.g., solos inférteis ou ácidos) (GRIME, 2001). Essas situações ambientais favorecem ciclos de vida longos, com conservação de recursos, relacionados a órgãos duráveis e adaptações ecofisiológicas para otimização no uso de recursos. Finalmente, plantas ruderais (R) compreendem espécies com ciclos de vida curtos, com capacidade de rápida produção de biomassa, tendo como principal demanda conflitante a reprodução e sobrevivência (GRIME, 1977; 2001). Essa estratégia e típica de herbáceas que são favorecidas em ambientes com distúrbios frequentes (GRIME, 2001).

Baseado nessas características básicas, Grime (2001) sugere que plantas R e S correspondem aos extremos opostos das estratégias r e K (PIANKA, 1970), respectivamente, enquanto espécies C abrange posições intermediárias. Ainda, as demandas conflitantes observadas em escala global segundo o espectro global de forma e função das plantas são explicadas pela teoria CSR, constituindo os principais componentes das estratégias CSR (PIERCE et al., 2012; 2013; 2017; REICH, 2014; DÍAZ et al., 2016). Neste sentido, plantas R e S representam dois extremos de conservação e aquisição do espectro econômico foliar, respectivamente (WRIGHT et al., 2004; CERABOLINI et al., 2010), enquanto um eixo ortogonal relacionado tamanho das folhas apresenta valores intermediários criando esse espaço triangular predito pela teoria CSR (GRIME et al., 1997; CERABOLINI et al., 2010; PIERCE et al., 2013) (Figura 1a).

O esquema da Figura 1a apresenta a relação entre o padrão global do espectro foliar de forma e função adaptado de Pierce et al. (2013). Assim, é possível evidenciar que plantas competidoras tendem a ser plantas com elevado crescimento vegetativo, folhas grandes e um espectro econômico intermediário; ao passo que plantas ruderais e tolerantes ao estresse tendem a ser menores, sendo as ruderais com economia foliar aquisitiva, evidente pela elevada área foliar específica; enquanto as espécies tolerantes ao estresse conservam recursos, vide o elevado conteúdo de massa seca (Figura 1a).

Dentro dessas premissas, Grime (1977; 1985) previu a distribuição das plantas (e líquens) ao longo desse espaço triangular (Figura 1b). Arvores e arbustos são esperadas para variar ao longo de estratégias competitivas e de tolerância ao estresse, ao mesmo tempo que herbáceas e samambaias estariam distribuídas ao longo de todo o triangulo, evitando os extremos de estratégias (GRIME, 1977; 1985; CERABOLINI et al., 2010; Figura 1b).

Especificamente para samambaias, a maioria das espécies apresentam um caráter perene, associada um crescimento lento, com baixas taxas fisiológicas, baixa capacidade fotossintética quando comparado as angiospermas (PAGE, 2002; TOSENS et al., 2016). Ainda, samambaias possuem uma elevada tolerância a ambientes com baixa disponibilidade de nutrientes, ácidos ou muitas vezes tóxicos para outras plantas (PAGE, 2002). Dada essas características, Grime previu que as samambaias estariam dispostas ao longo de estratégias competitivas e tolerantes ao estresse, sendo um dos fatores que limitaram a dominância dessas plantas no sub-bosque (GRIME, 1985; Figura 1b).

Liquens e briófitas são esperados para apresentar distribuições similares na base do triangulo indicando uma baixa capacidade competitiva, mais relacionados com estratégias ruderais e tolerantes ao estresse (GRIME, 1985; Figura 1b), diferindo apenas pela posição mais próxima de estratégias de tolerância ao estresse por parte dos liquens.

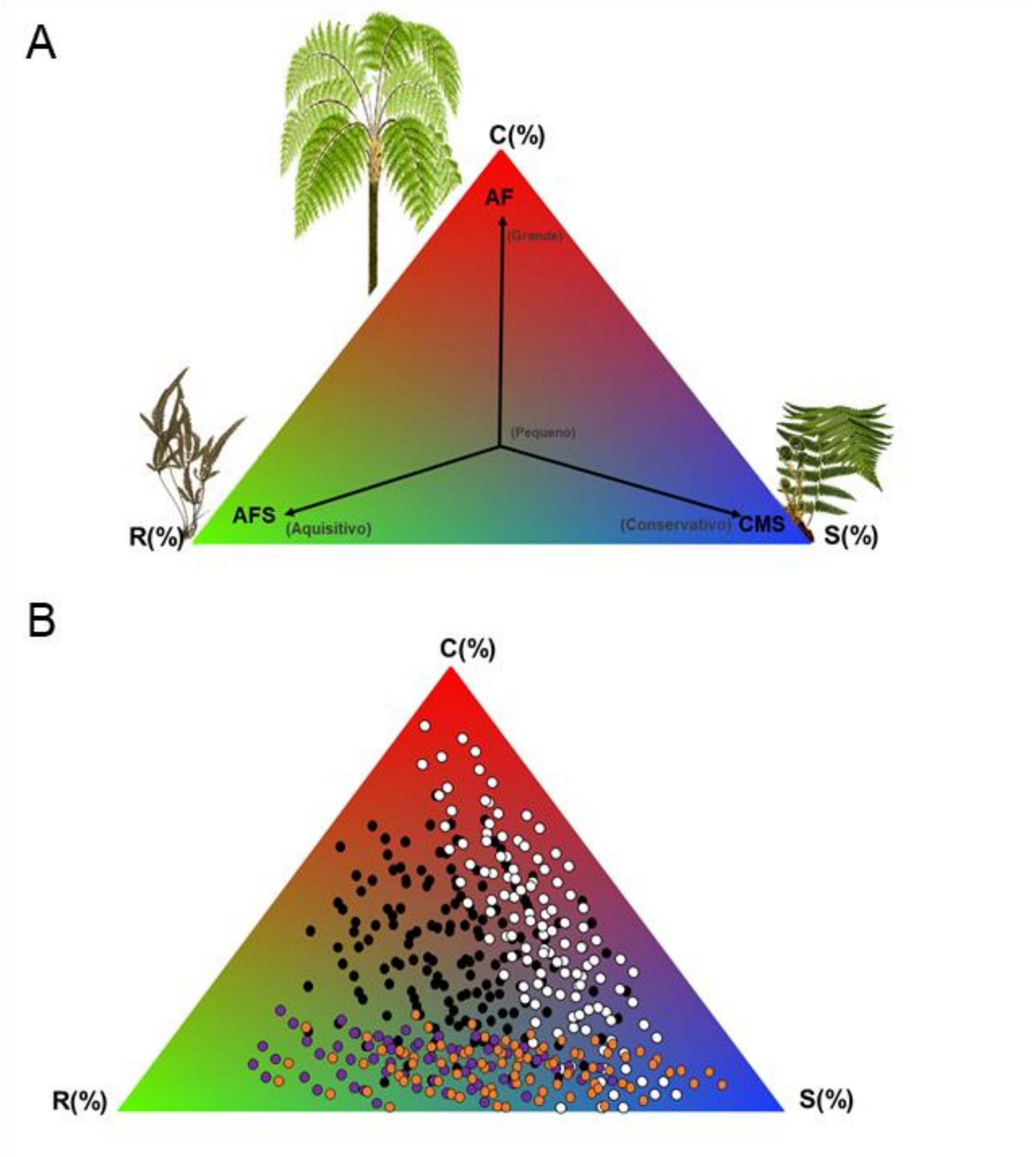


Figura 1: Esquema teórico das Estratégias CSR propostas por Grime indicando: (A) as relações entre o espectro global de forma e função das plantas e as estratégias CSR como (CERABOLINI et al., 2010; Pierce et al. 2013) e (B) a distribuição esperada das plantas de acordo com a forma de vida (Adaptado de GRIME, 1985). C: competitiva; S: tolerante ao estresse; R: ruderal; AF: área foliar: CMS: conteúdo de massa seca; AFS: área foliar específica.● : Herbáceas perenes e samambaias; ○ : árvores e arbustos; 🟠 : briófitas;🟣 : líquens.

Em síntese, a teoria CSR apresenta diversas vantagens como teoria unificadora para entender estratégias ecológicas, pois: 1. corrobora observações evidências globais a respeito da importância de demandas conflitantes em relação ao tamanho e espectro econômico dos atributos funcionais; 2. apresenta um link direto e intuitivo com as condições ambientais onde as estratégias emergem; 3. Apresenta um aporte teórico robusto; 4. Consiste num método simples, realístico e facilmente reprodutível ao redor do globo que pode ser aplicado ao longo de diferentes escalas ecológicas espaciais, temporais e de acordo com a complexidade biológica (i.e., de espécies à ecossistemas); 5. Nenhuma teoria ecológica atual é capaz de responder simultaneamente os espectros globais de forma e função (PIERCE et al., 2013; 2017).

Dada essas vantagem, o esquema CSR tem sido amplamente utilizado em diferentes escalas espaciais e contextos, seja para intender os padrões de dominância de espécies (e.g., ROSADO; MATOS, 2017); para identificar as estratégias ecológicas filtradas ao longo de seres sucessionais (e.g., PRÉVOSTO et al., 2011; CACCIANIGA et al., 2016; CHAI et al., 2016); bem como para investigar como os gradientes ambientais selecionam as estratégias ecológicas (e.g., NEGREIROS et al., 2014). Além disso, as estratégias CSR podem ser escalonadas para a comunidade em escala local de modo a sumarizar a assinatura funcional das comunidades para uma comparação de situações contrastantes, regras de montagem, bem como a influência das estratégias ecológicas na resistência e resiliência dos ecossistemas (e.g., HODGSON et al., 1999; CACCIANIGA et al., 2006; SCHMIDT et al. 2017).

A fim de facilitar e difundir o uso das estratégias CSR ao redor do globo, Pierce et al. (2017) propuseram a tabela ‘StrateFy’, uma ferramenta para detectar as estratégias CSR para qualquer forma de vida, em qualquer ambiente. O protocolo para o cálculo das estratégias CSR segundo o ‘StrateFy’ é calibrado globalmente e pode ser mensurado para arvores ou pequenas ervas, a partir de atributos de fácil mensuração (“soft traits”) e elevada relevância (WRIGHT et al., 2004; PIERCE et al., 2013; 2017).

Apesar da acurácia das estratégias ecológicas em identificar o impacto dos atributos funcionais no fitness e sobrevivência dos indivíduos, bem como possibilitar um link direto entre ecológica e seleção natural usando os espectros de tamanho e de economia foliar (CERABOLINI et al., 2010; PIERCE et al., 2012; CORNELISSEN; CORNWELL, 2014; DÍAZ et al., 2016), esses padrões estão calibrados a partir de uma escala global, de modo que dependendo do contexto em que as estratégias são aplicadas, essas demandas conflitantes básicas podem não ser evidenciadas, havendo uma sobreposição de estratégias ou o surgimento de características não suportadas pelo modelo (e.g., plantas grandes com um elevado conteúdo de massa seca, o que inviabilizaria o uso das estratégias CSR nesse contexto (PIERCE et al., 2017).

Desde modo, a utilização do método CSR via ‘StrateFy’ deve ser aplicado em diferentes contextos ecológicos, com diferentes grupos a fim de testar sua aplicabilidade, generalidade, identificar suas limitações e idiossincrasias (PIERCE et al., 2013).

2.5 ESCALONANDO ATRIBUTOS FUNCIONAIS PARA AS COMUNIDADES

Os avanços no desenvolvimento de estratégias ecológicas foram concomitantes ao avanço na utilização de abordagens funcionais para entender regras de montagem e outros processos ao nível de comunidade (ACKERLY; CORNWELL, 2007; LAURETO; CIANCIARUSO; SAMIA, 2015). Adicionalmente, estudos tem destacado a importância de atributos das espécies no funcionamento do ecossistema (DÍAZ; CABIDO, 2001).

De fato, as espécies podem ser ecologicamente entendidas como um conjunto de indivíduos que apresentam uma série de atributos que afetam a forma como esses indivíduos estão distribuídos nos ambientes, como se comportam frente as mudanças ambientais, bem como a forma como eles interagem entre si (MCGILL et al., 2006).

Essa abordagem acabou levando a uma remontagem das comunidades de um ponto de vista funcional (FUKAMI et al., 2005; MCGILL et al., 2006). Apesar da importância de abordagens taxonômicas para entender regras de montagem e outros processos, uma abordagem funcional pode ser mais significativa do que abordagens unicamente baseadas na riqueza e composição de espécies, devido a sua capacidade de generalidade e previsibilidade (MCGILL et al., 2006).

2.5.1 Métricas funcionais ao nível comunitário e suas aplicabilidades

Atendendo a demanda crescente, bem como visando tornar as abordagens funcionais mais robustas, diversas métricas foram desenvolvidas para mensurar e avaliar as variações individuais ou em conjunto dos atributos funcionais nas comunidades, por meio da diversidade funcional (MOUCHET et al., 2010). Apesar do termo ser empregado de forma genérica, primeiramente a diversidade funcional (DF) pode ser entendida como a medida dos componentes da biodiversidade que influenciam o funcionamento de um ecossistema (TILMAN, 2001). Esse conceito inclui a diversidade de atributos que representam a diversidade de nichos ou funções (MCGILL et al., 2006; PETCHEY; GASTON, 2006). A DF vem sendo amplamente utilizada para entender regras de montagem, o papel das espécies no funcionamento do ecossistema, bem como, como a biodiversidade responde a estreses ambientais e perturbações de origem natural ou antrópica (CADOTTE et al., 2009; FLYNN et al., 2011).

A DF das comunidades pode ser acessada a partir de métricas que quantificam a tendência central, dispersão, e distribuição de determinados atributos, ou de forma conjunta a partir de índices de diversidade funcional (DÍAZ et al., 2007; MOUCHET et al., 2010). A média ponderada da comunidade (CWM, do inglês community-weighted mean) é uma propriedade funcional recorrente nos estudos funcionais (e.g., DÍAZ et al., 2007; DE BELLO et al., 2013; WIDENFALK, 2015; CARREÑO-ROCABADO et al., 2016; SCHELLENBERGER COSTA et al., 2017). O CWM calcula a média de um dado atributo, ponderando a abundância das espécies na comunidade. A ideia por trás do CWM é de que diferentes espécies, especificamente as abundantes, contribuem de forma desproporcional para a funcionalidade do ecossistema ("mass ratio hyphotesis"; GRIME, 1998). Normalmente, CWM é utilizado em conjunto com medidas de dispersão dos atributos funcionas, como o desvio padrão, coeficiente de variação, curtose e assimetria (CARREÑO-ROCABADO et al., 2016).

Apesar de estudos recentes criticaram o uso do CWM, essa métrica tem sido amplamente difundida em estudos funcionais sob diferentes perspectivas, como para avaliar regras de montagem ao longo de gradientes ambientais (ACKERLY; CORNWELL, 2007; LEBRIJA-TREJOS et al., 2010), para avaliar o efeito da diversidade funcional no funcionamento do ecossistema (DÍAZ; CABIDO, 2001; LAVOREL et al., 2011), ou para avaliar o efeito das ações antrópicas sobre o funcionamento do ecossistema (CARREÑO-ROCABADO et al., 2016).

Embora a análise individual dos atributos funcionais seja uma ferramenta eficiente para identificar respostas das comunidades aos gradientes ambientais, bem como para inferir processos ecossistêmicos (BUTTERFIELD; SUDING, 2013), a utilização de índices "mult-trait" (i.e., que avaliam diversos atributos ao mesmo tempo) tem sido usados para representar a multidimensionalidade do nicho (VILLEGER et al., 2008).

A DF pode ser obtida a partir de diferentes índices (MOUCHET et al., 2010). Mouchet e colaboradores (2010) realizaram uma revisão sobre o uso dos índices de diversidade funcional, como são calculados o quão relacionados eles são entre si e suas principais propriedades para predizer regras de montagem, gradientes ambientais e perturbações antrópicas. Ainda que o intuído deste estudo não seja definir cada métrica, é importante entender as propriedades básicas das principais mensurações relacionadas à DF. Mason et al. (2005) identificaram três componentes básicos da DF (i.e., riqueza funcional, equabilidade funcional e divergência funcional) que são complementares, nãos ao relacionados entre si e quantificam diferentes aspectos da DF (Mason et al., 2005; MOUCHET et al., 2010).

A riqueza funcional indica o espaço funcional ocupado pelas espécies na comunidade, a equabilidade funcional indica o quão equável é a distribuição das abundâncias das espécies no espaço funcional, enquanto a divergência funcional corresponde a dispersão das espécies ao longo do espaço multivariado dos atributos, ponderado pelas abundâncias das mesmas

(MOUCHET et al., 2010). Ainda, índices que relatam essas facetas da diversidade funcional como riqueza funcional (Fric), a entropia quadrática de Rao (Q; mede tanto riqueza quanto divergência funcional; MASON et al., 2013), a equabilidade funcional (Feve) e a divergência funcional (Fdiv) são bons indicadores de regras de montagem (MOUCHET et al., 2010)

Especificamente para a riqueza funcional, estudos tem demonstrado o impacto desta faceta e seus índices explanatórios sobre o funcionamento do ecossistema (e.g., CORNWELL; ACKERLY, 2009; DE BELLO et al., 2010; ROSCHER et al., 2012; BUTTERFIELD; SUDING, 2013). A riqueza funcional, principalmente quando associada ao funcionamento do ecossistema, traz à tona uma discussão sobre o papel da redundância funcional. A redundância funcional indica o quão similares são as espécies em relação aos seus papéis no ecossistema (LAWTON; BROWN, 1993) e tem implicações diretas sobre o impacto da perda de espécies no funcionamento do ecossistema (PETCHEY et al., 2007) e na conservação da biodiversidade (ROSENFELD, 2002).

É importante ressaltar que os índices descritos acima refletem o componente alpha da diversidade funciona. Semelhantemente a faceta taxonômica (e demais facetas da biodiversidade), a estrutura funcional das comunidades também pode ser particionada em seus componentes alpha, beta e gama. Especificamente a diversidade beta funcional (i.e., diferenças funcionais entre as comunidades) tem sido considerada uma faceta chave na identificação da contribuição relativa de gradientes ambientais ao longo de diferentes escalas espaciais (PAVOINE; BONSALL, 2011; SWENSON et al., 2011; MÜNKEMÜLLER et al., 2012; VILLEGER et al., 2013), isto porque a diversidade beta pode evidenciar o caráter dinâmico da biodiversidade (SOININEN et al., 2018).

Atualmente, diferentes abordagens têm sido utilizadas para analisar a diversidade beta funcional (VILLEGER et al., 2013) e as diferentes métricas podem envolver analises de dissimilaridade, baseada na composição de traços (ANDERSON et al., 2006; SWENSON et al., 2011), avaliar a sobreposição das comunidades num espaço funcional multidimensional (VILLÉGER et al., 2011), ou estimar a diversidade beta funcional a partir de índices baseados na entropia funcional, via matrizes de distancia funcional ponderadas pela abundancia das espécies (RICOTTA; SZEIDL, 2009; MARCON; HÉRAULT, 2015). Especificamente os índices derivados de entropia, estes tem sido difundidos devido sua fácil conversão em diversidade verdadeira da perspectiva dos números de Hill, que podem facilmente padronizar as diferentes facetas (taxonômica, funcional, filogenética) ao longo dos diferentes componentes (alpha, beta e gama) (CHAO et al., 2014; MARCON; HÉRAULT, 2015).

Finalmente, uma nova geração de métodos tem tentado incorporar o papel da estocasticidade nos índices funcionais (e filogenéticos) amplamente difundidos (MASON et al., 2013; BOTTA-DUKÁT, 2018). Um dos principais métodos é o SES (GOTELLI; MCCABE, 2002), do inglês “standardized effect size”, que analisa os índices, neste caso de diversidade funciona, ponderando o efeito do caso a partir de comparações dos valores reais com os valores observados a partir de modelos nulos (MASON et al., 2013; BOTTA-DUKÁT, 2018).

2.6 RELAÇÕES ENTRE A DIVERSIDADE FUNCIONAL E A DIVERSIDADE TAXONÔMICA

Entender os processos envolvidos na montagem da estrutura funcional da comunidade, bem como compreender as relações entre a biodiversidade e o funcionamento do ecossistema, emerge como uma importante questão dentro da ecologia, sobretudo no atual cenário de mudanças climáticas e degradação de habitats devido às atividades antrópicas (DÍAZ et al., 2007). O efeito mais visível desses processos é a perda da biodiversidade e uma vez que tal processo é irreversível, há uma preocupação sobre como a perda de espécies pode afetar o funcionamento do ecossistema.

Uma forma de avaliar essa questão é através da DF, que quando combinado com métodos complementares (e.g., diversidade taxonômica) pode ajudar na compreensão de como a biodiversidade interage com os processos ecossistêmicos e subsidiar medidas mais eficazes de conservação (DÍAZ; CABIDO, 2001; ROSENFELD, 2002; MOUCHET et al., 2010). A relação entre a DF e a diversidade de espécies pode ser expressa de três maneiras: (I) através de uma função linear, neste caso, um aumento da riqueza específica resulta num aumento da riqueza de atributos da comunidade; (II) pode resultar numa função não linear (i. e. assintótica), convergindo num patamar; (III) ou simplesmente serem variáveis independentes (MOKANY et al., 2008).

Na primeira situação, diz-se que a comunidade apresenta baixa redundância funcional, ou seja, a perda de espécies influencia negativamente o funcionamento do ecossistema. Já nas duas últimas situações, diz-se que a comunidade apresenta elevada redundância funcional, neste caso, a comunidade apresenta um conjunto de espécies que contribuem de forma semelhante para uma dada função ecológica. A redundância funcional tende a conferir uma maior resiliência aos ecossistemas, uma vez que, em situações de perda local de espécies, essa perda pode ser compensada pela presença de outra espécie funcionalmente semelhante, i.e., com características funcionais semelhantes, mas com respostas funcionais diferentes (CADOTTE, 2001; FLYNN et al., 2009).

Comunidades com elevada riqueza específica tendem a apresentar uma maior diversidade funcional e geralmente uma baixa redundância funcional (FLYNN et al., 2009; CADOTTE, 2011). Entretanto, assembleias ricas em espécies podem conter uma maior proporção de espécies funcionalmente redundantes (e, portanto, semelhantes). Por outro lado, assembleias pobres em espécies podem ser mais prevalentes (YACHI; LOREAU, 2007).

Essas diferentes predições básicas foram evidenciadas em estudos prévios (e.g., DÍAZ; CABIDO, 2001; MAYFIELD et al., 2010), sabe-se que essas relações são contexto-dependentes (DE BELLO et al., 2006; CADOTTE et al., 2011), uma vez que diferentes facetas da biodiversidade podem variar de forma diferente (DE BELLO et al., 2006), e a maioria dos ecossistemas apresentam informações escarças (NAEEM, 2002).

Para analisar de forma mais acurada as relações entre a diversidade de espécies e a DF, bem como sua relação com o funcionamento do ecossistema e com as características dos habitats, é importante considerar todos os componentes da DF para identificação de como essa relação é expressa ao longo de diferentes componentes e qual melhor representa essas relações (MOUCHET et al., 2010).

2.7 A FLORESTA ATLANTICA NO NORDESTE DO BRASIL (FAN)

A Floresta Atlântica brasileira representa um dos *hotsposts* mundiais para a conservação da biodiversidade devido a intensa fragmentação desses ambientes que apresenta apenas 12% de sua cobertura natural, considerando áreas em regeneração e degradadas (MYERS et al., 2000; RIBEIRO et al., 2011). A fragmentação desse ecossistema teve início no processo de colonização ao longo de toda costa do País (TABARELLI et al., 2006). No Nordeste, essa degradação foi acentuada pelos ciclos econômicos desenvolvidos na região (monocultura de cana-de-açúcar) que persistem atualmente (TABARELLI et al., 2006). Deste modo, a Floresta Atlântica no Nordeste do Brasil (FAN) compreende remanescentes florestais em sua maioria pequenos (i.e., ≤ 50ha), isolados e circundados por uma matriz de baixa complexidade estrutural (e.g., monoculturas e áreas de pastos) ou áreas não-florestadas (TABARELLI et al., 2006; RIBEIRO et al., 2009).

Estudos anteriores demonstraram que as espécies remanescentes na FAN são afetadas pelos efeitos de borda e estão susceptíveis à homogeneização biótica da vegetação (e.g., OLIVEIRA et al. 2004; LÔBO et al. 2011; SILVA et al. 2011). Embora esses estudos tenham trazido importantes contribuições para subsidiar medidas de conservação para a FAN, eles foram focados em sua maioria no componente taxonômico da vegetação, e atualmente uma análise integrada entre as diferentes facetas da biodiversidade deve ser incentivada (MCGILL et al., 2006; CARVALHO et al., 2019). Sobretudo, estudos que incorporem dados funcionais (atributos funcionais relacionados com diferentes trade-offs), devem ser estimulados para uma análise mais detalhada sobre os padrões e processos estruturando a biodiversidade (FUKAMI et al., 2005; VILLÉGER et al., 2012). Ainda, estudos funcionais surgem como uma alternativa viável para entender os processos moldando a distribuição das espécies ao longo dos gradientes ambientais nos remanescentes florestais, visando identificar a vulnerabilidade dos ecossistemas e espécies, bem como prever os impactos das mudanças climáticas sobre esses ecossistemas, de modo a propor estratégias de conservação mais efetivas (MCGILL et al., 2006; DÍAZ et al., 2007; KRAFT et al. 2008; REISSS et al., 2009).

Estudos funcionais da vegetação da FAN tem indicado que a diversidade funcional de árvores pode ser reduzida em fragmentos devido ao efeito de borda gerando padrões convergentes, (GIRÃO et al., 2007), que podem levar à alterações nos atributos das espécies mas não necessariamente na diversidade funcional (MAGNAGO et al., 2014), ou levar a uma drástica erosão funcional (SANTOS et al., 2008). Contudo, além de divergentes, os estudos têm focado em arvores, enquanto outras formas de vida têm sido pouco estudadas (e.g., lianas, ervas, epífitas).

O estudo da estrutura funcional da biodiversidade da FAN levanta um importante dilema, visto que estudar toda biodiversidade seria um processo longo, a busca por grupos-resposta (i.e., espécies que podem ser agrupadas de acordo com a forma como respondem ao ambiente) (LAVOREL; GARNIER, 2002). Ainda, uma vez que a Floresta Atlântica é um dos biomas mais vulneráveis às mudanças climáticas (SCARANO; CEOTTO, 2015), é importante que esses grupos-resposta possam ser utilizados como substitutivos para toda a vegetação (“surrogate groups”).

2.8 SAMAMBAIAS NA FAN

As samambaias são um grupo de plantas vasculares que representam um componente abundante da flora, estando distribuídas ao longo de vários ecossistemas, especialmente no sub-bosque das florestas tropicais (SHARPE et al., 2010), podendo representar até 15% da biomassa total (HARMS et al., 2004). Amplamente distribuídas nos trópicos, no Brasil as samambaias ocorrem majoritariamente na Floresta Amazônica e Atlântica (LABIAK; PRADO, 1998). As samambaias têm sido extensivamente estudadas na Amazônia (e.g., TUOMISTO; POULSEN, 1996; LANDEIRO et al., 2012; ZUQUIM et al., 2014), enquanto os estudos na Floresta

Atlântica tem focado em estudos florísticos (e.g., SANTIAGO et al., 2014; PEREIRA et al., 2011; COSTA et al., 2013), populacionais (e.g., FARIAS et al., 2011; SILVA et al., 2019), bem como no impacto da fragmentação e dos efeitos de borda (SILVA et al. 2011; 2014), sendo as abordagens funcionais escassas.

2.8.1 Ecologia de samambaias numa perspectiva funcional

A despeito de sua representatividade, as abordagens funcionais na comunidade de samambaias ainda estão avançando de forma lenta. Pioneiramente, Grime (1985) analisou as estratégias ecológicas responsáveis pela contribuição da flora local. O autor constatou que as samambaias da flora local estavam distribuídas ao longo de estratégias competitivas e tolerantes ao estresse, e especula que algumas características como o crescimento lento e a intolerância à distúrbios seriam fatores responsáveis pela pouca contribuição de samambaias para a floral loca. Embora o estudo tenha sido importante para introduzir as samambaias dentro do contexto CSR, nenhum estudo até nosso conhecimento replicou essa abordagem para identificar padrões gerais para as samambaias.

Adicionalmente, atualmente sabemos que as samambaias podem habitar uma ampla faixa de variações climáticas, substratos e de níveis luminosidade, tanto em ambientes dominados por angiospermas ou em locais onde muitas não conseguem sobreviver (PAGE, 2002), apresentando diversos atributos funcionais que potencializam a capacidade invasora dessas plantas (JONES et al., 2019). Ainda, diversas espécies de samambaias podem tolerar distúrbios ambientas, sendo em alguns casos, favorecidas por eles, como no caso de espécies que proliferam em bordas florestais (e.g., SILVA et al., 2011).

Alguns estudos utilizando abordagens funcionais trouxeram importantes informações em relação a regras de montagem e seleção de atributos a partir dos ambientes (e.g., KLUGE; KESSLER, 2007; 2011; ROCHA-URIARTT et al., 2016; CARVAJAL-HERNÁNDEZ et al., 2018). De fato, Kluge e Kessler (2007) observaram um padrão consiste na variação de atributos morfológicos de samambaias ao longo de um gradiente de altitude. Que também pode afetar a diversidade funcional, sem uma relação direta com grau de degradação ao longo desse gradiente (CARVAJAL-HERNÁNDEZ et al., 2018). Rocha-Uriartt et al. (2016) observaram que a estrutura das florestas riparias podem afetar significativamente a diversidade funcional de samambaias epífitas, indicando que a conservação desses ambientes é crucial para a manutenção da diversidade funcional de samambaias epífitas.

Ainda, Kluge e Kessler (2011) ao analisar a montagem da comunidade de samambaias em um gradiente de altitude, considerando a diversidade filogenética, diversidade de atributos e o nicho, observaram que sob condições ambientais extremas (seca elevada sob baixas altitudes e geada em altitudes mais elevadas), espécies epífitas tendem a agrupar-se de acordo com características dos atributos, o que sugere uma filtragem ambiental. Contudo, em condições ambientais moderadas (elevações intermediárias no gradiente de altitude), houve uma elevada diferenciação, presumivelmente causada pela competição interespecífica e diferenciações nos atributos entre espécies aparentadas. Esse estudo denotou a contexto-dependência na regra de montagem da comunidade de samambaias, previamente especulada na teoria ecológica (e.g., MASON et al., 2007), como corroborou a premissa de convergência e divergência, mesmo num contexto de filtragem ambiental (DE BELLO et al., 2009).

Embora esses estudos prévios tenham trazido contribuições substanciais para o corpo teórico envolvendo padrões funcionais em samambaias, eles foram baseados em atributos categóricos específicos, que embora significativos, falham em não possibilitar uma comparação com outras herbáceas em relação a regras de montagem e seleção de atributos a partir dos ambientes falharam ao não utilizar atributos amplamente utilizados para possibilitar uma comparação direta com outras herbáceas. Curiosamente, estudos demonstraram que as samambaias estão sob as mesmas demandas conflitantes previstas para angiospermas (e.g., KARST; LECHOWICZ, 2007; REICH, 2014; TOSENS et al., 2016) estando incluídas no espectro global de forma e função das plantas (DÍAZ et al., 2016).

Apesar disto, poucos estudos utilizaram atributos foliares amplamente utilizados, mesmo os “soft traits”, que podem ser facilmente obtidos. Neste sentido, destaco os de Kessler et al. (2007), que incluíram “soft traits” ao reportarem os padrões de atributos foliares de samambaias em relação a humidade e temperatura; e de Seral et al. (2017), que observaram alterações significativas dos atributos foliares em samambaias saxícolas ibéricas.

Essa escassez de estudos com abordagens funcionais utilizando as premissas das demandas conflitantes, não só contribuem para uma importante lacuna teórica para as samambaias especificamente, como também impacta a síntese de padrões gerais dentro da ecologia de comunidades, bem como da ecologia funcional. Baseado nisso, Bruelheide et al. (2018) destacaram que embora o corpo teórico da ecologia funcional tenha aumentado vertiginosamente nos últimos anos, algumas questões básicas (e.g., como atributos funcionais estão arranjados ao longo de diferentes espécies coexistindo? Como a diversidade funcional se relaciona com outros componentes da biodiversidade e como eles, em conjunto, afetam o funcionamento do ecossistema? Como os fatores ambientais afetam os atributos funcionais?) permanecem em aberto para diversos grupos e diversos sistemas naturais.

Especificamente para samambaias, Zhang et al. (2017) utilizaram uma série de importantes “hard traits” para identificar os processos estruturando comunidades de samambaias ao longo de um gradiente de luminosidade e disponibilidade hídrica, indicando a influência da filtragem ambiental e exclusão de competidores mais fracos nos padrões funcionas. Apesar deste importante achado, o papel dessas plantas como grupos resposta ainda é subestimado, visto que estudos tem demonstrado o papel das samambaias como importantes indicadoras das condições ambientais, especialmente edáficas (e.g., TUOMISTO; POULSEN, 1996; SALOVAARA et al., 2004; ZUQUIM et al., 2014), sendo ainda reconhecidas como importantes grupos substitutivos para florestas mega diversas (LANDEIRO et al., 2012).

Adicionalmente, embora samambaias contribuam com apenas uma pequena fração da biomassa e produtividade no ecossistema (KESSLER et al., 2014), pouco se sabe sobre o papel dessas espécies em outros processos ecossistêmicos, embora estudos destaquem o papel de samambaias arborescentes como engenheiras do ecossistema e reguladoras de interações multitróficas (e.g., MEHLTRETER et al., 2005; FARIAS et al., 2018).

3 FUNCTIONAL TRAITS BUT NOT FUNCTIONAL UNIQUENESS EXPLAIN FERNS NICHE SEGREGATION ALONG LOCAL AND BROAD SCALE ENVIRONMENTAL GRADIENTS

MANUSCRITO A SER SUBMETIDO AO PERIÓDICO FLORA

FUNCTIONAL TRAITS BUT NOT FUNCTIONAL UNIQUENESS EXPLAIN FERNS NICHE SEGREGATION ALONG LOCAL AND BROAD SCALE ENVIRONMENTAL GRADIENTS

Lucas Erickson Nascimento da Costa[1*]; Rafael de Paiva Farias[1,2]; Michael Kessler[3]; Iva Carneiro Leão Barros[1]

[1] Departamento de Botânica, Universidade Federal de Pernambuco. Ave. Professor Moraes Rêgo, 50560-901, Recife, PE, Brazil.

[2] Department of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland.

Corresponding author: lucasbiologicasufpe@hotmail.com

lucasbiologicasufpe@hotmail.com

Telephone number: +55 81 2126 8348

Fax number: +55 81 2126 8946

Highlights

- **Ferns exhibited strong niche segregation towards local and broad-scale environmental variables**
- **Species realized niche position was related to shifts in functional traits**
- **Both response and effect traits explained niche segregation patterns**

Abstract

Plant ecological niche and functional diversity are powerful approaches in the understanding of plant distribution, coexistence mechanisms, and ecosystem functioning. The ecological niches in plants are typically determined from the broadest scales (e.g. rainfall and temperature) to the fine ones (edaphic conditions). In this study, using ferns, an ecological indicator group, abundant and functionally important in the tropical understory, we tested species niche segregation based on local and broad-scale environmental gradients and determined the role of functional traits and functional uniqueness on observed patterns. We assessed the fern diversity in three tropical forests in Northeast Brazil (Atlantic Forest) and obtained a robust set of environmental data at local (e.g. edaphic) and broad scales (bioclimatic), as well as ten functional traits from rhizome and leaves. We evidenced strong niche segregation among fern species, although niche breadths overlapped. Fern's niche position was affected by species traits, especially, specific leaf area, leaf nitrogen concentrations, rhizome type and leaf division. Our results denoted the importance of hole plant traits on niche segregation patterns. Further, both response and effect traits responded to different multidimensional niche axes indicating that different traits might be selected according to the niche axis under observation.

Keywords: abiotic niche, aluminum, Atlantic Forest, ecological specialization, edaphic niche, ecosystem functioning, niche overlap, response-effect trait.

Introduction

Ecological niches *lato sensu* assumes a central role in ecology and evolution, and their extensions permeate in multi approaches, such as physiological tolerances, variations in diversity (taxonomic, functional and phylogenetic) and specific intra-inter interactions (Chase and Leibold 2003). Species niche can be differentiated in fundamental and realized niches (Hutchinson 1957). While the fundamental niche describes the physiological competence of the species, the realized niche comprises the environmental species were the species is occurring (Hutchinson 1957; Chase and Leibold 2003). The niches are determined from the broader to the fine scales (Harmáčková et al. 2019). From broad scales, abiotic conditions and historical effects affect species distribution (Devictor et al. 2010; Harmáčková et al. 2019), while niche partitioning allows species coexistence at fine scales (Harmáčková et al. 2019).

The understanding of species niche brings important contributions to the knowledge of mechanisms allowing species coexistence and to estimate the future distribution of species in the scenario of climate change (Letten et al. 2015; Violle and Jiang 2009). Due to the multidimensionality of the niche, several factors should be considered when the species niche is analyzed (Clark et al., 2007; Violle and Jiang 2009). Information about species climatic niches is substantially more available (Peterson et al. 2011). However, Velazco et al. (2017) draw attention that climate-only ecological niche models are conceptually weak, and their respective spatial predictions may be unreliable, especially for species with edaphic requirements (Zuquim et al. 2019).

Therefore, niche approaches can be coupled with functional traits, since functional traits might be more easily linked to environmental conditions, rather than species identity (McGill et al. 2006; Violle and Jian 2009; Kearney et al. 2010). Both response (i.e., vary in response to environmental conditions; Lavorel and Garnier 2002) and effect traits (i.e., related to the effect of the species on the environment) can be considered in niche analysis, since

Yet, despite the importance of functional traits on community assembly and ecosystem functioning (Lavorel and Garnier 2002; McGill et al. 2006), few studies addressed the role of functional traits on species niche segregation, especially in species-rich ecosystems, as the tropical forest (Kraft et al. 2008; Sterck et al. 2011; Costa-Saura et al. 2016).

Here, our model system is tropical ferns, seedless vascular plants, with high dispersal potential, cosmopolitan distribution (Page 2002), but that exhibits a stronger response to environmental gradients at both large (Kluge and Kessler 2007), and fine-scale, especially from edaphic conditions (Zuquim et al. 2014). This plant group is abundant in forest understory (Sharpe et al. 2010), typically occurring along with specific habitat and playing a wide range of interactions with lichens, herbivorous or epiphytes plants (Mehltreter et al. 2005; Santos et al. 2018). In addition, fern biomass may be an important component of litter in tropical forests (Silva et al. 2019). Using ferns, we intended to analyze niche segregation patterns in a trait-based perspective. We look at the fine-scale and all the advantages of this approach for the prediction of changes in flora can be extended to our geographic space, the Atlantic Forest in the eastern part of Northeast Brazil, an area historically and intensely degraded, which remains with a few fragments, small and mostly without effective management actions (see Ribeiro et al. 2009). We thus tested the fern niche segregation based on local and broad-scale environmental gradients and determined the role of functional traits observed pattern. Additionally, we analyzed whether more functional unique species (i.e., functionally apart from other species) would be segregated along similar niches. Regarding previous studies about the role of the environment on functional traits (e.g., Weiher and Keddy 1995; Violle and Jiang 2009), we addressed the hypothesis that ferns niche is trait-based determined. Thus, we expect that species niche segregation will be coupled with shifts in functional traits.

Methods

Study area, field and herbarium procedures

Our study was performed in three Atlantic forest areas located in Pernambuco state, northeastern Brazil. Study sites are classified as Lowland Forest (Rio Formoso district: 8º34'S; 35º7'W, 100 m a.s.l.) and Submontane Forest (Bonito district: 8°29´S; 35°41’W; São Vicente Férrer district: 7°35’S; 35°29’S, between 450-550 m a.s.l.). The climate is hot and humid with a mean annual temperature of 22–27ºC and an annual rainfall of 1200–1800 mm.

We established 22 plots (10 × 20 m) with a minimum distance of 100 m apart from each other. In each plot, we counted fern species and collected approximately 12 undamaged full-expanded mature leaves from different individuals per species. Fern species vouchers were deposited at the UFP Herbarium, with names following the International Plant Names Index (IPNI) database.

Plant trait data

We measured a set of ten functional traits (response and effects) from rhizome and leaves. We classified rhizomes in three types: erect/short creeping (1), creeping (2) and tree-like (3), which indicates performance to competition for space and light (Kluge and Kessler 2007). We categorized leaves in three types from lamina dissection: entire (1), once-pinnate, to pinnate-pinnatifid (2), and twice or more pinnate (3), reflecting distinct tolerance to harsh conditions, especially temperature and humidity fluctuations (Kramer et al. 1995; Kluge and Kessler 2007). Moreover, we classified leaves in three types from laminar morphology: monomorphic (1), hemidimorphic (2) and dimorphic (3), an indication of resource demand to reproductive events and spore dispersion (Kramer et al. 1995). Measurements of rhizomes types, lamina dissection and lamina morphology followed the protocols of Kluge and Kessler (2007) and were obtained from consults in the literature. Further, we measured the leaf area (LA), the specific leaf area (SLA) the leaf dry matter content (LDMC), the leaf water content (LWC), leaf phenol concentrations, and the leaf nitrogen (N) and phosphorus (P) concentrations. These traits potentially indicate trade-offs for resource acquisition, stress tolerance and ecosystem functioning (Pérez-Harguindeguy et al. 2013; Díaz et al. 2016). The LA, SLA LDMC and LWC were measured following methods defined by Pérez-Harguindeguy et al. (2013). Leaf N and P concentrations were measured using adapted protocols from Kjeldahl (Bremner and Mulvaney 1982), and Bezerra-Neto and Barreto (2011), respectively. Phenol concentrations were measured according to Amorim et al. (2008), using a spectrophotometer Genesys 10S UVVIS, Thermo Scientific, Waltham, USA, calibrated at a wavelength of 760 nm. Due to logistic questions, no data on N, P and phenol concentrations were measured to only three species (*Alsophila sternbergii*, *Lindsaea falcata* and *Meniscium longifolium*), instead, we obtained them from mean of genus for the formers, and as the mean for the family for the latter.

Local and broad-scale environmental data

We measured in each plot several environmental variables (i.e. local scale; Table A1), as follows: number of trees, the basal area of the trees (proxy to understory luminosity and forest structure), rock coverage (proxy to habitat heterogeneity due to rock outcrops), and a set of edaphic variables (i.e. soil pH, soil contents of Ca, Mg, Al, K, P, and Na, as well as, percentages of sand, silt, and clay). The basal area was calculated following Gama et al. (2007). Rock coverage was measured as the percentage of the plot covered by rocks following the Blaun–Blanket scale (Kent and Coker 1992). Edaphic variables were obtained from surface soil samples (0-20 cm depth) collected in five points of the plot and mixed to a composite sample (500 g). Samples were air-dried, cleaned from roots and detritus, and homogenized. The dataset of edaphic variables was obtained standard methods according to Embrapa (2017). In addition, we calculated the exchangeable bases (EB), the effective cation-exchange capacity (CEC(t)), the base saturation (BS), and Al-saturation (AlS). For more details on methods see Costa et al. (2019).

We used a total of 10 bioclimatic variables (Table A.2) obtained from WORLDCLIM databases (http://www.worldclim.org/bioclim) to each plot in at 1km spatial resolution (Fick and Hijmans 2017), representing environmental data at a broad scale.

Data analysis

We selected the most meaningful environmental variables in both local and broad scales based in Principal Component Analysis - PCA ("princomp" in *factoextra*). We excluded variables with low contribution to PCA axes or weakly correlated (≤0.4). Based on PCA results (Figure A.1-2), the most representative local variables were rock coverage, soil pH and other edaphic variables (i.e. AlS, EB, K, Mg, and sand content). Meanwhile, the most meaningful environmental variables of the broad-scale were the annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, and annual precipitation (Figure A.2).

We calculated the functional uniqueness of the species based on a trait distance matrix (using Gower distance) and community matrix ("uniqueness" *funrar*). Functional uniqueness represents how isolated the species is in the functional space and how changes in abundance change the contribution of species to functional redundancy, similar to functional originality (Mouillot et al. 2013). We used this index to identify the role of the species in the overall functional diversity. We classified species as high and low unique according to the upper (75th) and lower (1st) quartiles of uniqueness considering all sampled species, respectively. Species with intermediate values were classified as medium unique. To test the consistency of possible species groups based in functional unique values, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) using uniqueness and groups (high, medium and low) as factors with 1000 permutations ("adonis" in *vegan*).

Finally, we estimated species realized niche and niche breadths via Outlying Mean Index (OMI) considering local and broad-scale environmental variables ("niche" function in *ade4*). The OMI consists in an analysis that determines the position of the species in niches (realized and breadths), via comparisons between environmental conditions where the species occur related to the overall environmental distance captured in the whole dataset (Dolédec et al. 2000). Species scores on the first two OMI axes were tested as response variables (i.e. niche position) in order to analyze whether species niche was correlated with functional uniqueness (tested with simple correlations). Furthermore, to test the significance of functional traits on species niche, we used species functional traits as explanatory variables in general linear models ("lm" in *lme4*). Data were analyzed using R v.3.3.3 (R Development Core Team 2015), considering a significance level of $p \leq 0.05$.

Results

We sampled 37 fern species distributed among 18 families (Table B.1). The LA exhibited a mean of 84.23 ± 42.39 mm^2, with a coefficient of variation (CV) of 50.3%, the highest between quantitative traits, which was followed by SLA (CV = 33.41%, 234.92± 78.49 mm^2/mg). Leaf P values showed the lowest variation among species (CV = 7.69%; 0.83±0.06 g/kg DW). Most of the species presented erect of short creeping rhizomes (70.6%), once pinnate (51.3%) monomorphic leaves (64.9%). All species traits were summarized in Table B.1.

The functional uniqueness mean was 0.104 ± 0.054, with a high coefficient of variation (52.09%). Ten species were classified as high unique, other ten species as low unique, while the remainder (17 spp.) showed medium values (Table B.1; Figure B.1). Species differed in functional distances when considered the functional uniqueness among groups (high, medium and low uniqueness), but this relation was week (pseudo-F = 2.171; p = 0.043; $R^2 = 0.11$; Table B.2), indicating that high, medium and less unique species do not constitute conspicuous functional groups (i.e., are not similar in terms of functional traits). Instead, they are diffused and overlapped (Figure B.1).

The first two axes from the Outlying Mean Index were meaningful and captured 67.03% of the total variation (Figure 1; Figure A.3). The first axis had an association (i.e. $r \geq 0.4$) with eight of the 11 environmental variables tested, which exhibited a high covariation (Figure A.3). This association was positive only to aluminum saturation (0.66). Conversely, annual temperature (- 90), maximum temperature of warmest month (- 0.69), minimum temperature of coldest month (- 0.90), annual precipitation (- 0.76), soil rock coverage (- 0.70), soil sand (- 0.62), soil pH (- 0.74) and exchangeable bases (- 0.50) had negative associations. The second axis was negative associated with the annual precipitation (- 0.44) and soil sand (- 0.55), and positively with soil contents of Mg (0.75) and K (0.79), as well as soil exchangeable bases.

We identified that fern species were consistently segregated among niches, even though niche breadths overlapped across the two niche gradients (Figure 1). *Neoblechnum brasiliense* and *Pecluma robusta*, for example, exhibited the wide niche breadths in the first axis (Figure 1A). Meanwhile, *Gleichenella pectinata* and *N. brasiliense* exhibited the wide niche breadths in the second axis (Figure 1B). Furthermore, we identified that epiphyte ferns (i.e. *Serpocaulon catharinae*, *Serpocaulon* sp., *Elaphoglossum iguapense,* and *Pecluma robusta*) were weakly associated with AlS (Figure 1A), differentially from those terrestrial ones. Tree ferns (Cyatheaceae) and species of Thelypteridaceae were distributed across the entire gradient (Figure 2), while *Anemia* species represent an example that placed in extremes opposite positions (Figure 4B).

We found no significant correlations between functional uniqueness and both niche axis (1^{st} axes: r = 0.033, p = 0.846; 2^{nd} axis: r = 0.035, p = 0.834). On the other hand, the first niche axis was related to species SLA and N (Table 1), while the second axis was related to rhizome type and leaf laminar division (Table 1).

Discussion

In our study from tropical ferns in forests intensely degraded (Atlantic Forest, Brazil's Northeaster), ferns species exhibits niche segregation when considered local and broad-scale environment, which was mainly explained by shifts towards hole plant traits regarding different niche multidimensional axes.

The lack of associations between functional uniqueness of the species and their degree of isolation along functional space or niche position indicates that the contribution of the species to overall functional diversity is mediated the proportion of species exhibiting a given trait or trait range and not due to trait substitutions (Mouillot et al. 2013). Yet, these results also denoted that high, medium and less unique species do not represent a different functional group (de Bello et al. 2010), according to the set of traits analyzed.

The several environmental variables both local and broad-scale contributing to niche structure in ferns, with high covariation between them, reveals the difficult the interpretation of specific relationships. Like this, we corroborated previous studies that suggested that multiple meaningful factors compounding niche axes are needed (Viole and Jiang 2009; Boulangeat et al. 2012) since plants tend to share similar requirements (Silvertown 2004; Clark et al. 2007;

Boulangeat et al. 2012). Furthermore, we reinforce that variables with low contribution potentially may affect species niche segregation (Westoby et al. 2002).

The niche segregation reported, with considerable overlaps in niche breadths evidenced for some species which differed according to observed niche axis, represents a stronger niche specialization to ferns. Ecological specialization is a key mechanism to allow species coexistence (Chase and Leibold 2003), especially in closely related lineages, such as ferns (Page 2002). In fact, ferns are well-known from responses to edaphic gradients (Zuquim et al. 2014; Costa et al. 2019; Moulatlet et al. 2019), as corroborated in this study at the local scale. On the other hand, a broader niche breadth favors species to occur in large ranges of environmental conditions (Vázquez 2006). Further, some species placed across extreme ranges of niche distribution may indicate niche specialization (Fariñas et al. 2015), explained by changes in mean niche conditions occupied by the species in environmental gradient (Hof et al. 2010).

The local and broad-scale environmental variables covariates that driven niche segregation in ferns have been frequently reported to explain plant diversity, such as is the to temperature (Testo and Watkins 2013), substrates (Tuomisto et al. 2002), pH (Tuomuisto et al. 2002; Moulatlet et al. 2019), and soil sand content (Costa et al. 2005). The segregation of fern species towards edaphic nutrient availability (e.g. soil cation concentrations) was previously reported (e.g. Tuomisto et al. 2002; Zuquim et al. 2014). These consistent patterns highlight the role of these plants as reliable ecological indicators of this edaphic condition (Zuquim et al. 2014; Moulatlet et al. 2019).

The aluminum that driven niche segregation in ferns represents one of the most inhibitors of plant growth (Alleoni et al. 2010), since under acid soils ($pH \leq 5.0$), as reported for most habitats in this study. Typically, ferns can tolerate environments with aluminum saturation, limiting to general seed plants (Schmitt et al. 2017). Furthermore, this tolerance to aluminum saturated habitats is less evidenced in epiphytes than terrestrial species (Schmitt et al. 2017; Moulatlet et al. 2019), as reported in our study. Niche segregation within the genus found in our study also had been reported along with edaphic gradients in Amazon (Tuomisto et al. 1998; Tuomisto 2006), particularly to *Adiantum* and *Polybotrya*. The niche differentiation among closely related species might be widespread among fern lineages. Further, the high niche breadths to some can be explained by the wide distribution species, such as *Neoblechnum* *brasiliense* widely spread (see distribution in Dittrich 2005) across different habitats in the Brazilian Atlantic Forest.

Furthermore, specifically to high unique species, the trait divergence combined with niche segregation), it is resorbable to expect that ferns can keep high contributors to ecosystem functioning towards different environmental conditions, which increases niche complementarity allowing coexistence and might enhancing the contribution of ferns to ecosystem functioning (Loreau and Hector 2001; Cardinale et al. 2007; Cardinale 2011). Although previous studies denoted the importance of redundancy to ecosystem resilience (Walker 1995), these might favor ferns contribution to overall ecosystem function, particularly in conditions where other plants might be limited, such as acid habitats under aluminum saturation (Schmitt et al. 2017).

Ferns niche segregations affected by both response and response/effect functional traits corroborated previous studies (e.g. Thuiller et al. 2004; Vázquez 2006). SLA and N are components of the leaf economic spectrum (Wright et al. 2004) and can be considered, at the same time, effect and response traits. Previous studies demonstrated the effect of edaphic and climate variables on SLA (e.g. Rosbakh et al. 2015; Gong and Gao 2019). Yet, since this trait is related to plant ecosystem properties, as productivity and litter decomposition (Garnier et al. 2004), these results indicate that, under aluminum saturation conditions, ferns productive is reduced and litter decomposition increases, due to nutrient conservation (Westoby et al. 2002; Poorter et al. 2009). Regarding N content, this functional trait has direct effects on photosynthesis (Reich et al. 1995). The opposite response of leaf N in relation to SLA in ferns, indicates that leaf N under aluminum saturated soils are focused on biomass allocation, enhancing leaf longevity (Franco et al. 2005), instead of the metabolic process (Reich et al. 1998).

Rhizome type can reflect the competitive ability of the species (Kluge & Kessler 2007), and especially to our dataset, these results denoted the role of water availability (via increasing precipitation) to tree ferns, which was previously reported (Bystriakova et al. 2011). Our results added another layer to the interpretation of the role of climate niche to tree ferns, by denoting that tree-like rhizome were more associated with climate rather local edaphic conditions. Moreover, laminar dissection can be interpreted to adaptations to harsh environments (Kramer et al., 1995), but this interpretation in our study might be ambiguous. Laminar dissecting increased with nutrient availability, which might be a sign that nutrient availability allows more complex leaf architectures.

CONCLUSION

Our results evidenced the relationship between whole plant functional traits and ferns niche segregation across local and broad-scale environments, despite species contribution to functional diversity, which brings new insights to the role of ferns on ecosystem function in a niche complementarity framework. Curiously, despite the reliability of trait-base approaches in the understanding of species responses, community patterns and ecosystem function (Westoby et al. 2002; Poorter and Bongers 2006), few studies had addressed functional trait-niche responses (Thuiller et al. 2004; Violle and Jiang 2009). Moreover, we argue that both response and effect traits should be analyzed in order to achieve more accurate responses when determined traits are analyzed (Costa-Saura et al. 2016). Previous studies highlighted the importance of predictive models combining local and climatic variables to predict future species distribution, especially for species with edaphic specificities (Zuquim et al. 2019). We argue that these approaches should also include functional traits (Heilmeier 2019) in other to allow more integrative explanations about the distribution of species, of traits, and spatial process in niche dynamic (Chase & Leibold 2003), towards a more comprehensive understanding of the general impacts of climate change on ecosystem functioning. This represents an urgent request to the Brazilian Atlantic Forest, which is one of the top hotspots susceptible to climate change (Béllard et al. 2014).

Acknowledges

We thank the Laboratório de Química do Solo of the Universidade Federal Rural de Pernambuco for supporting soil analysis; To Cucau and Trapiche Mills for logistic support during the fieldwork. The first author thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, National Council for Scientific and Technological Development) to the doctorate scholarship and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) for doctorate international ‘sandwich’ internship (process 88881.189293/2018-01).

Funding: This study was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) under the Finance Code 001.

Author Contributions

LENC, MK, and ICLB conceived the ideas and designed the experiments. LENC and RPF collected the data and conducted the statistical analyses. LENC wrote the first draft of the manuscript. All authors discussed the results and significantly contributed to the writing of the manuscript.

References

Alleoni, L. R., Cambri, M. A., Caires, E. F., & Garbuio, F. J. (2010). Acidity and aluminum speciation as affected by surface liming in tropical no-till soils. Soil Science Society of America Journal, 74(3), 1010-1017.

Amorim, E. L., Nascimento, J. E., Monteiro, J. M., Peixoto Sobrinho, T. J. S., Araújo, T. A., & Albuquerque, U. P. (2008). A simple and accurate procedure for the determination of tannin and flavonoid levels and some applications in ethnobotany and ethnopharmacology. Functional Ecosystems and Communities, 2(1), 88-94.

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., & Courchamp, F. (2014). Vulnerability of biodiversity hotspots to global change. Global Ecology and Biogeography, 23(12), 1376-1386.

Bezerra-Neto, E., Barreto, L. P. (2011) Análises químicas e bioquímicas em plantas. UFRPE, Recife.

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L., & Thuiller, W. (2012). Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. Journal of Biogeography, 39(1), 204-214.

Bremner , J. M., Mulvaney, C. S. (1982). Nitrogen total. In: Page, A. L. (ed) Methods of soil analysis, 2nd edn. Soil Science Society of America, Madison, pp 595–624.

Bystriakova, N., Schneider, H., & Coomes, D. (2011). Evolution of the climatic niche in scaly tree ferns (Cyatheaceae, Polypodiopsida). Botanical Journal of the Linnean Society, 165(1), 1-19.

Cardinale, B. J. (2011). Biodiversity improves water quality through niche partitioning. Nature, 472(7341), 86-89.

Cardinale, B. J., Wright, J. P., Cadotte, M. W., Carroll, I. T., Hector, A., Srivastava, D. S., ... & Weis, J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences, 104(46), 18123-18128.

Chase, J. M., & Leibold, M. A. (2003). Ecological niches: linking classical and contemporary approaches. University of Chicago Press.

Clark, J.S., Dietze, M., Chakraborty, S., Agarwal, P.K., Ibanez, I., LaDeau, S. and Wolosin, M. (2007), Resolving the biodiversity paradox. Ecology Letters, 10: 647-659.

Costa, F. R., Magnusson, W. E., & Luizao, R. C. (2005). Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology, 93(5), 863-878.

Costa, L. E. N., Arnan, X., de Paiva Farias, R., & Barros, I. C. L. (2019). Community responses to fine-scale environmental conditions: Ferns alpha and beta diversity along Brazilian Atlantic forest remnants. Acta Oecologica, 101, 103475.

Costa-Saura, J. M., Martinez-Vilalta, J., Trabucco, A., Spano, D., & Mereu, S. (2016). Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species. Perspectives in Plant Ecology Evolution and Systematics, 21, 23–30.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H., Bardgett, R. D., ... & da Silva, P. M. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. Biodiversity and Conservation, 19(10), 2873-2893.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., ... & Mouquet, N. (2010). Defining and measuring ecological specialization. Journal of Applied Ecology, 47(1), 15-25.

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., ... & Garnier, E. (2016). The global spectrum of plant form and function. Nature, 529(7585), 167-171.

Dittrich, V. A. D. O. (2005). Estudos taxonômicos no gênero Blechnum L.(Pterophyta: Blechnaceae) para as regiões sudeste e sul do Brasil.

Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community analysis: a new method. Ecology, 81(10), 2914-2927.

Empresa Brasileira de Pesquisa Agropecuária [EMBRAPA] (2017) Manual de métodos de análise de solos, 3rd edn. Embrapa CNPS, Rio da Janeiro.

Fariñas, T. H., Bacher, C., Soudant, D., Belin, C., & Barillé, L. (2015). Assessing phytoplankton realized niches using a French national phytoplankton monitoring network. Estuarine, coastal and shelf science, 159, 15-27.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International journal of climatology, 37(12), 4302-4315.

Franco, A. C., Bustamante, M., Caldas, L. S., Goldstein, G., Meinzer, F. C., Kozovits, A. R., ... & Coradin, V. T. (2005). Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. Trees, 19(3), 326-335.

Gama, J. R. V., Souza, A. L. D., Calegário, N., & Lana, G. C. (2007). Fitossociologia de duas fitocenoses de floresta ombrófila aberta no município de Codó, Estado do Maranhão. Revista Árvore, 31(3), 465-477.

Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint J-P (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637.

Gong, H., & Gao, J. (2019). Soil and climatic drivers of plant SLA (specific leaf area). Global Ecology and Conservation, 20, e00696.

Harmáčková, L., Remešová, E., & Remeš, V. (2019). Specialization and niche overlap across spatial scales: Revealing ecological factors shaping species richness and coexistence in Australian songbirds. Journal of Animal Ecology, 88(11), 1766-1776.

Heilmeier, H. (2019). Functional traits explaining plant responses to past and future climate changes. Flora.

Hof, C., Rahbek, C. and Araújo, M.B. (2010), Phylogenetic signals in the climatic niches of the world's amphibians. Ecography, 33: 242-250.

Hutchinson, G. E. (1957). Cold spring harbor symposium on quantitative biology. Concluding remarks, 22, 415-427.

Kraft, N. J., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. Science, 322(5901), 580-582.

Kearney, M., Simpson, S. J., Raubenheimer, D., & Helmuth, B. (2010). Modelling the ecological niche from functional traits. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1557), 3469-3483.

Kent, M. & Coker, P. (1992). Vegetation description and analysis. Belhaven, London, UK.

Kluge, J. & Kessler, M. (2007) Morphological characteristics of fern assemblages along an elevational gradient: patterns and causes. Ecotropica, 13, 27–43.

Kramer, K. U., Schneller, J. J., & Wollenweber, E. (1995). Farne und Farnverwandte. G. Thieme.

Lavorel, S. and Garnier, E. (2002), Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology, 16: 545-556.

Letten, A.D., Keith, D.A., Tozer, M.G. and Hui, F.K. (2015), Fine-scale hydrological niche differentiation through the lens of multi-species co-occurrence models. J Ecol, 103: 1264-1275.

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. Nature, 412(6842), 72-76.

Mehltreter, K., Flores-Palacios, A., & García-Franco, J. G. (2005). Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. Journal of Tropical Ecology, 21(6), 651–660.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. Trends in ecology & evolution, 21(4), 178-185.

Mouillot, D., Graham, N. A., Villéger, S., Mason, N. W., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. Trends in ecology & evolution, 28(3), 167-177.

Moulatlet, G., Zuquim, G., Tuomisto, H. (2019). The role off soils for Pteridophyte distribution in Tropical American Forests. Fern Gazette, 21(1),1-20.

Moulatlet, GM, Zuquim, G, Figueiredo, FOG, et al. Using digital soil maps to infer edaphic affinities of plant species in Amazonia: Problems and prospects. Ecol Evol. 2017; 7: 8463–8477.

Page, C. N. (2002). Ecological strategies in fern evolution: a neopteridological overview. Review of palaeobotany and palynology, 119(1-2), 1-33.

Pérez-Harguindeguy, N., Díaz, S., Gamier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... & Urcelay, C. (2013). New handbook for stand-ardised measurement of plant functional traits worldwide. Australian Journal of Botany 61: 167-234.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., & Araújo, M. B. (2011). Ecological niches and geographic distributions (MPB-49) (Vol. 49). Princeton University Press.

Poorter L, Bongers F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology, 87(7):1733-43.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New phytologist, 182(3), 565-588.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P. B., Walters, M. B., Kloeppel, B. D., & Ellsworth, D. S. (1995). Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia, 104(1), 24-30.

Reich, P. B., Walters, M. B., Tjoelker, M. G., Vanderklein, D., & Buschena, C. (1998). Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Functional Ecology, 12(3), 395-405.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142(6): 1141-1153

Rosbakh, S., Römermann, C., & Poschlod, P. (2015). Specific leaf area correlates with temperature: new evidence of trait variation at the population, species and community levels. Alpine Botany, 125(2), 79-86.

Santos, M. G., Hanson, P., Maia, V.C & Mehltreter, K. (2018). A Review of Galls on Ferns and Lycophytes," Environmental Entomology 48(1), 53-60.

Schmitt, M., Mehltreter, K., Sundue, M., Testo, W., Watanabe, T., & Jansen, S. (2017). The evolution of aluminum accumulation in ferns and lycophytes. American journal of botany, 104(4), 573-583.

Sharpe JM, Mehltreter K, Walker LR (2010) Ecological importance of ferns. In: Mehltreter K, Walker LR, Sharpe JM (eds) Fern Ecology, 1st edn. Cambridge University Press, Cambridge, pp. 1–21

Silva, M.M.; Farias, R.P.; Costa, L.E.N.; Barros, I.C.L. 2019. Leaf phenological traits of the tree fern Cyathea praecincta (Cyatheaceae) in a Brazilian lowland tropical forest. Australian Journal of Botany, 66 (8), 618-627.

Silvertown, J. (2004) Plant coexistence and the niche. Trends in Ecology & Evolution, 19, 605–611.

Sterck, F., Markesteijn, L., Schieving, F., & Poorter, L. (2011). Functional traits determine trade-offs and niches in a tropical forest community. Proceedings of the National Academy of Sciences, 108(51), 20627-20632.

Testo, W., & Watkins, J. (2013). Understanding mechanisms of rarity in pteridophytes: Competition and climate change threaten the rare fern Asplenium scolopendrium var. americanum (Aspleniaceae). American Journal of Botany, 100(11), 2261-2270.

Thuiller, W., Lavorel, S., Midgley, G. U. Y., Lavergne, S., & Rebelo, T. (2004). Relating plant traits and species distributions along bioclimatic gradients for 88 Leucadendron taxa. Ecology, 85(6), 1688-1699.

Tuomisto, H. (2006). Edaphic niche differentiation among Polybotrya ferns in western Amazonia: implications for coexistence and speciation. Ecography, 29(3), 273-284.

Tuomisto, H., Poulsen, A. D., & Moran, R. C. (1998). Edaphic Distribution of Some Species of the Fern Genus Adiantum in Western Amazonia 1. Biotropica, 30(3), 392-399.

Tuomisto, H., Ruokolainen, K., Poulsen, A. D., Moran, R. C., Quintana, C., Cañas, G., & Celi, J. (2002). Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuní National Park, Ecuadorian Amazonia. Biotropica, 34, 516-533.

Vázquez, D. P. (2006). Exploring the relationship between nichie breadth and invasion success. In Conceptual ecology and invasion biology: reciprocal approaches to nature (pp. 307-322). Springer, Dordrecht.

Velazco SJE, Galvão F, Villalobos F, De Marco Júnior P (2017) Using worldwide edaphic data to model plant species niches: An assessment at a continental extent. PLoS one 12(10): e0186025.

Violle C., Jiang L. (2009) Towards a trait-based quantification of species niche. Journal of Plant Ecology 2: 87–93.

Walker, B. (1995). Conserving biological diversity through ecosystem resilience. Conservation biology, 9(4), 747-752.

Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos, 159-164.

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(1), 125-159.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... & Flexas, J. (2004). The worldwide leaf economics spectrum. Nature, 428(6985), 821-827.

Zuquim, G., Costa, F.R.C., H. Tuomisto, G. M. Moulatlet & F. O. G. Figueiredo (2019). The importance of soils in predicting the future of plant habitat suitability in a tropical forest. Plant Soil, 1-20.

Zuquim, G., Tuomisto, H., Jones, M.M., Prado, J., Figueiredo, F.O., Moulatlet, G.M., Costa, F.R., Quesada, C.A. and Emilio, T. (2014), Predicting environmental gradients with fern species composition in Brazilian Amazonia. J Veg Sci, 25: 1195-1207.

Tables

Table 2: Results from the general linear models regarding fern species niche position and functional traits. Significant p values regarding the regression coefficient (*β*) and standard error (SE) were highlighted in bold. CI: Confident intervals. La: leaf area; SLA: specific leaf area; LDMC: leaf dry matter content. Note that leaf water content (LWC) was not computed due to collinearity with LDMC.

Fixed Effects	*β*	SE	95% CI		p-value
			Lower	Upper	
Axis 1					
Intercept	7.729	6.502	-5.613	21.070	0.245
LA	0.002	0.013	-0.024	0.028	0.895
SLA	-0.018	0.006	-0.031	-0.004	**0.011**
LDMC	-0.034	0.070	-0.178	0.109	0.626
Leaf N	2.597	0.925	0.699	4.494	**0.009**
Leaf P	-9.559	7.045	-24.014	4.897	0.186
Phenols	-0.041	0.097	-0.241	0.158	0.676
Rhizome	0.175	0.675	-1.210	1.560	0.798
Laminar dissection	-0.625	0.648	-1.955	0.705	0.344
Laminar morphology	0.306	0.460	-0.638	1.251	0.511
Axis 2					
Intercept	2.337	3.907	-5.679	10.353	0.555
LA	-0.011	0.008	-0.027	0.004	0.149
SLA	-0.002	0.004	-0.010	0.006	0.601
LDMC	-0.079	0.042	-0.165	0.007	0.069
Leaf N	-0.034	0.556	-1.175	1.106	0.951
Leaf P	0.475	4.233	-8.211	9.161	0.911
Phenols	0.039	0.058	-0.080	0.159	0.505
Rhizome	-1.090	0.406	-1.922	-0.257	**0.012**
Laminar dissection	1.316	0.389	0.517	2.115	**0.002**
Laminar morphology	-0.069	0.277	-0.637	0.498	0.804

Figures

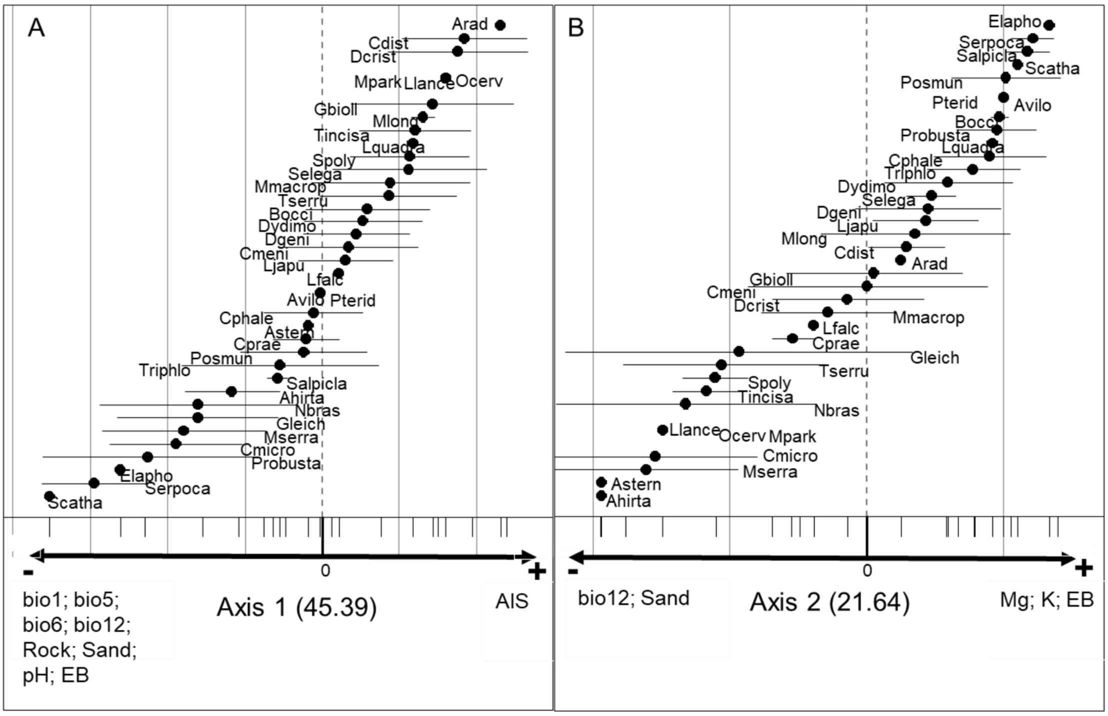


Figure 2: Fern species niche segregation towards the first two axes of the outlying mean index indicating niche position and breadths. Positively and negatively associated environmental conditions were pointed in each axes extremes. Dashed lines indicate shifts toward negative and positive positions. EB: soil exchangeable bases; Rock: soil rock coverage; bio1: annual temperature; bio5: maximum temperature of the warmest month; bio6: minimum temperature of the coldest month; bio12: annual precipitation. Species full names are available from Table A.1 in Appendix A.

Appendix A

Table A1: Summary of the local and broad scale environmental variables analyzed in general linear mixed effect models. LL: Rio Formoso district; SBM: São Vicente Féerrer district; SBB: Bonito district; Rock: soil rock coverage; EB: exchangeable bases; AlS: soil aluminum saturation; bio1: annual temperature; bio5: maximum temperature of the warmest month; bio6: minimum temperature of coldest month; bio12: annual precipitation.

Plot	Area	Local-scale							Broad-scale			
		Rock (%)	Sand (%)	pH	Mg (mg/dm3)	K (mg/dm3)	EB (cmolc/dm3)	AlS(%)	bio1	bio5	bio6	bio12
1	LL	50	82.4	5.18	193.985	100.190	4.310	36.341	25.6	30.1	20.8	1804
2	LL	70	63.8	4.19	132.230	302.758	6.426	33.370	24.4	29.7	19.1	1280
3	LL	0	62.9	3.93	244.342	168.741	6.280	40.139	24.1	28.6	19.4	2108
4	LL	0	76.1	4.06	321.215	134.378	5.659	35.514	24.1	28.6	19.4	2108
5	LL	45	86.9	5.1	196.190	114.984	3.317	17.536	24	28.5	19.2	2015
6	LL	45	85.8	5.44	217.9955	248.777	5.315	13.659	24	28.5	19.2	2015
7	LL	30	68.3	4.89	412.0887	227.500	8.823	6.233	23.9	28.5	19.2	2020
8	SBM	0	58.6	4.21	636.902	189.033	8.774	36.959	22.7	29.5	16.6	1020
9	SBM	0	62.8	3.48	323.709	148.5106	4.391	63.811	22.7	29.5	16.6	1020
10	SBM	0	54.9	3.54	116.460	196.768	4.531	54.895	22.3	29.0	16.2	1006
11	SBM	0	58.1	3.44	195.401	209.120	5.035	62.832	22.7	29.5	16.6	1020
12	SBM	0	65.8	4.48	542.319	264.353	6.141	9.051	22.3	29.0	16.2	1006
13	SBM	30	61.9	4.66	474.878	344.790	5.855	9.460	22.3	29.0	16.2	1006
14	SBM	45	58.8	4.65	494.8459	200.756	5.200	18.584	22.5	29.3	16.4	1016
15	SBB	10	78.1	3.8	210.781	203.161	5.653	38.932	20.2	26.4	14.7	1015
16	SBB	0	55.3	3.26	198.865	186.793	3.083	31.818	20.2	26.4	14.7	1015
17	SBB	17	57.9	4.43	194.286	127.189	4.136	44.389	20.2	26.4	14.7	1015
18	SBB	0	58.0	4.85	297.475	142.769	6.261	46.875	20.2	26.4	14.7	1015
19	SBB	0	62.8	3.88	246.288	160.278	4.922	49.105	20.5	26.7	15.0	1063
20	SBB	0	67.5	3.55	101.153	82.825	2.209	34.834	20.3	26.5	148	1032

21	SBB	0	61.8	3.89	145.454	101.253	2.683	73.067	20.3	26.5	148	1032
22	SBB	0	62.5	3.72	513.649	255.532	5.496	54.317	21.2	27.5	156	973

Table A2: Code for environmental variables extracted from the Worldcilm3 at 1km spatial resolution. Reference: Fick, S.E. and Hijmans, R.J. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology.

Code	Variables
bio1	Annual Mean Temperature
bio4	Temperature Seasonality (standard deviation *100)
bio5	Max Temperature of Warmest Month
bio6	Min Temperature of Coldest Month
bio8	Mean Temperature of Wettest Quarter
bio9	Mean Temperature of Driest Quarter
bio12	Annual Precipitation
bio13	Precipitation of Wettest Month
bio14	Precipitation of Driest Month
bio15	Precipitation Seasonality (Coefficient of Variation)

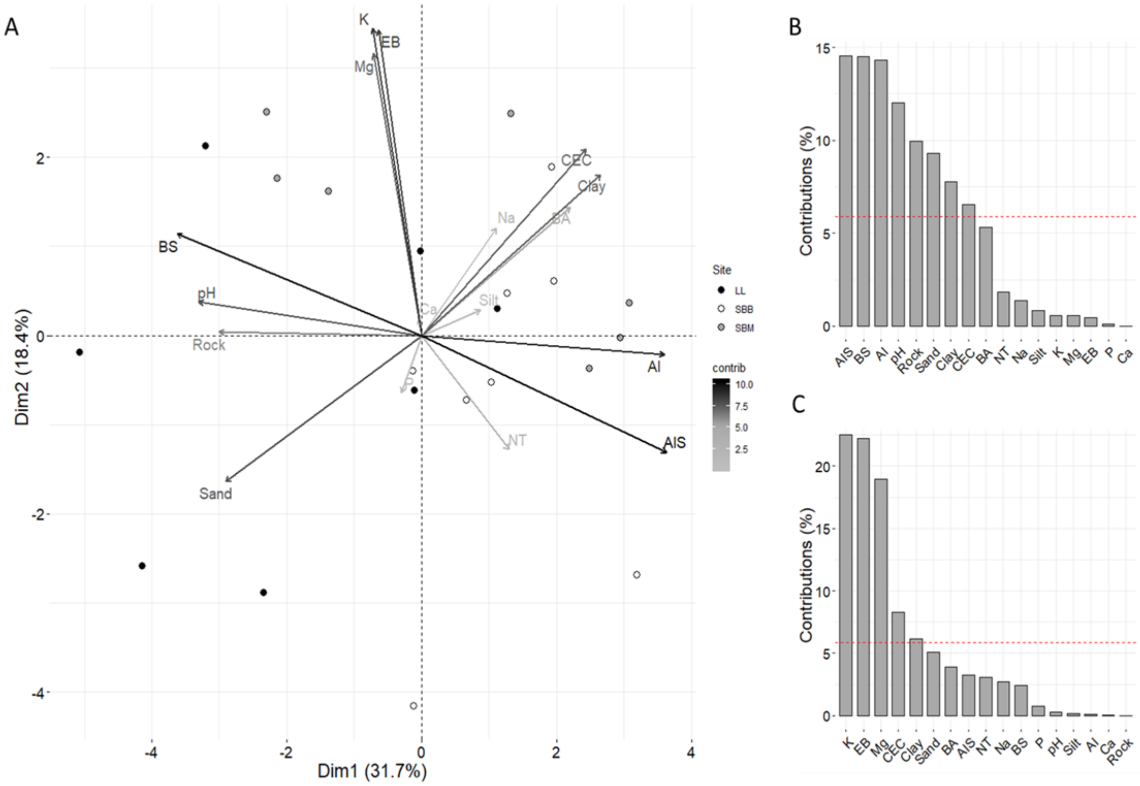


Figure A.1: Principal component analysis of local environmental variables sampled from Atlantic Forest remnants in the northeastern Brazil (A) and contribution of each variable to the first two axes (B-C). Contribution (contrib) values over the dashed red line indicate significant variables to the respective axis. Rock: rock coverage; BA: basal area; EB: exchangeable bases; CEC: effective cation exchange capacity; BS: base saturation; Al-S: soil aluminum saturation.

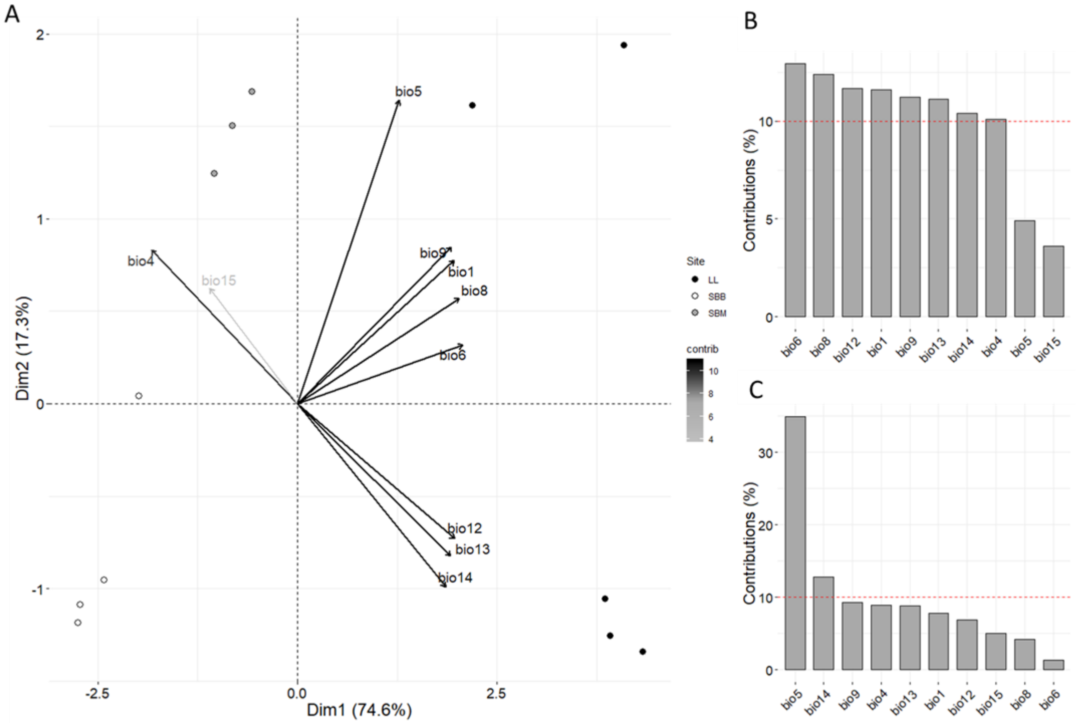


Figure A.2: Principal component analysis of broad-scale environmental variables sampled from Atlantic Forest remnants in the northeastern Brazil (A) and contribution of each variable to the first two axes (B-C). Contribution (contrib) values over the dashed red line indicate significant variables to the respective axis. Variables were extracted from the Worldcilm3 at 1km spatial resolution. To consult Table A.2 to check variable code descriptions.

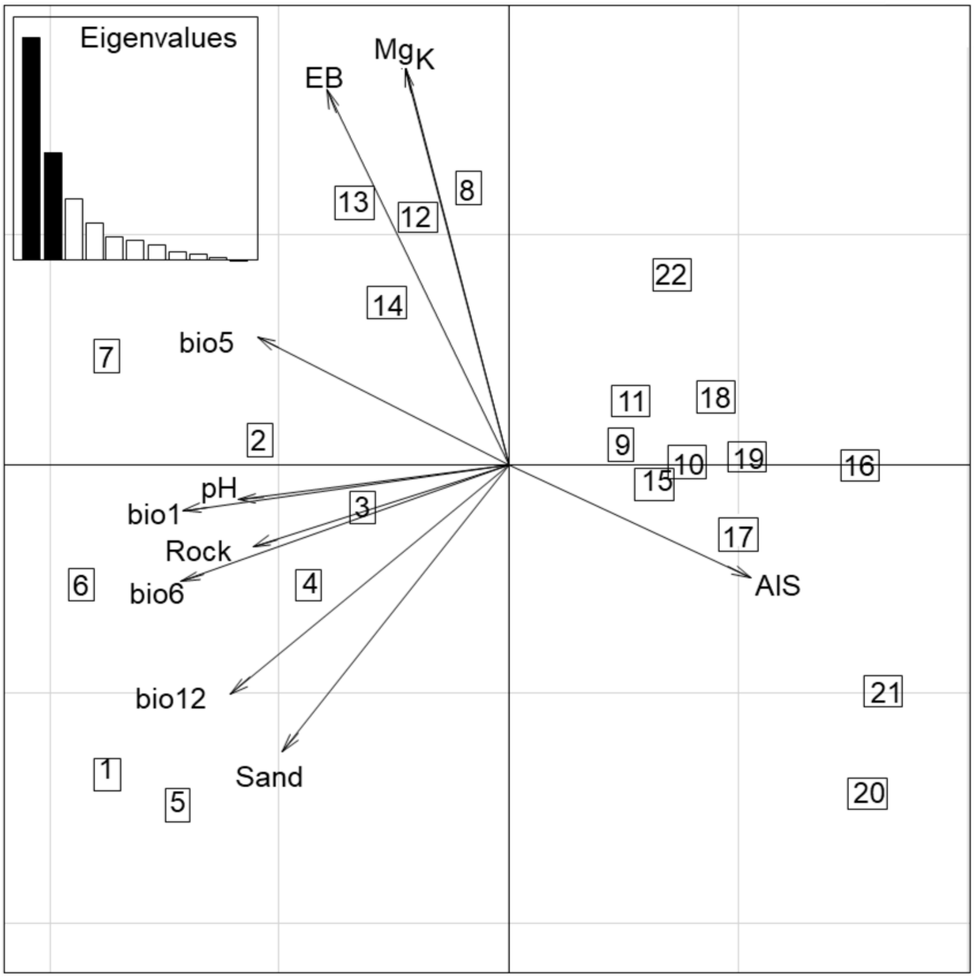


Figure A.3: Results from environmental variables analyzed in the outlying mean index using local and broad-scale environmental variables and the 22 fern assemblages sampled among Atlantic Forest remnants in northeastern Brazil. Note that the first two axes were the most meaningful. EB: soil exchangeable bases, AlS: soil aluminum saturation; Rock: soil rock coverage, bio1: annual temperature, bio5: maximum temperature of the warmest month, bio6: minimum temperature of the coldest month, bio12: annual precipitation.

4 CSR ECOLOGICAL STRATEGIES IN SPECIES AND COMMUNITIES: A FERN TALE IN THE BRAZILIAN ATLANTIC FOREST

MANUSCRITO SUBMETIDO AO PERIÓDICO OECOLOGIA

Scaling up CSR ecological strategies from species to assemblages: A fern tale in the Brazilian Atlantic Forest

Lucas E.N Costa[1*], Rafael P. Farias[1], Michael Kessler[2], Iva C.L. Barros[1]

[1] Departamento de Botânica, Universidade Federal de Pernambuco. Ave. Professor Moraes Rêgo, 50560-901, Recife, PE, Brazil.

[2] Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland.

Lucas E.N Costa

lucasbiologicasufpe@hotmail.com

Telephone number: +55 81 2126 8348

Fax number: +55 81 2126 8946

LENC, MK and ICLB conceived the ideas and designed the experiments. LENC and RPF collected the data and conducted the statistical analyses. LENC wrote the first draft of the manuscript. All authors discussed the results and significantly contributed to the writing of the manuscript.

Abstract

Grime’s CSR ecological strategies approach provides a meaningful framework to understand plant responses to stress, disturbances, and competition. Thus, CSR ecological strategies have the potential to (i) be expanded worldwide among plant groups, such as ferns, the second largest group of vascular plants, and (ii) cover diverse scenarios of environmental conditions. In this study, we investigated the CSR strategies in ferns in highly disturbed and fragmented Atlantic Forests in northeastern Brazil. We analyzed CSR strategies in the individual species and the assemblage and related CSR patterns to a set of local environmental factors. In 22 plots, we assessed CSR strategies based on leaf traits (leaf area -LA, specific leaf area - SLA, leaf dry matter content - LDMC), and community weighted means. Most of the species (80%) were assigned to a mixed R/CR strategy, and the remainder to R/SR (14%), R/CSR (4%), and R (2%). When scaled up to the assemblage level, the R/CR strategy included 91% of the assemblages. The percentages of CSR strategies were correlated with leaf traits following the leaf economic spectrum framework, where (i) the C-strategy was positively correlated with LA, and negatively with LDMC, (ii) the S-strategy was positively correlated with LDMC, and (iii) the R-strategy was positively correlated with SLA. C and R strategies at the assemblage level were affected negatively by soil pH and positively by soil potassium content, respectively. Our results reveal the reliability of Grime’s CSR strategies to describe ruderal strategies in Atlantic forest ferns and highlight the role of microhabitat conditions on the functional signature of the assemblages.

Keywords edaphic conditions·Grime’s triangle·leaf economic spectrum·local scale·trait trade-offs

Introduction

Plants interact with their abiotic and biotic environments via functional traits, i.e., morphophysiological characteristics that affect the performance of the individuals, which can be related to any ecosystem function performed by the species (Violle et al. 2007). In leaves, there are important functional traits closely related to species performance and ecosystem processes, such as carbon and nitrogen fluxes (e.g. Wright et al. 2004; Shipley et al. 2006; Cadotte 2017). Globally, there are consistent leaf trait trade-offs, such as the well-known global spectrum of plant form and function (Wright et al. 2004; Díaz et al. 2016; Bruelheide et al. 2018). This global pattern reflects trade-offs between the acquisition and conservation of resources, creating the gradient of the leaf economic spectrum (Wright et al. 2004; Reich 2014; Díaz et al. 2016).

Trade-offs among functional traits have helped in the understanding of the role of environmental and evolutionary selection on species strategies (Cerabolini et al. 2010; Pierce et al. 2013). Pierce et al. (2013) demonstrated that the leaf economic spectrum and plant size can be explained by Grime's theoretical CSR triangle which predicts the occurrence of three main plant strategies, namely competitive (C), stress-tolerant (S), and ruderal (R (Grime et al. 1997; Grime 2001). The C strategy is related to the resource allocation within habitats with variability in resource availability, whereas the stress tolerance strategy (S) represent high resource conservation and high tolerance to stress, being selected in habitats with low resource availability. The ruderal strategy (R) is a high acquisition strategy in high resource habitats (Grime et al. 1977). Interestingly, averages of CSR strategies for the species can be scaled up to the community level in order to summarize vegetation strategies under different environmental conditions, like succession, edaphic gradients, and disturbance (e.g., Caccianiga et al. 2006; Pierce et al. 2013; Cerabolini et al. 2016; Rosado and de Mattos 2017; Schmidt et al. 2017). In order to facilitate the applicability of the CSR strategies worldwide, Pierce et al. (2017) proposed the ‘StrateFy’ scheme to detect plant strategies following CSR predictions with an analysis weighted across biomes. Most of the studies using CSR strategies and specifically the ‘StrateFy’ tool are focused on seed plants (e.g., Caccianiga et al. 2006; Pierce et al. 2013; Cerabolini et al. 2016; Rosado and de Mattos 2017), whereas other groups, such as ferns, have so far been neglected.

Ferns amount to approximately 10.578 species worldwide (PPG I 2016) and represent an important component of the tropical forest understory, where they can account for up to 15% of total biomass (Harms et al. 2004). Interestingly, despite having different leaf anatomy and stomatal control mechanisms compared to angiosperms (Brodribb and Holbrook 2004), the leaf economic spectrum does not appear to differ between ferns and angiosperms (Tosens et al. 2016). Ferns present ecological characteristics such as low grow rates and the ability to inhabit a range of low nutrient microhabitats as well as to tolerate unusually high levels of excess mineral elements which would be toxic to other plants (Page 2002; Schmitt et al. 2017). Moreover, environmental conditions as climate and soil affect both fern species distribution and community composition (Richard et al. 2000; Poulsen et al. 2006; Tuomisto et al. 2002, Kessler et al. 2011; Zuquim 2014).

As the comparison across different taxa is essential to test the applicability of the CSR scheme in different taxa and geographic contexts in other to identify generalities and idiosyncrasies on the selection of ecological strategies (Pierce et al. 2013), our study aimed to classify ferns in different microhabitats in the Atlantic forest of northeastern Brazil according to the CSR strategies. Further, we analyzed the reliability of scaling-up CSR strategies from species to the assemblage level in other to summarize the functional signature of local assemblages and testing whether the strategies of the assemblages are related to local environmental conditions. Due to the ecological particularities of ferns and based on previous studies, our hypothesis was that ferns will mainly display stress tolerance strategies (S) in

Grime’s CSR scheme, in other words, traits favoring species persistence. Further, we expected that when scaled up to assemblage level, ecological strategies will be driven by microhabitat conditions, especially edaphic ones, creating shifts in the functional signature of the assemblages along with different local environmental conditions.

Materials and methods

Study area and data sampling

We carried out our study in Atlantic forest remnants at three sites in Pernambuco state, northeastern Brazil (Figure 1). The climate of the three sites is hot and wet (As’ Köppen scheme). Detailed information about elevation, annual rainfall, and annual temperature of the three sites are available from the supplementary material (Table 1). We established 22 plots of 10 m x 20 m at three sites (eight plots in Bonito, seven in both Rio Formoso and São Vicente Férrer). Plots at the same site were at least 100 m apart and plot establishment was based on the microhabitats inhabited by ferns such as shaded forest interior, slopes, ravines, and marshes (Pereira et al. 2014).

We measured the number and the basal area of trees with a diameter at breast height ≥ 15 cm, the percentage of the soil in the plot covered by rocks and rock outcrops, and collected soil samples in five points of the plot that were combined for analyses. Soil samples (500 g) were analyzed following the methods described by EMBRAPA (2017) for soil pH, concentrations of Ca, Mg, Al, available P, and exchangeable K and Na, as well as percentages of clay, silt, and sand. We also calculated soil base saturation (BS), soil aluminum saturation (AlS), soil exchangeable bases (EB), and soil cation-exchange capacity (CEC).

All the ferns recorded in each plot were counted and identified, with vouchers deposited at the herbarium UFP. We registered all epiphytic species that were possible to count and collect without tree climbing techniques. Species identification was based on specialized literature and consulting specialists. The species names and authors were confirmed using The International Plant Names Index.

For leaf traits measurement, we selected five leaves of each species per plot from different individuals. Following Pérez-Harguindeguy et al. (2013), we selected mature and fully expanded sterile leaves with no traces of herbivory. For the species with less than five individuals in the plot, additional leaves were collected in the areas surrounding the plot. From the collected leaves we measured leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC) following Pérez-Harguindeguy et al. (2013).

Data analyses

In other to classify ferns according to the CSR strategies, we applied the ‘StrateFy’ spreadsheet (Pierce et al. 2017), calculating the proportion of CSR strategies of each species per plot via their LA, SLA, and LDMC trait values. The ‘StrateFy’ method was developed based on well-known trade-offs (e.g. the leaf economic spectrum). However, due to the high degree of variation in leaf traits across ecosystems, some degree of distortion in multivariate relations can lead to unusual combinations (e.g. large leaves with extremes in the leaf economic spectrum). In such cases, the trade-offs related to CSR strategies are not clearly visible and the applicability of the method can be questioned. To test whether ferns were under the trade-offs predicted by the CSR strategies scheme, we analyzed the relationships between leaf traits and CSR scores via simple regressions. Leaf trait trade-offs were also analyzed via multivariate associations with a principal component analysis (PCA) using spectral decomposition (*princomp* in the factoextra package of R software) in order to examine the correlations between leaf traits considering species per plot and using linear correlations between leaf traits (Figure S1).

We calculated the relative proportion of CSR strategies at the assemblage level using the community-weighted mean values (CWM) of LA, SLA, and LDMC. CWM was calculated following $CWM = \sum_{i=1}^{S} wi \text{ X } xi$, where *S* represents the total number of species in the plot, *wi* is the species abundance of the *ith* species in the plot, and *xi* the trait value of the *ith* species in the plot.

In order to analyze the relationship between the assemblage CSR values and microhabitat conditions, we used generalized linear mixed models (GLMM) using the *glmer* function in the lme4 package of R, including study site as a random effect and microhabitat conditions as fixed effects. Before the GLMM analyses, we ran a principal component analysis (PCA) in order to assess the contribution of the variables to the principal components (*princomp* function in the factoextra package). In order to select the microhabitat variables for the GLMM analyses, we excluded variables with low contributions to the first two axes of the PCA (Table S2; Figure S2). After this, we calculated the variance inflation factor (VIF) of the model with the *vif* function and removed variables with VIF up to 10 (clay content, CEC, and BS) in order to avoid multicollinearity in the final model. The fixed effects expressed in percentages (rock coverage and soil contents of clay, sand, and silt) were normalized using root square transformation, whereas the others were log10+1 normalized. The percentages of R and S-strategies were normalized using arcsine of log10 transformation and tested with Gaussian distribution error. It was not possible to normalize assemblage percentages of C strategies, which was tested with a gamma distribution error. For all analyses, were considered $p \leq 0.05$ as significant. The statistical analyses were performed using R version 3.4.4 (R Development Core Team 2017).

Results

According to Grime’s triangle, all the 40 ferns species recorded in this study (Table S2) were placed in the corner of the R strategy with tendencies towards the C strategy or, in few cases, the S strategy (Figure 2A, Table S3). Most of the species were assigned to a mixed R/CR strategy (80%), followed by R/SR (14%), R/CSR (4%), while only *Diplazium cristatum* showed an exclusive R strategy in some plots (2%) (Table S3). Most of the species that occurred in different plots consistently exhibited the same strategy (Table S3). However, some species showed slight variations in the strategies according to the plot of occurrences, such as *D. cristatum*, which varied between R and R/CSR, *Lomariopsis japurensis* between R/SR and R/CR, and *Steiropteris polypodioides* between R/SR and R/CR (Table S3). When scaled up to the assemblage level, the R strategy was dominantl, ranging from 62.5% to 81.4%, with a mean of 69.8±3.7%, followed by the C strategy (range11.6-24.4%; mean 20.3±3.2%), and the S strategy (range 4.7-23.7%; mean 9.9±4.1%), which was consistent with the results at the species level. The R/CR strategy covered 91% of the assemblages, whereas R and R/CSR accounted for 4.5% each.

We found correlations between the percentages of CSR strategies and the species leaf traits (Figure 2B-E). The degree of competitiveness (C%) of the species was positively correlated with LA (R^2 = 0.93, p = < 2.2e-16, Figure 2B), and negatively with LDMC (R^2 = 0.22, p = < 1.32e-07, Figure 2C). The increase of the ruderal strategy (R%) was associated with an increase in SLA (R^2 = 0.20, p = 4.43e-07, Figure 2D), whereas stress tolerance (S%) was positively correlated with LDMC (R^2 = 0.96, p = < 2.2e-16, Figure 2E). The leaf traits showed the triangular spacing predicted by the CSR theory (Figure 2A). LDMC was the most important variable to explain the first PCA axis, with negative associations (r = -0.85; Figure 2A). SLA and LA equally explained the second PCA axis (Figure 2A), with a negative association for SLA (r = -0.68) and positive one for LA (r = 0.71).

We found significant effects of microhabitat conditions on the percentages of C and R strategies of the fern assemblages, specifically in relation to soil pH for the former and soil K levels for the latter (Table 1). The occurrence of the S strategy in the fern assemblages was not explained by any of the variables.

Discussion

Our hypothesis that due to their long life span and occurrence in the forest understory ferns would mainly exhibit a stress tolrence strategy was refuted. Instead, the 40 species studied in the Atlantic forests remnants of northeastern Brazil exhibited a strong tendency towards the ruderal strategy (R). The same pattern was maintained when the strategies were scaled up to the assemblages, highlighting the importance of high acquisition strategies for the ferns inhabiting the Atlantic Forest. Interestingly, shifts in the ecological strategies of the assemblages were associated only with local soil properties, demonstrating the importance of fine-scale soil conditions for the selection of ecological strategies in ferns.

The associations between leaf traits and CSR strategies in ferns (i.e. acquisitive-conservative gradients, mediated by the size of the plant’s organs) corroborate the

pattern described in the worldwide leaf economics spectrum (Díaz and Cabido 2001; Reich 2014), which is expected within the CSR theory (Pierce et al. 2013). It indicates that ferns in the Atlantic forest are under the trade-offs predicted by CSR theory, highlighting the applicability of this method to this taxonomic group. Previous studies have confirmed the applicability of the leaf economic spectrum to ferns (e.g. Tosens et al. 2016), but our study showed that most of the species overlapped in the middle of the “fast-slow” gradient, mediated by LA, which compounds the orthogonal gradient that mediates the plant size (Díaz et al. 2016). The leaf economic spectrum ranges from herbs to trees, i.e., extremes of vascular plant life form (Wright et al. 2004; Díaz et al. 2016). In this sense, analyses within the same life form can give different results and some overlap might be expected. Indeed, Díaz et al. (2016) observed some degree of trait overlap when considering plant lineages (i.e. angiosperms, gymnosperms, and ferns) and life forms (woody versus non-woody plants). The positive relationship between SLA and R strategies and LDMC and -strategies in our study is in accordance with expectations from the CSR theory (Pierce et al. 2013). Since SLA is an important indicator of the leaf economic spectrum (Wright et al. 2004), high values of the ferns indicate acquisitive strategies and leaves that are cheap to construct (Pérez-Harguindeguy et al. 2013), i.e., R strategists. On the other hand, LDMC indicates conservative strategies and high values in ferns indicate low-growth long-lived leaves tolerant to environmental stress, especially nutritional stress (Hodgson et al. 2011; Pérez-Harguindeguy et al. 2013), i.e. K strategists. The correlation between LA and C strategies indicates that an increase in LA strengenths fern species competitiveness and that C strategists are located in the middle of the leaf economic spectrum gradient (Cerabolini et al. 2010; Pierce et al. 2013). Moreover, individual trait correlations support this result, due to the absence of correlation between LA and SLA and the negative correlation between LA and LDMC.

The occurrence of ferns towards ruderal strategies disagrees with the results of Grime (1985), who found that ferns have stress-tolerance strategies. These divergent results might be related to habitat conditions of ferns in the two studies. The temperate forest studied by Grime (1985) and the tropical forest studied here show large differences in dynamics and perturbation. The ferns sampled by Grime (1985) occurred in habitats with low disturbance. However, ferns exhibit widely different life forms (Page 2002) and inhabit a wide range of environmental conditions along edaphic, elevational, and vegetational gradients (e.g. Tuomisto and Poulsen 1996; Kessler 2001; Tuomisto et al. 2002, 2006; Kluge et al. 2006), which might affect the CSR strategies of the species. Indeed, some ferns occur in disturbed habitats such as forest edges in tropical forests (Silva et al. 2011) and become invasive in several habitats (Jones et al. 2019). Our study area comprises disturbed and fragmented forest remnants surrounded by the monoculture of sugar cane or non-forested areas (Silva and Tabarelli 2000; Silva et al. 2011). Previous studies have shown that fragmentation and disturbance, such as edge effects, can reduce ferns diversity and shift species composition, filtering tolerant species (e.g. Silva et al. 2011, 2014). Furthermore, most of the ferns in

Atlantic forest in northeastern of Brazil are widely distributed in other Brazilian vegetation types such as the southern Atlantic Forest and Amazonian forest (Pereira et al. 2013), a fact that might explain the high overlap toward a ruderal strategy, with competitive and stress tolerance strategies playing a secondary role.

Interestingly, the dominance of one specific CSR strategy, as evidenced by the fern in our study, is a strong environmental signal (Schmidt et al. 2017). Therefore, the predominance of the R strategy among the ferns in the study region can be indicative of an adaptation to microhabitat conditions. Species typically reported to favour shady and wet microhabitats (e.g. *Danaea geniculata*, *Tectaria incisa*, and *Meniscium serratum*) shared the same strategy of more generalist species and some ferns typically found in open areas (e.g. *Blechnum occidentale*, *Gleichenella pectinata*, and *Pteridium arachnoideum* subsp. *arachnoideum*). It is important to highlight that species of shady and wet microhabitats tend to have small leaves with high water content, increasing leaf SLA in shade environments, as reported by Sessa and Givnish (2014), and consequentially favoring an interpretation as ruderal strategists.

The similarity of strategies between the species and assemblage levels suggest the presence of a strong environmental filter since it is expected that trade-offs at the species level can be decoupled at the community level, leading to a divergence in species strategies at the assemblages, which favors species coexistence (Bruellheide et al. 2018). The dominance of ruderal strategies in the assemblages is mainly determined by the abiotic environment, the availability of microsites for the establishment, and propagule limitations (Kelemen et al. 2013). Due to the high spore production and dispersal ability of ferns (Page 2002), we believe that environmental factors drive overall assemblage strategies.

The negative correlation between the C strategies (%) at the assemblage level and soil pH might be explained by the preference of many ferns for acidic soils, as previously reported (e.g. Tuomisto et al. 2002; Poulsen et al. 2006; Costa et al. 2019). Soil pH can affect the availability of several nutrients and some toxic elements, and acid soils are related to some limiting conditions, such as lower fertility (Barrow 2017). The higher competitiveness in fern assemblages under more acid soils might be related to the high tolerance of these plants to nutrient disequilibrium (Page 2002, Kessler et al. 2014). The increase in ruderal strategy associated with increases in soil K content can be related to the role of this fundamental macronutrient in regulating plant photosynthesis and resource acquisition, playing a critical role in plant growth, especially under abiotic stresses (Wang et al. 2013). Moreover, K is strongly related to soil water content, increasing water use efficiency (Sardans and Peñuelas 2015), which is a key factor in fern ecology, affecting both the gametophyte development, sporophyte establishment and surviving, because fern sporophytes have low evaporative control (Page 2002).

In conclusion, our results highlight the reliability of CSR analysis to identify fern ecological strategies, reporting a high overlap between species and a predominance of ruderal strategies. Whether this holds true for other ferns will need further investigations from a wide range of environmental conditions. The CSR strategies scheme has been widely applied to summarize general species strategies and vegetation trends along successional and environmental gradients, as well as for tracking changes in the functional signature of the communities (Caccianiga et al. 2006; Negreiros et al. 2014; Chai et al. 2016; Pierce et al. 2017; Schmidt et al. 2017). .

Acknowledgments

We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, National Council for Scientific and Technological Development) to doctorate scholarship and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) for doctorate ‘sandwich’ internship (process 88881.189293/2018-01); To the Laboratório de

Química do Solo of the Universidade Federal Rural de Pernambuco for supporting soil analysis; To Cucau and Trapiche Mills for logistic support during the fieldwork.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

References

Barrow NJ (2017) The effects of pH on phosphate uptake from the soil. Plant soil 410:401–410. https://doi:10.1007/s11104-016-3008-9

Brodribb TJ, Holbrook NM (2004) Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. New Phytol 162:663–670. https://doi:10.1111/j.1469-8137.2004.01060.x

Bruelheide H, Dengler J, Purschke O et al. (2018) Global trait–environment relationships of plant communities. Nat Ecol Evol. 2:1906–1917. https://doi:10.1038/s41559-018-0699-8

Caccianiga M, Luzzaro A, Pierce S, Ceriani RM, Cerabolini B (2006) The functional basis of a primary succession resolved by CSR classification. Oikos 112:10–20. https://doi:10.1111/j.0030-1299.2006.14107.x

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. Ecol Lett 20:989–996. https:// doi:10.1111/ele.12796

Cerabolini BEL, Brusa G, Ceriani RM, De Andreis R, Luzzaro A, Pierce S (2010) Can CSR classification be generally applied outside Britain? Plant Ecol 210:253–261. https://doi:10.1007/s11258-010-9753-6

Cerabolini BEL, Pierce S, Verginella A, Brusa G, Ceriana RM, Armiraglio S (2016) Why are many anthropogenic agroecosystems particularly species rich? Plant Biosyst 150:550–557. https://doi:10.1080/11263504.2014.987848

Chai Y, Yue M, Wang M, Xu J, Liu X, Zhang R, Wan P (2016) Plant functional traits suggest a change in novel ecological strategies for dominant species in the stages of forest succession. Oecologia 180:771–783. https://doi:10.1007/s00442-015-3483-3

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655. https://doi: 10.1016/S0169-5347(01)02283

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Wright SJ, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD, Gorné LD (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi:10.1038/nature16489

Empresa Brasileira de Pesquisa Agropecuária [EMBRAPA] (2017) Manual de métodos de análise de solos, 3rd edn. Embrapa CNPS, Rio da Janeiro.

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. https://doi: 10.1086/283244

Grime JP (1985) Factors limiting the contribution of pteridophytes to a local flora. P Roy Soc Edinb B 86:403–421. https://doi:10.1017/S0269727000008393

Grime JP (2001) Plant Strategies, Vegetation Processes and Ecosystem Properties. Wiley, Chichester.

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79:259–281. https://doi:10.2307/3546011

Harms KE, Powers JS, Montgomery RA (2004) Variation in small sapling density, understory cover, and resource availability in four neotropical forests. Biotropica 36:40–51. https://doi:10.1111/j.1744-7429.2004.tb00294.x

Hodgson JG, Montserrat-Martí G, Charles M, Jones G, Wilson P, Shipley B, Sharafi M, Cerabolini BEL, Cornelissen JHC, Band SR, Bogard A, Castro-Díez P, Guerrero-Campo J, Palmer C, Pérez-Rontomé MC, Carter G, Hynd A, Romo-Díez A, Espuny LT, Pla FR (2011) Is leaf dry matter content a better predictor of soil fertility than specific leaf area? Ann Bot 108:1337–1345. https://doi:10.1093/aob/mcr225

Jones MM, Szyska B, Kessler M (2011) Microhabitat partitioning promotes plant diversity in a mid-elevation tropical montane forest. Glob Ecol Biogeogr 20:558–569. https://doi:10.1111/j.1466-8238.2010.00627.x

Jones EJ, Kraaij T, Fritz H, Moodley D (2019). A global assessment of terrestrial alien ferns (Polypodiophyta): species’ traits as drivers of naturalisation and invasion. Biol Invasions 21:861–873. https://doi:10.1007/s10530-018-1866-1

Kelemen A, Török P, Valkó O, Miglécz T, Tóthmérész B (2013) Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. J Veg Sci 24:1195–1203. https://doi:10.1111/jvs.12027

Kessler M (2001) Pteridophyte species richness in Andean forests in Bolivia. Biodivers Conserv 10:1473-1495. https://doi: 10.1023/A:1011811224595

Kessler M, Kluge J, Hemp A, Ohlemüller R (2011) A global comparative analysis of elevational species richness patterns of ferns. Glob Ecol Biogeogr 20:868–880. https://doi: 10.1111/j.1466-8238.2011.00653.x

Kessler M, Salazar L, Homeier J, Kluge J (2014) Species richness-productivity relationships of tropical terrestrial ferns at regional and local scales. J Ecol 102:1623–1633.

Kluge J, Kessler M, Dunn R (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate, and species pool effects for pteridophytes on an elevational gradient in Costa Rica. Glob Ecol Biogeogr 15:358–371. https://doi:10.1111/j.1466-822X.2006.00223.x

Laboratório de Meteorologia de Pernambuco [LAMEPE] (2012) Available from http://www.itep.br/meteorologia/lamepe [accessed 11 Dec 2017].

Negreiros D, Le Stradic S, Fernandes GW, Rennó HC (2014) CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. Plant Ecol 215:379–388. https://doi:10.1007/s11258-014-0302-6

Page CN (2002) Ecological strategies in fern evolution: a neopteridological overview. Rev Palaeobot Palynol 119:1–33. https://doi:10.1016/S0034-6667(01)00127

Pereira AFN, Silva IAA, Santiago ACP, Barros ICL (2013) Richness, geographic distribution and ecological aspects of the fern community within the Murici Ecological Station in the state of Alagoas, Brazil. Acta Bot Bras 27:788–800. https://doi:10.1590/S0102-33062013000400019

Pereira AFN, Silva IAA, Santiago ACP, Barros ICL (2014) Efeito de borda sobre a comunidade de samambaias em fragmento de Floresta Atlântica (Bonito, Pernambuco, Brasil) Interciência 39:281–287. Available from https://www.redalyc.org/articulo.oa?id=33930412012 [accessed 06 Jul 2019].

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC, (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:67–234. https://doi: 10.1071/BT12225

Pierce S, Brusa G, Vagge I, Cerabolini BEL (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Funct Ecol 27:1002–1010. https://doi: 10.1111/1365-2435.12095

Pierce S, Negeiro D, Cerabolini BEI, Kattge J, Díaz S, Kleyer M, Shipley B, Wright SJ, Soudzilovskaia NA, Onipchenko VG, van Bodegom PM, Frenette-Dussault C, Weiher E, Pinho BX, Cornelissen JHC, Grime JP, Thompson K, Hunt R, Wilson PJ, Buffa G, Nyakunga OC, Reich PB, Caccianiga M, Mangili F, Ceriani RM, Luzzaro A, Brusa G, Siefert A, Barbosa NPU, Chapin FS III, Cornwell WK, Fang J, Wilson FG, Garnier E, Stradic SL, Peñuelas J, Melo FPL, Slaviero A, Tabarelli M, Tampucci D (2017) A global method for calculating plant CSR ecological strategies applied across biomes world-wide. Funct Ecol 31:444–457. https://doi:10.1111/1365-2435.12722

Poulsen AD, Tuomisto H, Balslev H (2006) Edaphic and Floristic Variation within a 1-ha Plot of Lowland Amazonian Rain Forest. Biotropica 38:468-478. https://doi:10.1111/j.1744-7429.2006.00168.x

PPG I (2016) A community-derived classification for extant lycophytes and ferns. J Syst Evol 5:563–603. https://doi: 10.1111/jse.12229

Reich PB (2014) The world-wide 'fast-slow' plant economics spectrum: a trait manifesto. J Ecol 102:275–301. https://doi: 10.1111/1365-2745.12211

Richard M, Bernand T, Bell G (2000) Environmental heterogeneity and the spatial structure of fern species diversity in one hectare of old-growth forest. Ecography 23:231–245. https://doi: 10.1111/j.1600-0587.2000.tb00279.x

Rosado BH, de Mattos EA (2017) On the relative importance of CSR ecological strategies and integrative traits to explain species dominance at local scales. Funct Ecol 3:1969–1974. https://doi:10.1111/1365-2435.12894

Sardans J, Peñuelas J (2015) Potassium: a neglected nutrient in global change. Glob Ecol Biogeogr 24:261–275. https://doi:0.1111/geb.12259

Schmidt J, Fassnacht FE, Lausch A, Schmidtlein S (2017) Assessing the functional signature of heathland landscapes via hyperspectral remote sensing. Ecol Indic 73:505–512. https://doi: 10.1016/j.ecolind.2016.10.017

Sessa EB, Givnish TJ (2014) Leaf form and photosynthetic physiology of *Dryopteris* species distributed along light gradients in eastern North America. Funct Ecol 28:108–123. https://doi:10.1111/1365-2435.12150

Shipley B, Lechowicz MJ, Wright I, Reich PB (2006) Fundamental trade-offs generating the worldwide leaf economics spectrum. Ecology 87:535–541. https://doi:10.1890/05-1051

Silva JMC, Tabarelli M (2000) Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404:72–74. https://doi:10.1038/35003563

Silva IAA, Pereira AFN, Barros ICL (2011) Edge effects on fern community in an Atlantic Forest remnant of Rio Formoso, PE, Brazil. Braz J Biol 71:421–430. https://doi: 10.1590/S1519-69842011000300011

Silva IA, Pereira AFDN, Barros ICL (2014) Fragmentation and loss of habitat: consequences for the fern communities in Atlantic forest remnants in Alagoas, north-eastern Brazil. Plant Ecol Divers **7**:509–517. https://doi:10.1080/17550874.2013.862750

Tosens T, Nishida K, Gago J, Coopman RE, Cabrera HM, Carriquí M, Laanisto L, Morales L, Nadal M, Rojas R, Talts E, Tomas M, Hanba Y, Niinemets Ü, Flexas J (2016) The photosynthetic capacity in 35 ferns and fern allies: mesophyll CO^2 diffusion as a key trait. New Phytol 209:1576–1590. https://doi:10.1111/nph.13719

Tuomisto H (2006) Edaphic niche differentiation among *Polybotrya* ferns in western Amazonia: implications for coexistence and speciation. Ecography 29:273–284. https://doi: 10.1111/j.2006.0906-7590.04390

Tuomisto H, Poulsen AD (1996) Influence of edaphic specialization on pteridophyte distribution in neotropical rain forests. J Biogeogr 23:283–293. https://doi:10.1046/j.1365-2699.1996.00044.x

Tuomisto H, Ruokolainen K, Poulsen AD, Moran RC, Quintana C, Cañas G, Celi J (2002) Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuní national park, Ecuadorian Amazonia. Biotropica 34:516–533. https://doi:10.1111/j.1744-7429.2002.tb00571.x

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882–892. https://doi:10.1111/j.0030-1299.2007.15559

Wang M, Zheng Q, Shen Q, Guo S (2013) The critical role of potassium in plant stress response. Int. J. Mol. Sci. 14:7370–7390. https://doi: 10.3390/ijms14047370

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas, EJ, Villar, R (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi: 10.1038/nature02403

Zuquim G, Tuomisto H, Jones MM, Prado J, Figueiredo FOG, Moulatlet GM, Costa FRC, Quesada CA, Emilio T (2014) Predicting environmental gradients with fern species composition in Brazilian Amazonia. J Veg Sci 25:1195–1207. https://doi:10.1111/jvs.12174

Tables

Table 1: Results of the final model examining the effects of local environmental conditions in the percentages of CSR strategies of ferns assemblages in Atlantic Forest remnants in the northeastern of Brazil. Each variable in the model is followed by its respective coefficient (β), the standard error (SE), lower and upper confident intervals (CI) and the p-value. Significant values are highlighted in bold. Rock = soil rock coverage; EB = soil exchangeable bases; AlS = soil aluminium saturation. Note S-strategies were not exhibited because no significant variables were retained in the model.

Model factors	β	*SE*	*95% CI*		*p*-value
			Lower	*Upper*	
C-strategies					
AlS	-0.5834	0.5827	-1.7255189	0.5586319	.317
Soil pH	-60.1795	23.4790	-106.1975111	-14.1615691	**.010**
Rock	0.2383	0.2925	-0.3350398	0.8117039	.415
Soil Sand	2.1538	1.3532	-0.4983394	4.8060038	.111
EB	3.6340	6.8702	-9.8314129	17.0994079	.597
Soil K	-10.1761	6.4184	-22.7558365	2.4036724	.113
Soil Mg	-0.6568	4.0202	-8.5361520	7.2225694	.870
R-strategies					
AlS	-1.945e-05	1.488e-04	-3.109895e-04	0.0002720991	.896
Soil pH	-1.317e-03	6.099e-03	-1.327105e-02	0.0106370973	.829
Rock	1.389e-05	8.746e-05	-1.575278e-04	0.0001852980	.874
Soil Sand	-1.969e-04	3.814e-04	-9.444303e-04	0.0005505697	.606
EB	-2.755e-03	1.982e-03	-6.638650e-03	0.0011293272	.164
Soil K	3.405e-03	1.706e-03	6.220062e-05	0.0067476714	**.046**
Soil Mg	5.370e-04	1.112e-03	-1.642564e-03	0.0027165329	.629

Figures

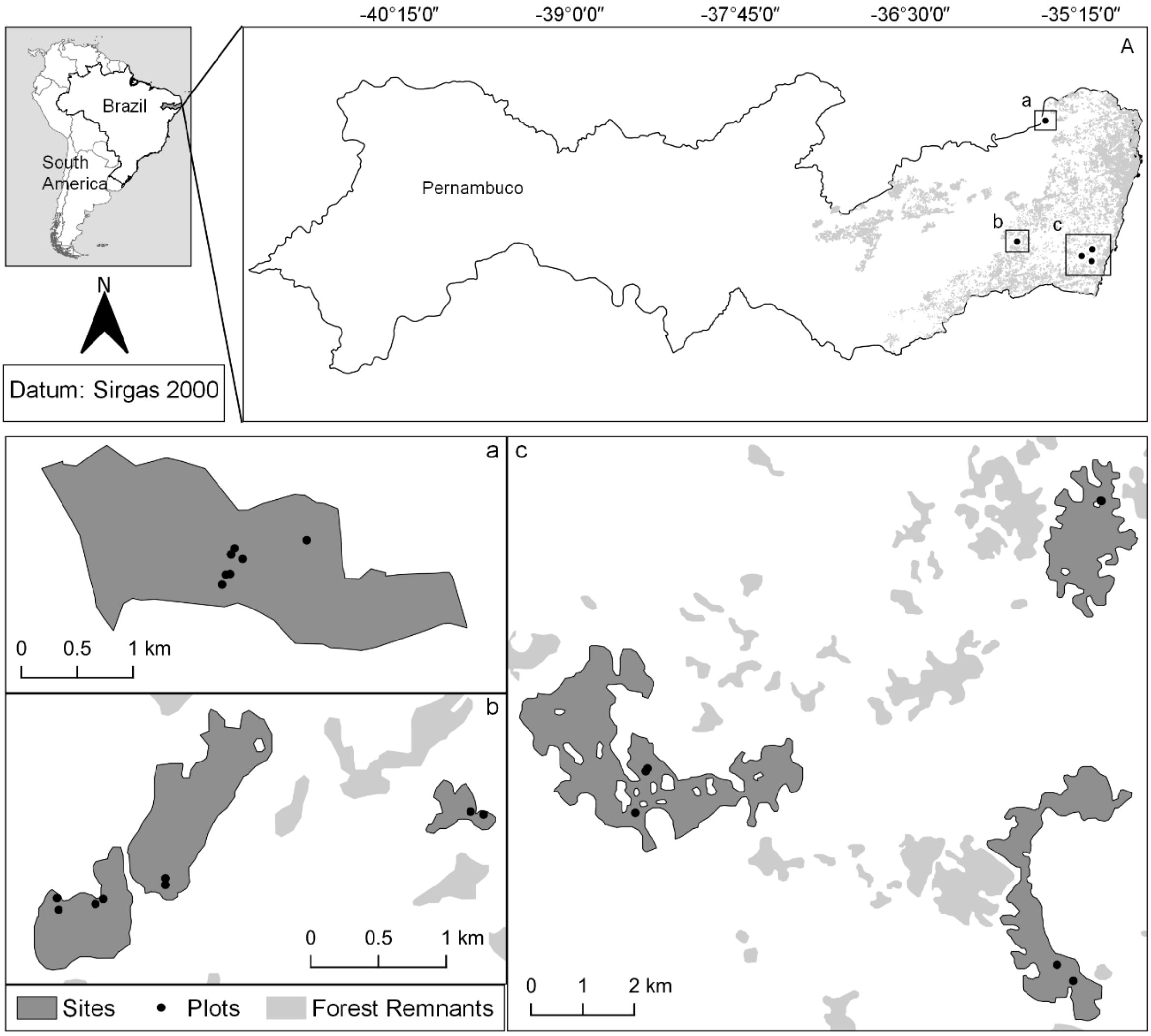


Figure 1.

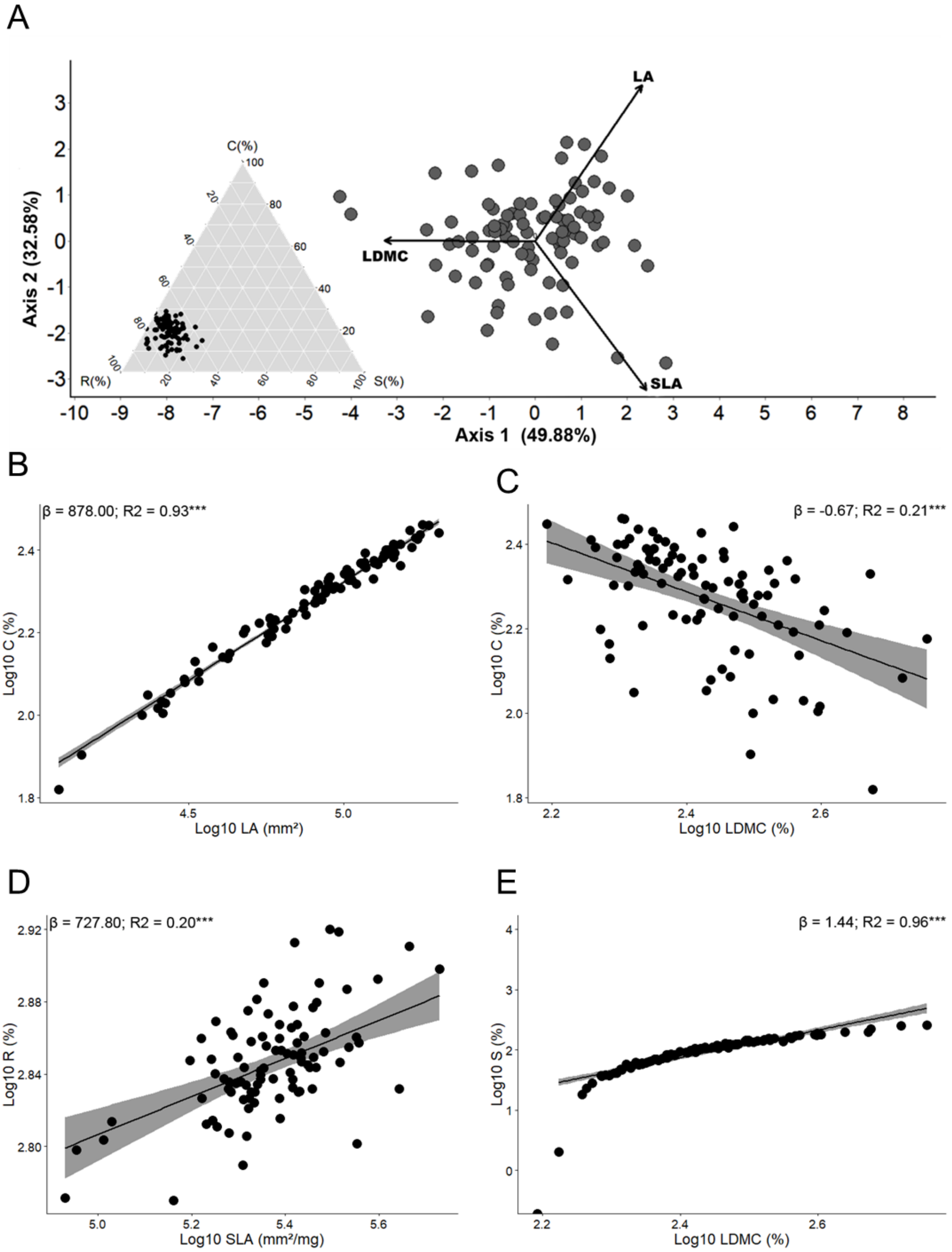

A
Axis 2 (32.58%)
Axis 1 (49.88%)
LA
LDMC
SLA
C(%)
R(%)
S(%)
B
β = 878.00; R2 = 0.93***
Log10 C (%)
Log10 LA (mm²)
C
β = -0.67; R2 = 0.21***
Log10 C (%)
Log10 LDMC (%)
D
β = 727.80; R2 = 0.20***
Log10 R (%)
Log10 SLA (mm²/mg)
E
β = 1.44; R2 = 0.96***
Log10 S (%)
Log10 LDMC (%)

Figure 2.

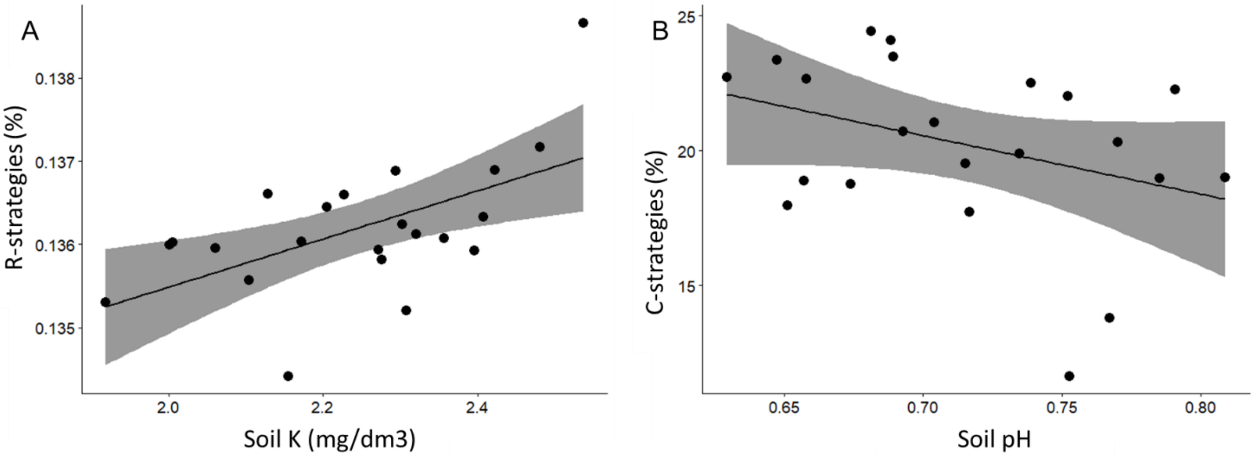

A
R-strategies (%)
0.138
0.137
0.136
0.135
2.0
2.2
2.4
Soil K (mg/dm3)
B
C-strategies (%)
25
20
15
0.65
0.70
0.75
0.80
Soil pH

Figure 3.

Figures legends

Figure 1: Figure 1: Locations of the Atlantic forest remnants studied in the northeastern Brazil, highlighting the state of Pernambuco and plots distribution in the three forest areas: São Vicente Férrer (a), Bonito (b), and Rio Formoso (c). Light grey patches are the remain Atlantic Forest and dark patches are the study areas.

Figure 2: Principal component diagrams of trait trade-offs and ternary plot with fern species CSR strategies position (A) and results of the simple regressions between leaf traits and CSR scores (B-E). *** represents $p < 0.0001$.

Figure 3: Influence of (A) soil K content and (B) soil pH in the R-strategies and C-strategies of ferns assemblages in Atlantic forest remnants in the northeastern of Brazil. Note that metric values and 95% confidence intervals (in grey) were plotted according to general linear mixed effect models results. R-strategies values were arcsine of log10 normalized, while log10+1 normalization was applied to soil K and pH values.

Supplementary material

Table S1. Climatic and vegetation type of the three sites in the Atlantic Forest in northeastern Brazil. Climatic information was obtained from the Laboratório de Meteorologia do Estado de Pernambuco (Lamepe) (available on http://www.itep.br/meteorologia/lamepe).

Site	Geographic Coordinates	Mean Annual Temperature	Mean Annual Rainfall	Mean Elevation	Vegetation Type
Rio Formoso	08°38'45.2"S; 35°10'29.9"W	24.4ºC	2000 mm	75 m	Lowland forest
Bonito	08°30'16.2"S; 35°43'14.6"W	21.5ºC	1150 mm	750 m	Submontane forest
São Vicente Férrer	07°37'02.5"S; 035°30'47.0"W	24.0 ºC	1155 mm	650 m	Submontane forest

Table S2: Local environmental variables of the fern microhabitats in Atlantic forest remnants in the northeastern of Brazil selected in the generalized mixed effect models. Note that soil rock coverage and sand content were root square transformed, while the other variables were log10+1 normalized. EB = soil exchangeable bases; AlS = soil saturation by aluminum; LL = lowland Atlantic forest remnants, SBB = submontane forest remnants in a fragmented landscape; SBM = submontane forest in a protected area. VIF = variance inflation factor.

Plot	Area	Rock	Sand	pH	EB	AlS	K	Mg
1	LL	7.07	9.08	0.79	0.63	6.03	2.00	2.29
2	LL	8.37	7.99	0.71	0.81	5.78	2.48	2.12
3	LL	0	7.93	0.69	0.80	6.33	2.23	2.39
4	LL	0	8.72	0.70	0.75	5.96	2.13	2.51
5	LL	6.71	9.32	0.78	0.52	4.19	2.06	2.29
6	LL	6.71	9.26	0.81	0.72	3.69	2.39	2.34
7	LL	5.48	8.26	0.77	0.94	2.50	2.36	2.61
8	SBB	0	8.21	0.66	0.34	5.90	1.92	2.00
9	SBB	0	7.86	0.69	0.43	8.55	2.00	2.16
10	SBB	0	7.90	0.67	0.74	7.37	2.41	2.71
11	SBB	3.16	8.83	0.68	0.75	6.24	2.31	2.32
12	SBB	0	7.43	0.63	0.49	5.64	2.27	2.30
13	SBB	4.12	7.61	0.73	0.62	6.66	2.10	2.29
14	SBB	0	7.61	0.77	0.80	6.85	2.15	2.47
15	SBB	0	7.93	0.69	0.69	7.00	2.20	2.39
16	SBM	0	7.66	0.72	0.94	6.08	2.28	2.80
17	SBM	0	7.92	0.65	0.64	7.99	2.17	2.51
18	SBM	0	7.41	0.66	0.66	7.41	2.29	2.07
19	SBM	0	7.62	0.65	0.70	7.93	2.32	2.29
20	SBM	0	8.11	0.74	0.79	3.01	2.42	2.73
21	SBM	5.48	7.87	0.75	0.77	3.07	2.54	2.68
22	SBM	6.71	7.67	0.75	0.72	4.31	2.30	2.69
VIF:		**2.61**	**1.40**	**3.49**	**3.13**	**2.37**	**2.93**	**2.39**

Table S3: Fern species sampled in 22 plots along Atlantic forest remnants in the northeastern of Brazil followed by leaf trait values and CSR strategies according to Stratefy spreadsheet (Pierce et al. 2017). LA = Leaf area; SLA = specific leaf area; LDMC = leaf dry matter content. Note that leaf traits were log10 normalized. Pierce et al. 2017- A global method for calculating plant CSR ecological strategies applied across biomes world-wide. Functional Ecology 31(2):444-457.

Plot	**Family**	**Species**	**LA (mm^2)**	**SLA (mm^2/mg)**	**LDMC (%)**	**C:S:R**	**Strategy**
1	Anemiaceae	*Anemia hirta* (L.) Sw.	3.417	4.557	1.595	10 : 18 : 72 %	R/SR
	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.184	4.335	1.357	26 : 6 : 68 %	R/CR
	Blechnaceae	*Blechnum occidentale* L.	4.016	4.452	1.411	21 : 9 : 70 %	R/CR
	Cyatheaceae	*Cyathea microdonta* (Desv.) Domin	4.184	4.554	1.550	23 : 14 : 63 %	R/CR
	Tectariaceae	*Tectaria incisa* Cav.	3.677	4.665	1.272	16 : 3 : 81 %	R/CR
2	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.142	4.433	1.308	25 : 4 : 71 %	R/CR
	Blechnaceae	Blechnum *occidentale* L.	3.941	4.354	1.438	20 : 10 : 70 %	R/CR
	Tectariaceae	*Tectaria incisa* Cav.	3.919	4.730	1.223	21 : 0 : 79 %	R/CR
	Thelypteridaceae	*Steiropteris polypodioides* (Raddi) Salino & T.E. Almeida	3.424	4.359	1.574	11 : 18 : 72 %	R/SR
3	Cyatheaceae	*Cyathea phalerata* Mart.	3.873	4.380	1.426	19 : 10 : 71 %	R/CR
	Cyatheaceae	*Cyathea praecincta* (Kunze) Domin	3.945	4.441	1.363	20 : 7 : 73 %	R/CR
	Dryopteridaceae	*Cyclodium meniscioides* (Willd.) C.Presl	3.875	4.339	1.292	20 : 4 : 76 %	R/CR
	Marattiaceae	*Danaea geniculata* Raddi	3.763	4.363	1.380	17 : 8 : 75 %	R/CR
	Lindsaeaceae	*Lindsaea lancea* (L.) Bedd.	3.755	4.341	1.559	16 : 16 : 68 %	R/SR
	Dryopteridaceae	*Polybotrya osmundacea* Willd.	4.021	4.404	1.365	22 : 7 : 71 %	R/CR
	Thelypteridaceae	*Meniscium macrophyllum* Kunze	4.131	4.411	1.352	24 : 6 : 69 %	R/CR
4	Cyatheaceae	*Cyathea praecincta* (Kunze) Domin	4.098	4.348	1.379	24 : 8 : 69 %	R/CR

	Family	*Species*	*LA*	*SLA*	*LDMC*	*C:S:R*	*Strategy*
4	Dryopteridaceae	*Cyclodium meniscioides* (Willd.) C.Presl	3.952	4.288	1.336	21 : 6 : 7rr3 %	R/CR
	Marattiaceae	*Danaea geniculata* Raddi	4.003	4.387	1.331	22 : 6 : 72 %	R/CR
	Thelypteridaceae	*Meniscium macrophyllum* Kunze	4.065	4.417	1.345	23 : 6 : 71 %	R/CR
	Thelypteridaceae	*Steiropteris polypodioides* (Raddi) Salino & T.E. Almeida	3.154	4.472	1.495	8 : 14 : 78 %	R/SR
5	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	3.927	4.316	1.484	19 : 13 : 68 %	R/CR
	Cyatheaceae	*Cyathea microdonta* (Desv.) Domin	3.906	4.536	1.426	19 : 10 : 72 %	R/CR
	Gleicheniaceae	*Gleichenella pectinata* (Willd.) Ching	3.769	4.231	1.639	15 : 20 : 65 %	R/SR
	Thelypteridaceae	*Meniscium serratum* Cav.	3.766	4.425	1.415	17 : 10 : 74 %	R/CR
6	Cyatheaceae	*Alsophila sternbergii* (Sternb.) D.S. Conant	4.309	4.310	1.470	28 : 11 : 62 %	R/CR
	Anemiaceae	*Anemia hirta* (L.) Sw.	3.079	4.482	1.677	7 : 22 : 71 %	R/SR
	Blechnaceae	*Blechnum occidentale* L.	3.914	4.295	1.481	19 : 13 : 68 %	R/CR
	Cyatheaceae	*Cyathea microdonta* (Desv.) Domin	4.184	4.554	1.550	23 : 14 : 63 %	R/CR
	Marattiaceae	*Danaea nodosa* (L.)Sm.	3.763	4.363	1.380	17 : 8 : 75 %	R/CR
	Tectariaceae	*Tectaria incisa* Cav.	3.677	4.665	1.272	16 : 3 : 81 %	R/CR
	Thelypteridaceae	*Meniscium serratum* Cav.	3.766	4.425	1.415	17 : 10 : 74 %	R/CR
7	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.072	4.449	1.374	23 : 7 : 70 %	R/CR
	Blechnaceae	*Blechnum occidentale* L.	3.973	4.279	1.462	21 : 12 : 68 %	R/CR
	Cyatheaceae	*Cyathea microdonta* (Desv.) Domin	4.184	4.554	1.550	23 : 14 : 63 %	R/CR
	Dryopteridaceae	*Cyclodium meniscioides* (Willd.) C.Presl	3.957	4.284	1.324	22 : 5 : 73 %	R/CR
	Marattiaceae	*Danaea geniculata* Raddi	4.184	4.554	1.550	23 : 14 : 63 %	R/CR
	Lindsaeaceae	*Lindsaea lancea* (L.) Bedd.	3.625	4.250	1.567	14 : 17 : 69 %	R/SR
	Family	*Species*	*LA*	*SLA*	*LDMC*	*C:S:R*	*Strategy*

7	Metaxyaceae	*Metaxya parkeri* (Hook. & Grev.) ex J. Sm.	3.965	4.285	1.478	20 : 12 : 68 %	R/CR
	Dryopteridaceae	*Olfersia cervina* (L.) Kunze	4.011	4.327	1.327	23 : 5 : 72 %	R/CR
	Thelypteridaceae	*Christella hispidula* (Decne) Holttum	3.487	4.532	1.436	12 : 11 : 77 %	R/CR
	Thelypteridaceae	*Meniscium macrophyllum* Kunze	4.164	4.551	1.258	26 : 2 : 72 %	R/CR
	Thelypteridaceae	*Steiropteris polypodioides* (Raddi) Salino & T.E. Almeida	3.908	4.375	1.485	19 : 12 : 69 %	R/CR
8	Polypodiaceae	*Pecluma robusta* (Fée) M.Kessler & A.R.Sm.	4.097	4.162	1.673	21 : 20 : 59 %	R/CSR
	Polypodiaceae	*Serpocaulon catharinae* (Langsd. & Fisch.) A.R.Sm.	4.100	4.416	1.392	23 : 8 : 69 %	R/CR
	Polypodiaceae	*Serpocaulon* sp.	4.100	4.416	1.392	23 : 8 : 69 %	R/CR
9	Dryopteridaceae	*Elaphoglossum iguapense* Brade	4.057	4.030	1.456	23 : 12 : 65 %	R/CR
	Polypodiaceae	*Pecluma robusta* (Fée) M.Kessler & A.R.Sm.	3.812	4.322	1.598	16 : 18 : 66 %	R/SR
	Polypodiaceae	*Serpocaulon* sp.	4.127	4.517	1.345	24 : 6 : 70 %	R/CR
	Tectariaceae	*Triplophyllum dicksonioides* (Fée) Holttum	4.165	4.458	1.382	25 : 7 : 68 %	R/CR
10	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.275	4.324	1.308	29 : 4 : 67 %	R/CR
	Blechnaceae	*Telmatoblechnum serrulatum* (Rich.) Perrie et al.	3.610	4.352	1.493	14 : 14 : 73 %	R/CR
	Cyatheaceae	*Cyathea phalerata* Mart.	4.111	4.429	1.423	23 : 9 : 68 %	R/CR
	Dryopteridaceae	*Cyclodium meniscioides* (Willd.) C.Presl	4.070	4.284	1.264	25 : 2 : 73 %	R/CR
	Lindsaeaceae	*Lindsaea quadrangulares* Raddi	4.042	4.317	1.562	21 : 15 : 64 %	R/CSR
	Dryopteridaceae	*Polybotrya osmundacea* Willd.	3.941	4.312	1.429	20 : 10 : 70 %	R/CR
	Thelypteridaceae	*Meniscium longifolium* Desv.	3.929	4.312	1.521	19 : 14 : 67 %	R/CR
	Thelypteridaceae	*Meniscium serratum* Cav.	3.836	4.391	1.447	18 : 11 : 71 %	R/CR
11	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.161	4.347	1.315	26 : 5 : 70 %	R/CR
	Family	*Species*	*LA*	*SLA*	*LDMC*	*C:S:R*	*Strategy*
	Dryopteridaceae	*Cyclodium meniscioides* (Willd.) C.Presl	4.255	4.223	1.304	29 : 4 : 67 %	R/CR
	Polypodiaceae	*Pecluma robusta* (Fée) M.Kessler & A.R.Sm.	3.879	4.255	1.605	18 : 18 : 65 %	R/CSR

12	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.275	4.324	1.308	29 : 4 : 67 %	R/CR
	Dryopteridaceae	*Polybotrya osmundacea* Willd.	4.021	4.269	1.408	22 : 9 : 69 %	R/CR
	Blechnaceae	*Salpichlaena volubilis* (Kaulf.) J.Sm.	3.949	4.196	1.387	21 : 8 : 70 %	R/CR
13	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	3.774	4.280	1.537	16 : 15 : 68 %	R/CR
	Blechnaceae	*Blechnum occidentale* L.	4.016	4.435	1.392	21 : 8 : 70 %	R/CR
	Cyatheaceae	*Cyathea microdonta* (Desv.) Domin	4.184	4.554	1.550	23 : 14 : 63 %	R/CR
14	Anemiaceae	*Anemia villosa* Humb. & Bonpl. ex Willd.	3.532	3.954	1.721	12 : 25 : 63 %	R/SR
	Gleicheniaceae	*Gleichenella pectinata* (Willd.) Ching	3.750	3.930	1.758	15 : 26 : 59 %	R/CSR
	Pteridaceae	*Pteridium arachnoideum* subsp. *arachnoideum* (Kaulf.) Maxon	4.014	4.012	1.522	22 : 15 : 64 %	R/CSR
15	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.216	4.426	1.192	28 : 0 : 72 %	R/CR
	Blechnaceae	*Telmatoblechnum serrulatum* (Rich.) Perrie et al.	4.027	4.333	1.483	21 : 12 : 67 %	R/CR
	Cyatheaceae	*Cyathea phalerata* Mart.	4.139	4.466	1.340	25 : 6 : 70 %	R/CR
	Dryopteridaceae	*Polybotrya osmundacea* Willd.	4.067	4.486	1.297	23 : 4 : 73 %	R/CR
	Blechnaceae	*Salpichlaena volubilis* (Kaulf.) J.Sm.	4.239	4.280	1.422	27 : 9 : 64 %	R/CR
16	Pteridaceae	*Adiantopsis radiata* (L.) Fée	3.400	4.299	1.599	10 : 19 : 71 %	R/SR
	Blechnaceae	*Blechnum occidentale* L.	3.820	4.348	1.512	17 : 14 : 69 %	R/CR
	Dryopteridaceae	*Ctenitis distans* (Brack.) Ching	3.413	4.387	1.529	11 : 16 : 74 %	R/SR
	Marattiaceae	*Danaea geniculata* Raddi	3.727	4.252	1.399	17 : 9 : 74 %	R/CR
	Dryopteridaceae	*Polybotrya osmundacea* Willd.	3.991	4.244	1.530	20 : 14 : 65 %	R/CR
	Family	*Species*	*LA*	*SLA*	*LDMC*	*C:S:R*	*Strategy*
	Saccolomataceae	*Saccoloma elegans* Kaulf.	3.925	4.327	1.506	19 : 13 : 68 %	R/CR
	Tectariaceae	*Triplophyllum dicksonioides* (Fée) Holttum	3.632	4.414	1.472	14 : 13 : 73 %	R/CR
17	Dryopteridaceae	*Ctenitis distans* (Brack.) Ching	3.413	4.387	1.529	11 : 16 : 74 %	R/SR
	Marattiaceae	*Danaea geniculata* Raddi	3.763	4.221	1.421	17 : 10 : 72 %	R/CR

	Lomariopsidaceae	*Lomariopsis japurensis* (Mart.) J.Sm	3.484	4.321	1.465	12 : 13 : 75 %	R/SR
	Dryopteridaceae	*Polybotrya osmundacea* Willd.	3.991	4.244	1.530	20 : 14 : 65 %	R/CR
	Saccolomataceae	*Saccoloma elegans* Kaulf.	3.869	4.305	1.499	18 : 13 : 69 %	R/CR
	Polypodiaceae	*Serpocaulon* sp.	4.100	4.416	1.392	23 : 8 : 69 %	R/CR
	Tectariaceae	*Triplophyllum dicksonioides* (Fée) Holttum	3.531	4.418	1.453	13 : 12 : 75 %	R/CR
18	Dryopteridaceae	*Ctenitis distans* (Brack.) Ching	3.349	4.468	1.499	10 : 14 : 76 %	R/SR
	Marattiaceae	*Danaea geniculata* Raddi	3.682	4.354	1.335	16 : 6 : 78 %	R/CR
	Dryopteridaceae	*Didymochlaena truncatula* (Sw.) J.Sm.	3.906	4.459	1.313	20 : 5 : 75 %	R/CR
	Athyriaceae	*Diplazium cristatum* (Desr.) Alston	4.162	4.389	1.455	24 : 10 : 65 %	R/CR
	Thelypteridaceae	*Goniopteris biolleyi* (Christ) Pic.Serm.	3.440	4.598	1.429	11 : 11 : 78 %	R/CR
19	Dryopteridaceae	*Ctenitis distans* (Brack.) Ching	3.349	4.468	1.499	10 : 14 : 76 %	R/SR
	Cyatheaceae	*Cyathea abreviata* I. Fern.	4.220	4.644	1.368	26 : 7 : 68 %	R/CR
	Marattiaceae	*Danaea geniculata* Raddi	3.763	4.221	1.421	17 : 10 : 72 %	R/CR
	Dryopteridaceae	*Polybotrya osmundacea* Willd.	4.137	4.435	1.298	25 : 4 : 71 %	R/CR
	Saccolomataceae	*Saccoloma elegans* Kaulf.	3.869	4.305	1.499	18 : 13 : 69 %	R/CR
	Thelypteridaceae	*Meniscium macrophyllum* Kunze	4.247	4.430	1.328	27 : 5 : 68 %	R/CR
20	Marattiaceae	*Danaea geniculata* Raddi	3.576	4.420	1.285	15 : 4 : 82 %	R/CR
	Athyriaceae	*Diplazium cristatum* (Desr.) Alston	3.520	4.514	1.286	13 : 4 : 83 %	R
	Thelypteridaceae	*Goniopteris biolleyi* (Christ) Pic.Serm.	3.440	4.598	1.429	11 : 11 : 78 %	R/CR
	Family	*Species*	*LA*	*SLA*	*LDMC*	*C:S:R*	*Strategy*
	Thelypteridaceae	*Meniscium macrophyllum* Kunze	4.247	4.430	1.328	27 : 5 : 68 %	R/CR
21	Dryopteridaceae	*Didymochlaena truncatula* (Sw.) J.Sm.	3.906	4.459	1.313	20 : 5 : 75 %	R/CR
	Athyriaceae	*Diplazium cristatum* (Desr.) Alston	3.366	4.496	1.322	11 : 6 : 83 %	R
	Lomariopsidaceae	*Lomariopsis japurensis* (Mart.) J.Sm	3.780	4.242	1.470	17 : 13 : 70 %	R/CR

	Thelypteridaceae	*Goniopteris biolleyi* (Christ) Pic.Serm.	3.487	4.532	1.436	12 : 11 : 77 %	R/CR
22	Blechnaceae	*Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich	4.232	4.387	1.350	27 : 6 : 67 %	R/CR
	Blechnaceae	*Blechnum occidentale* L.	4.016	4.435	1.392	21 : 8 : 70 %	R/CR
	Dryopteridaceae	Ctenitis distans (Brack.) Ching	3.349	4.468	1.499	10 : 14 : 76 %	R/SR
	Cyatheaceae	Cyathea sp.	4.220	4.644	1.368	26 : 7 : 68 %	R/CR
	Thelypteridaceae	Meniscium longifolium Desv.	3.929	4.312	1.521	19 : 14 : 67 %	R/CR
	Thelypteridaceae	Meniscium macrophyllum Kunze	4.069	4.461	1.355	23 : 6 : 71 %	R/CR

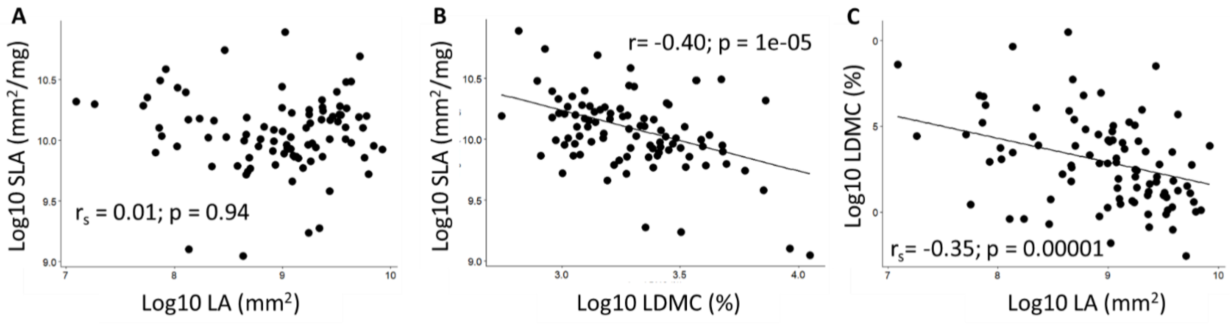


Figure S1: Correlation between ferns leaf traits in Atlantic forest remnants in the northeastern of Brazil using Spearman (r_S) and Pearson (r) correlation coefficients. SLA = Specific leaf area; LA = Leaf area; LDMC = Leaf dry matter content.

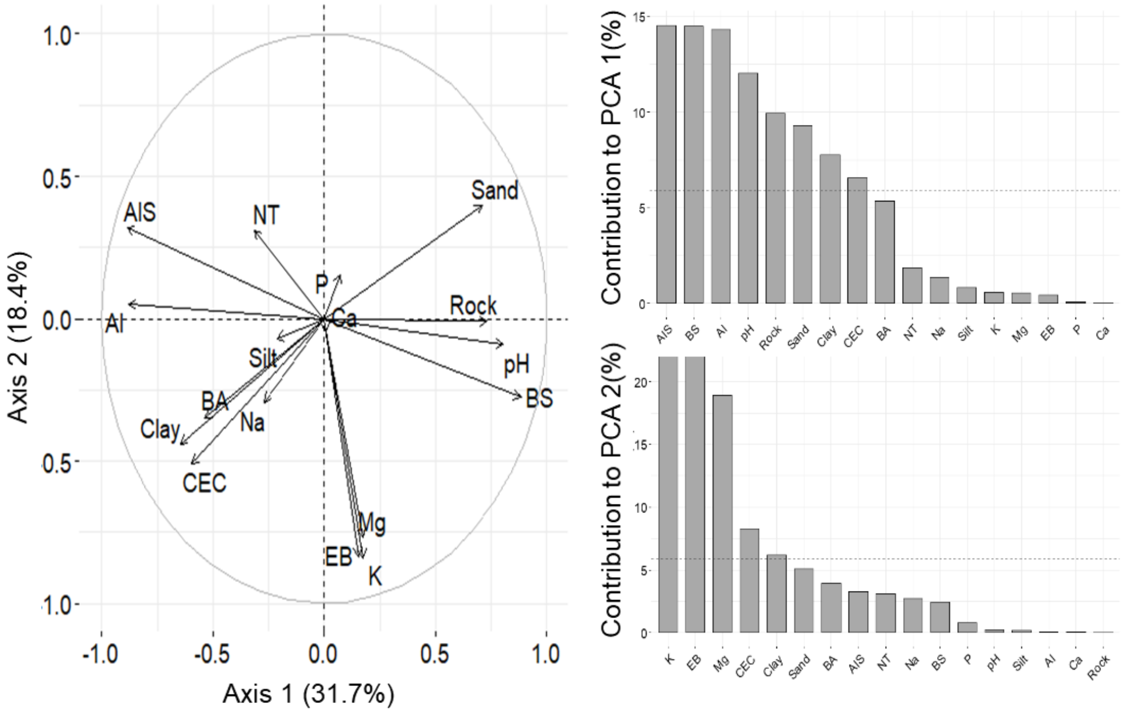


Figure S2: Principal component analysis (PCA) diagram and contributions of the local environmental variables to the first two axes of PCA. The dashed lines indicate the expected average contribution based on species distribution along with the principal components. Variables with a contribution above the dashed line can be considered as important in contributing to the component. BA: basal area; BS: soil bases saturation; NT: number of trees in the plot; Rock: rock outcrops cover (%) in the plot; CEC: soil cation-exchange capacity; Soil percentages of silt, sand and clay and soil concentrations of Al, Ca, K, Mg, and Na.

5 FUNCTIONAL TRAIT CONVERGENCE DOMINATES ALONG EDAPHIC GRADIENTS IN LOCAL FERN ASSEMBLAGES

MANUSCRITO SUBMETIDO AO PERIÓDICO BIOTRÓPICA

Functional trait convergence dominates along edaphic gradients in local fern assemblages

Lucas Erickson Nascimento da Costa[1], Rafael de Paiva Farias[1], Michael Kessler[2] & Iva Carneiro Leão Barros[1]

[1]Departamento de Botânica, Universidade Federal de Pernambuco. CEP 50670-420, Recife, Brasil.

[2]Department of Systematic and Evolutionary Botany, University of Zurich, CH-8008 Zurich, Switzerland.

Corresponding author: lucasbiologicasufpe@hotmail.com

Receveid:________________; Revised:________________; Accepted:________________.

Abstract

Numerous drivers affect the functional structure of plants, influencing species coexistence. Currently, a conceptual framework about mechanisms of species coexistence, functional diversity, and their interactions is required to forecast responses to environmental changes and to support more effective conservation and management strategies. Here, we analyzed leaf trait convergence and divergence among co-occurring fern species, the relationship between functional and taxonomic components, and the role of local environmental conditions on the functional diversity of the assemblages. We measured leaf traits in fern assemblages and local environmental conditions from various microhabitats in the Atlantic forest of northeastern Brazil. Functional trait convergence dominated in the fern assemblages. In general, there was a lack of phylogenetic signal on leaf traits (except leaf dry matter content). The taxonomic component influenced leaf trait variation, richness, redundancy and divergence functional. Edaphic conditions, especially soil pH and nutrients availability, drove the functional structure of fern assemblages. Overall, functional patterns were related to the diversity and species identity of the fern assemblages, with edaphic filters structuring functional patterns by mediating convergence-divergence patterns.

Keywords: assembly rules, Brazil, environmental filtering, functional diversity, leaf traits, phylogenetic signal, species coexistence, trait convergence-divergence.

Data Availability Statement

The data that support the findings of this study are openly available from the supplementary material.

INTRODUCTION

Functional leaf traits reflect basic trade-offs related to resource acquisition and competition, as evidenced by the leaf economic spectrum - LES (Wright et al., 2004; Díaz et al., 2016; Bruelheide et al., 2018). According to the LES trade-offs, plants are distributed along a gradient of strategies related to resource acquisition, with acquisitive and conservative species fundamentally opposed to one another (Reich, 2014; Díaz et al., 2016). Although these trade-offs might occur at different spatial scales (de Bello et al., 2009), interspecific trade-offs related to resource utilization and tolerance to abiotic stress are more apparent at the local scale (Kneitel & Chase, 2004), denoting the main mechanism structuring species coexistence.

Plant traits within assemblages may exhibit a convergence pattern, when structured by environmental filtering, since abiotic factors might narrow trait distributions (Cornwell & Ackerly, 2009; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010), or divergence, created from competition, reducing niche overlapping, and promoting a partition of resources between co-existing species (Stubbs & Wilson, 2004; Kraft, Valencia, & Ackerly, 2008; Adler, Ellner, & Levine, 2010). However, competition can also create convergence patterns if certain competitive strategies are superior under a given set of environmental conditions (Grime, 2006; Cornwell & Ackerly, 2009). Convergence and divergence might co-occur along environmental gradients (Mason, Lanoiselee, Mouillot, Irz, & Argillier, 2007), which increases the uncertainties about the processes regulating coexistence (Grime, 2006). Additionality, convergence and divergence patterns might be a response of phylogenetic structure (Webb, Ackerly, Mcpeek, & Donoghue, 2002). When closely related species share ecological characteristics, traits are clustered in the phylogeny, and thus, related species are prone to co-occur, while when the trait is overdispersed, different species might cooccur leading to a divergence pattern (Cavender-Bares, Keen, & Miles, 2006). Thus, the phylogenetic structure has to be considered alongside the ecological process (filters and competition) for a full understanding of the mechanisms regulating species coexistence.

Understanding the ecological rules of coexisting species may be reached from functional–taxonomic relationships (Diaz & Cabido, 2001). Species-rich communities tend to show high functional diversity because higher species numbers allows for for higher trait diversity (Yachi & Loreau, 2007). Nevertheless, species-rich communities might also exhibit high similarity of traits, generating functional redundancy (Flynn et al., 2009; Cadotte, Carscadden, & Mirotchnick, 2011). Conversely, species-poor communities tend to exhibit low functional diversity (Yachi & Loreau, 2007; Mokany, Ash, & Roxburgh, 2008) but may contain species inhabiting different niches (Yachi & Loreau, 2007).

Currently, ecologists are challenged to explain the mechanisms of species coexistence, functional diversity, and their interactions, particularly against the background of the environmental crisis, where this knowledge is required to forecast responses to environmental changes and to support more effective conservation and management strategies (Terborgh, Pitman, Silman, Schichter, & Núñez, 2002). This is the scenario of Brazilian Atlantic forest, a “top hotspot” for conservation priorities due to the intense degradation and fragmentation (Eisenlohr, Oliveira-Filho, & Prado, 2015), especially in the northeast, where habitats are highly fragmented, isolated, and surrounded by a matrix of agricultural systems (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Our study aims to contribute to the understanding of the mechanism structuring the local coexistence of ferns, which are an important component of the tropical understory (Sharpe, Mehltreter, & Walker, 2010) and species-rich in Atlantic Forest (Prado et al., 2015). We selected a set of LES traits in fern assemblages along Atlantic forest remnants in north-eastern Brazil in order (1) to analyze the functional patterns of either convergence or divergence in fern assemblages; (2) to identify if these LES traits are conserved in the phylogeny; (3) to analyze if LES trait diversity is correlated with the taxonomic structure of the assemblages (i.e., species richness, diversity, and composition); and (4) to analyze the effect of local environmental factors on LES trait diversity.

While the associations between environmental factors with ferns diversity and composition has been widely recognized (e.g., Tuomisto & Poulsen, 1996; Karst, Gilbert, & Lechowicz, 2005; Jones, Tuomisto, Clark, & Olivas, 2006), few studies have focused on environment-functional traits relationships (e.g., Kluge & Kessler, 2011; Zhang et al., 2017; Carvajal-Hernández, Gómez-Díaz, Kessler & Krömer, 2018). Some studies have documented the role of local environmental factors, especially soil and climatic conditions in determining fern community patterns of diversity and composition (Tuomisto & Poulsen, 1996; Karst, Gilbert, & Lechowicz, 2005; Kluge & Kessler, 2011), revealing the importance of the environmental filtering to fern community responses. Since our study sites have limited climatic variation, we proposed the hypothesis that environmental filtering via edaphic factors is the main driver of the LES traits in our local fern assemblages. Since edaphic niche preferences are common in ferns (e.g., Tuomisto & Poulsen, 1996; Zuquin et al., 2014), we expected that co-occurring species will be filtered according to local environmental conditions, and thus, would exhibit similar traits leading to a functional convergence within assemblages.

Ferns with similar edaphic niches might be closely related, indicating niche conservatism, as found by Lehtonem, Jones, Zuquim, Prado, & Tuomisto (2015). Thus, since LES traits also reflect niche preferences, we expected that closely related species would present similarities in LES traits values, creating a clustered pattern in phylogeny. Furthermore, we expected that the taxonomic structure of the fern assemblages such as species richness and diversity is not correlated to LES trait diversity of the assemblages due to overlap in trait values among co-occurring species (i.e., functional redundancy). However, since ferns species are good ecological indicators of environmental factors, including edaphic conditions (e.g., Zuquin et al., 2014), we expected that different species are selected along environmental gradients, so that shifts in the floristic composition will be related to changes in LES trait values and functional diversity.

Finally, since the environment selects different species strategies along environmental gradients (e.g., Kneitel & Chase, 2004; Cornwell, Schwilk, & Ackerly, 2006; Viani, Rodrigues, Dawson, Lambers, & Oliveira, 2014), we expected that changes in local environmental factors will lead to shifts in LES trait values and functional diversity of the fern assemblages, where, under stressful conditions (e.g., acidic soils, intense luminosity, or low nutrient availability), species will converge around conservative strategies, with low trait variation and low functional diversity. On the other hand, under more favorable conditions (e.g., shaded habitats, high water availability, and high nutrient availability), species will overlap around acquisitive strategies, with both high trait variation and functional diversity.

METHODS

Study area and data collection

We studied fern assemblages in three Atlantic forest areas in Pernambuco, northeastern Brazil. The climate and other main vegetational characteristics were summarized in Table 1. We conducted field sampling from July 2016 to June 2017 and established 22 plots (10 m x 20 m) in habitats suitable to ferns (e.g. shaded microhabitats, slopes, ravines, and marshy areas in the forest interior) following previous studies in northeastern Atlantic Forest remnants (e.g., Pereira, Silva, Santiago, & Barros, 2014; Silva, Pereira, & Barros, 2014). Plots in the same remnant were at least 100 m apart from each other.

In each plot, we measured the number and basal area of trees with a diameter at breast height - DBH ≥ 15 cm, as a proxy to luminosity and forest structure. Rock cover was sampled following the Braun–Blanket scale (Kent & Coker, 1994), due to the importance of rock outcrops in increasing habitat heterogeneity. Surface soil samples (0-20 cm depth) were collected in five points of each plot and mixed to a single composite sample (500 g). Soil samples were air-dried, cleaned from roots and detritus, and homogenized.

A set of 14 edaphic variables were measured (Table S1). Soil pH was assessed in a water solution. Concentrations of Ca, Mg and Al (exchangeable bases) were extracted with KCl 1 mol/L and determined using an atomic absorption spectrophotometer. The Mehlich 1 method was employed for the extraction of available P in the soil (determined by spectrophotometry) and exchangeable K and Na (measured using a flame photometer). Exchangeable bases, effective cation-exchange capacity (CEC(t)), base saturation, and Al-saturation were also measured. Soil texture (i.e. the percentage of clay, silt, and sand) was determined using the pipette method.

We counted and identified all ferns in the plots. For clonal species (especially those with creeping rhizome), each clump was counted as an individual (see Costa, Magnusson, & Luizao, 2005). Species identification was based on literature and specialists. Species names and authors were obtained from The International Plant Names Index (IPNI) and vouchers deposited at the UFP herbarium.

Trait selection

We selected and measured a set of LES (leaf economic spectrum) traits for species ferns. These traits are widely applied and related to resource acquisition, competitive ability, stress tolerance, and abiotic conditions of plants (Westoby, 1998; Hodgson et al., 2011; Pérez-Harguindeguy et al., 2013; Díaz et al. 2016). For each species per plot, we measured leaf area (LA), specific leaf area (SLA), leaf dry-matter content (LDMC), and leaf water content (LWC) in five individuals following Pérez-Harguindeguy et al. (2013). Individuals from areas close to the plots were used to complement the sample number if fewer than five individuals were encountered in a plot.

LA is an indicator of leaf construction cost, where small leaves indicate a reduction in water loss and an increase in the tolerance to nutritional stress (Cornelissen et al., 2003; Niinemets et al., 2007). SLA is an important descriptor of the LES, where high values are associated with high growth rates, whereas low values indicate low growth rate, high leaf longevity, and with long nutrient residence time (Poorter & Bongers, 2006; Pérez-Harguindeguy et al., 2013). LDMC represents resource use strategies, with high values denoting conservative strategies, characterized by low growth rates and high tolerance to abiotic stress, especially related to edaphic conditions (Hodgson et al., 2011; Pérez-Harguindeguy et al., 2013). Finally, LWC is associated with tolerance to hydric stress conditions (Ogburn & Edwards, 2012).

Taxonomic structure

We estimated species richness (SR), the Shannon-Wiener diversity index (H’), and Pielou’s evenness (J) for all plots (Table 2S). The floristic composition of all plots was reduced to multivariate axes using nonmetric multidimensional scaling (NMDS) (Figure S1). The NMDS was based on Bray-Curtis dissimilarity using abundance values (log10+1 transformed).

Functional structure

We calculated the community-weighted mean (CWM) and the abundance-weighted coefficient of variation (CV) to access the functional structure of the assemblages in each plot. CWM and CV were calculated as follows:

$$CWM = \sum_{i=1}^{S} wi \text{ X } xi \qquad CV = \frac{SD^*}{CWM}$$

where S is the total number of species in the plot, wi the species abundance of the ith species in the plot, and xi represents the trait value of the ith species in the plot. SD^* is the standard deviation of the abundance-weighted trait values, and CV was the SD* of the species in the plot divided by the CWM of the plot. CWM highlights the impacts of dominant species in the community (Díaz et al., 2007; Mason et al., 2012), whereas CV represents the extent of variability of a given trait related to CWM. Additionally, CV allows comparisons between traits expressed in different units and scales.

We selected these single-trait metrics due to their proven performance related to environmental gradients (Butterfield & Suding, 2013). Further, we coupled single-trait metrics with multi-trait functional diversity indexes: functional richness (FRiq), the standardized effect size Rao quadratic entropy (SESRao) and the functional redundancy (FRed), as measurements of functional space, functional divergence, and functional redundancy, respectively (de Bello, Lavergne, Meynard, Lepš, & Thuiller, 2010; Mason, de Bello, Mouillot, Pavoine, & Dray, 2013). The SESRao < 0 indicates functional convergence, while SESRao > 0 indicates functional divergence (Mason, de Bello, Mouillot, Pavoine, & Dray, 2013).

Data analyses

In order to analyze weather leaf traits of co-occurring species convergence or divergence, we used the standardized effect size (SES) on trait dissimilarity among co-occurring fern species. We calculated the trait dissimilarity between co-occurring species using euclidian distances and calculated the mean pairwise distance (MPD) per assemblages. Leaf traits were log10 normalized to avoid skewed values, similarly, the same was done to determine the functional diversity index.

SESMPD was calculated following Gotelli & McCabe (2002) as SES = (MPD_{obs} – MPD_{null})/MPD_{sdnull}, where MPD_{obs} is the observed mean pairwise distance for each assemblage, MPD_{null} is the mean of the MPD obtained from 1000 random null communities, and MPD_{sdnull} is the standard deviation of the MPD_{null}. Null trait MPD was obtained from shuffles in the row names on the trait matrix. This method kept the trait co-variance and overall phenotypes (Kembel et al., 2010). SESMPD < 0 suggest trait convergence, while, SESMPD > 0 indicates the prevalence of trait divergence.

We tested for the presence of a phylogenetic signal using Pagel's lambda in order to verify if closely related species would exhibit similar leaf trait values. We used Pagel's lambda index due to several advantages, including not being affected by the number of species in the phylogeny (Münkemüller et al., 2012). Pagel's lambda ranges from zero to one, where values close to zero indicate phylogenetic independence, whereas values close to one indicate a phylogenetic aggregation under a Brownian motion model (Münkemüller et al., 2012). Our phylogeny was obtained from a big phylogenetic tree with around 4000 fern species based on Testo & Sundue (2016) and expanded by Noben et al. (in review). We pruned the phylogenetic tree according to our sampled species. Sampled species that were missing in the phylogeny were substituted by the closely related sister species in the big phylogenetic tree. We did not calculate the phylogenetic signal of leaf LWC because this trait is mathematically inverse to LDMC and displayed the same phylogenetic structure.

The relationships between the functional and taxonomic structure of the fern assemblages were analyzed with a simple correlation using Pearson's r and Spearman's r_s according to the normality of the data. The relative abundance of the species was not tested because CWM, CV, and functional diversity indexes were abundance-weighted.

The effects of local environmental factors on the functional structure of fern assemblages were analyzed with generalized linear mixed models (GLMM). Although we aimed at understanding variation at the local scale (i.e. plot variation), the sampling area was included as the random effect, in order to control to some degree of aggregation in the variation of environmental conditions (Figure S2) and floristic patterns (Figure S1) among areas. We used the first axes of a principal component analysis PCA to summarize the main environmental conditions (Figure S2). Thus, we used the two first axes of the PCA as the fixed effects in the GLMM. We excluded from PCA those variables that were autocorrelated.

The environmental factors expressed in percentages were normalized with root square transformations (i.e. rock coverage, bases saturation, saturation by Al, and soil contents of sand, silt, and clay), whereas the others were log10+1 transformed. The leaf traits CWM and CV, as well as, the Fric, SESRao, and FRed were the response variables. Response variables with normal distribution were analyzed from a Gaussian distribution error and “identity” link. It was not possible to normalize the CWM-LDMC, CV-LDMC, CWM-LWC, and SESRao with conventional methods (e.g. root square, Log10, or trigonometric functions). Thus, they were tested with their specific distributions (i.e. gamma distribution) with the appropriated link function. For all the analyses, $p \leq 0.05$ was considered significant. All the statistical analyses were performed using the R statistical software (R Core Team, 2012).

RESULTS

In our 22 study plots, we recorded 2995 individuals of 36 fern species belonging to 15 families (Table S3). Species richness, diversity, and evenness, as well as the leaf traits CWM, CV and functional diversity indexes are summarized in Table S2.

Mean SESMPD among co-occurring fern within plots was -0.55±0.82, and both trait convergence and divergence were observed among local fern assemblages (Table S4; Figure 1). Trait convergence patterns were more common, which were significantly <0 for 14 out of 15 plots, suggest that trait variance within plots was generally lower than expected by chance. On the other hand, trait divergence was significant >0 for four out of seven plots, while the remaining plots exhibited marginal p values (Table S4; Figure 1).

No LES traits of the ferns exhibited aggregated patterns (i.e., $\lambda = 1$). However, leaf LDMC presented phylogenetic signal ($\lambda = 0.64$; $p = 0.02$). LA ($\lambda = 0.44$; $p = 0.29$) and SLA ($\lambda = 0.00$; $p = 1.00$) showed no significance and were close to random, indicating trait dispersion along the phylogeny.

Community weighted means (CWMs) of the assemblages were not correlated with fern species richness (SR), diversity (H'), or evenness (J') (Table 2). In contrast, these parameters were negatively correlated with trait CVs (Table 2). Moreover, FRic and FRed were positively associated with SR, whereas only FRed was significantly correlated with assemblage H' and J' (Table 2). SESRao was negatively related to both SR and H'. Considering floristic composition, increases in CWM-LA, CWM-SLA, and CWM-LWC were associated with floristic variations across fern assemblages (Table 2). Meanwhile, decreases in FRic and SESRao among assemblages were associated with floristic variation (Table 2).

The final model of the PCA for local environmental factors explained 70.9% of data variation in the two first axes (PC1: 47.4%; PC2: 23.5%) (Figure S2). The most important variables were soil pH on the first axis, and exchangeable bases and soil cation-exchange capacity on the second axis (Figure 2S). Regarding general characteristics of local plots, positive values along with the PC1 indicated microhabitats with the low tree basal area, covered by rock outcrops, and with less acidic sand soils (all plots presented acid soils). On the other hand, negative values represented microhabitats with the higher basal area and acidic conditions along with clay soils (opposite to soil sand content). The gradient along with the PC2 was explained by an increase in soil nutrient availability, i.e., positive associations between both the soil CEC and EB with this principal component (Figure 2S).

The functional structure of the fern assemblages was affected by local edaphic conditions (Table 3). Overall, increases in soil pH affected positively FRic and SESRao, as well as for allowing for higher ranges on LA and LWC among assemblages (Table 3). Further, soil pH promoted shifts along fern assemblages from convergence to divergence patterns (i.e., from SESRao <0 to SESRao >0). Conversely, more acid soils presented higher FRed and fewer variations on assemblages LA (Table 3). Soil nutrient availability increased FRic of the assemblages, despite the negative influence on CWM-LA and ranges of LA, SLA, and LWC (Table 3).

DISCUSSION

We found that both functional convergence and divergence of the leaf economic spectrum (LES) traits occur in the tropical fern assemblages studied by us. Such a co-occurrence has been reported in previous studies on other plant groups (e.g., de Bello et al., 2009), particularly in situations of marked abiotic gradients (Kluge & Kessler, 2011; Moraes et al., 2016). Nevertheless, functional convergence was predominant, highlighting the importance of environmental filtering and niche characteristics to functional patterns of ferns. Environmental filtering is often reported to act at large, i.e. regional, scales (Cornwell, Schwilk, & Ackerly, 2006; Mason, Lanoiselee, Mouillot, Irz, & Argillier, 2007). Here, we report environmental filtering in local fern assemblages, which agrees with similar local-scale patterns of species diversity and community composition of other fern assemblages (Richard, Bernard, & Bell, 2000;

Tuomisto et al., 2002; Poulsen, Tuomisto, & Balslev, 2006). In addition, trait divergence favors niche differentiation (e.g., Stubbs & Wilson, 2004; Sterk, Markesteijn, Schieving, & Poorter, 2011; de Bello et al., 2013) and differential use of resources represents an important local-scale trade-off for co-occurring species, especially for herbs (e.g. Cornwell & Ackerly, 2009; Kraft & Ackerly, 2010; Mason, de Bello, Doležal, & Lepš, 2011). Trait divergence reported in some fern assemblages in this study might be related to soft interspecific competition, contrary to the stronger competition expected at small scales (Cornell & Lawton, 1992; Petchey, Evans, Fishburn, & Gaston, 2007).

The lack of phylogenetic niche conservatism in most of the LES traits (except leaf dry matter content) in the tropical fern assemblages studied by us is in concordance with previous studies for other plant groups in other biomes, especially relating to traits with important ecological meaning (e.g., Silvertown et al., 2006; Cadote, Cavender-Bares, Tilman, & Oakley, 2009). One of the reasons for this may be the similarity in ecological and physiological strategies of ferns in tropical forests (Page, 2002), with variations in traits related to resource demands (Silvertown et al., 2006). Under similar environments, traits tend to be labile, presenting high phenotypic plasticity and displaying low phylogenetic signal (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009), as here reported. Thus, our results indicate that phylogenetic constraints did not limit the selected traits, highlighting the importance of other processes affecting local trait trade-offs, such as species interactions under environmental filtering.

Despite the complexity in the relationship between the functional and taxonomic structure of assemblages (Mokanym, Ash, & Roxburgh, 2008), it is well known that species richness can favor functional richness, due to increases in the functional space of the assemblages (Flynn et al., 2009; Cadotte, 2011). Carvajal-Hernández, Gómez-Díaz, Kessler & Krömer (2018) demonstrated this positive relationship between species-rich fern assemblages and functional diversity along elevational and disturbance gradients in tropical forests of Mexico. Our results corroborate this result for the local scale, highlighting that species-rich and diverse assemblages can also have higher functional redundancy and low functional divergence.

Our results also demonstrate that species-poor and less diverse assemblages were more functionally divergent, with lower functional richness and redundancy. Functional redundancy is crucial to ecosystem functioning because it ensures the functional stability of local assemblages while providing functional insurance against loss of ecosystem functions (Fonseca & Ganade, 2001; Petchey, Evans, Fishburn, & Gaston, 2007). Therefore, the studied fern assemblages might be prone to functional loss (Fonseca & Ganade, 2001), even though at present they can efficiently exploit different portions of the overall niche space, reducing the effect of competition, which favor local species coexistence (Diamond, 1975; Yachi & Loreau, 2007).

The functional structure of local fern assemblages was affected by soil pH and nutrient availability, corroborating previous studies on the functional diversity of plants (Viani, Rodrigues, Dawson, Lambers, & Oliveira, 2014; Moraes et al., 2016; Abrahão et al., 2019). Single-trait metrics exhibited singular responses, e.g., leaf area decreased with increasing nutrient availability. The outcomes of the trait-environment relationship might be complex because of the dimensions of trait trade-offs and multiple drives of community assembly (Le Bagousse-Pinguet et al., 2017; Laughlin & Messier, 2015). In such situations, multi-trait analyses might be more meaningful, as reported in our study.

Functional richness increased with higher soil pH and nutrient availability, indicating the importance of soil properties to the increase in the amount of functional space occupied by fern assemblages. These changes in functional space indicate the effect of assembly rules via changes in the taxonomic structure of the assemblages (Mouchet, Villéger, Mason, & Mouillot, 2010), which is reinforced by the positive correlation between species richness and functional richness.

These results further indicate that local fern assemblages incorporate different acquisition strategies even under environmental constraints, as reported for dryland assemblages by Le Bagousse-Pinguet et al. (2019). Finally, increases in soil acidity were associated with decreases in functional redundancy and functional divergence, with shifts in assemblages from convergent to divergent patterns. Similar patterns of turnover in functional convergence-divergence under edaphic gradients have previously been reported for other forest herbs (e.g., Moraes et al., 2016).

The functional convergence found here in fern assemblages along a soil pH gradient is in accordance with that reported on gradients of elevation, water availability, and light availability (Kluge & Kessler, 2011; Zhang et al., 2017). Further, the functional divergence of some assemblages under less acid soil conditions exemplifies the role of species interactions at small scales (Diamond, 1975; Cadotte, Carscadden, & Mirotchnick, 2011; Kessler, Salazar, Homeier, & Kluge, 2014), even in the presence of environmental filtering (Kang et al., 2017).

Our hypotheses were partially supported since we found a remarkable effect of environmental filtering via edaphic conditions structuring fern assemblages in Atlantic Forest remnants. However, we found no evidence of a phylogenetic structure on LES traits of the species. The taxonomic structure as a whole and not only species composition were related to the functional structure of the fern assemblages whereas functional divergence was constrained by edaphic factors.

Our results lead to important insights about the mechanism promoting fern species coexistence within local assemblages in Brazilian Atlantic Forest remnants. We found that trait convergence of LES traits is the dominant pattern within these fern assemblages, even though trait divergence also occurs. Further, while LES seems not to be phylogenetically constrained, the outcomes of the relationship between the functional and taxonomic structure of fern assemblages can be complex and not only species richness and diversity but also species identity is important to functional patterns, which might impact overall ecosystem functioning.

Finally, we found a remarkable effect of environmental filtering via edaphic conditions on the functional structure of local tropical fern assemblages, supporting either functional convergence or divergence. Most of the studies that reported environmental filtering have been conducted along strong gradients of succession or elevation as well as water, nutrient, or light availability (Kluge & Kessler, 2011; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010; Lohbeck et al., 2015; Zhang et al., 2017). Our study found that such patterns can also be found along weak edaphic gradients. We thus advocate that ferns might be a reliable response group (Lavorel & Garnier, 2002) to study the role of edaphic gradients on species coexistence via functional traits. This is crucial to understanding and forecasting how changes in local environmental conditions would affect local species coexistence, especially in the Atlantic Forest, where most of the remaining habitat is under the anthropic impact, much of which affects soil characteristics (Borrelli et al., 2017).

Tables

Table 1. Climatic and vegetation characteristics of the three study areas in the Atlantic Forest in northeastern Brazil. Climatic information was obtained from the Laboratório de Meteorologia do Estado de Pernambuco (Lamepe) (available on http://www.itep.br/meteorologia/lamepe).

	Geographic Coordinates	Mean Annual Temperature	Mean Annual Rainfall	Mean Elevation	Vegetation Type
Area I (LL)	08°38'45.2"S; 35°10'29.9"W	24.4ºC	2000 mm	75 m	Lowland forest
Area II (SB)	08°30'16.2"S; 35°43'14.6"W	21.5ºC	1150 mm	750 m	Submontane forest
Area III (SM)	07°37'02.5"S; 035°30'47.0"W	24.0 ºC	1155 mm	650 m	Submontane forest

Table 2. Coefficients of the pairwise correlations between the taxonomic and functional structure of 22 fern assemblages in Atlantic forest remnants in northeastern Brazil. The taxonomic properties were described by Species richness (SR), Shannon diversity index (H'), Pielou' evenness (J), and the two first axes of a non-metric multidimensional scaling (NMDS 1 and 2) based on Bray-Curtis dissimilarity index to represent community composition. The functional properties included the community-weighted means (CWM) and coefficient of variations (CV) of the leaf traits, as well as functional diversity index of functional richness (functional richness, "FRic"), functional redundancy (i.e., functional redundancy, "FRed"), and functional divergence (i.e., standardized effect size of Rao functional diversity, "SESRao"). LA: Leaf area; SLA: specific leaf area; LDMC: leaf dry matter content; LWC: leaf water content. Significant relationships (i.e., $p \leq 0.05$) are highlighted in bold. [1] We used Spearman's coefficient for non-normally distributed data. * $p \leq 0.01$;** $p \leq 0.001$.

		TAXONOMIC STRUCTURE				
		SR[1]	H'	J[1]	NMDS1	NMDS2[1]
FUNCTIONAL STRUCTURE	CWM-LA	-0.37	0.07	0.28	-0.06	**0.39**
	CV-LA	**-0.61***	**-0.80****	**-0.69****	-0.12	0.01
	CWM-SLA	-0.03	0.22	0.02	**0.50**	-0.19
	CV-SLA	**-0.53***	**-0.84****	**-0.87****	-0.29	0.14
	CWM-LDMC[1]	0.07	-0.11	-0.12	-0.39	0.33
	CV-LDMC[1]	**-0.43**	**-0.90****	**-0.88****	-0.12	0.09
	CWM-LWC[1]	0.13	0.23	0.13	**0.46**	0.03
	CV-LWC	**-0.62***	**-0.92****	**-0.85****	-0.29	0.11
	FRic	**0.51***	0.26	-0.08	-0.11	**-0.35**
	FRed	**0.60***	**0.89****	**0.78****	0.52	0.37
	SESRao[1]	**-0.59***	**-0.39**	-025	**-053**	-0.12

Table 3. Results of the Generalized Linear Mixed Models (GLMM) analyzing the influence of local environmental conditions (PCA axes) on community-weighted mean (CWM) and coefficient of variation (CV) of leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf water content (LWC), as well as functional richness (FRic), functional redundancy (FRed), and functional divergence (SESRao) in 22 fern communities in Atlantic forest remnants in northeastern Brazil. For each variable in the models were indicate the mean coefficient (β), the standard error (SE), the 95% confidence intervals (95% CI), and the p-value. Significant p (i.e., $p \leq 0.05$) are highlighted in bold. ns: no significative; *: $p \leq 0.0001$.

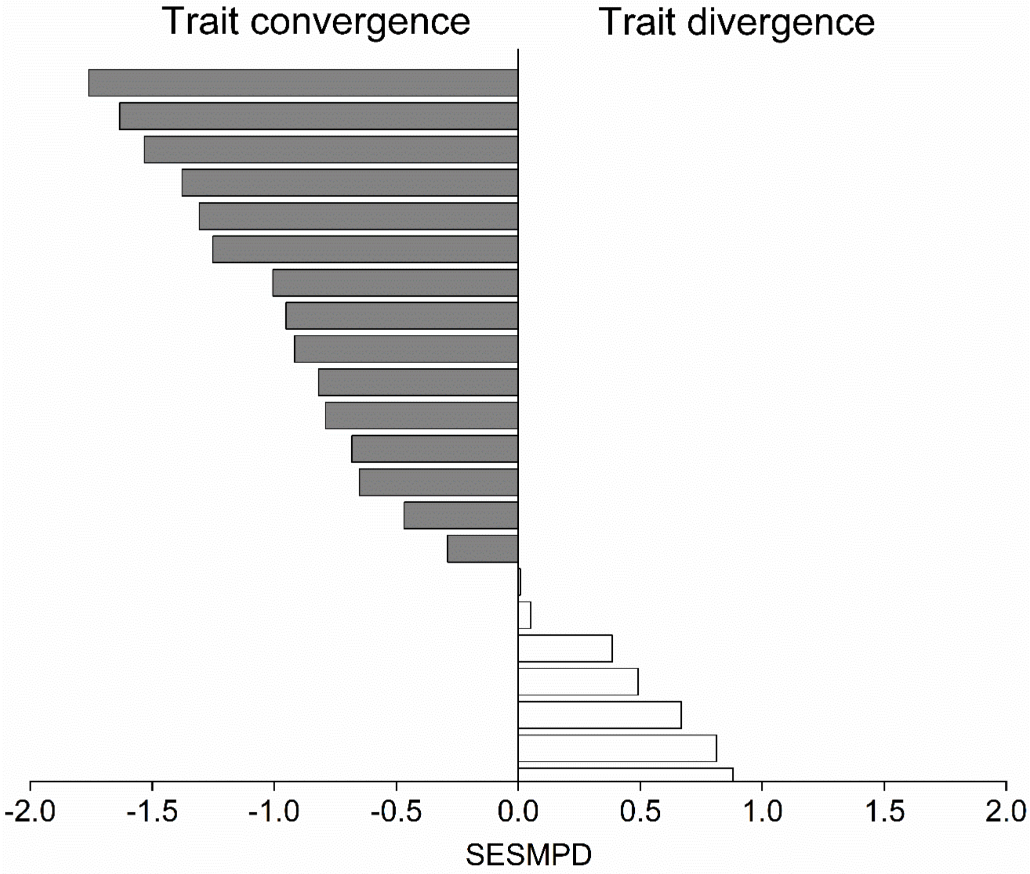
			95% CI		
Model factors	β	SE	Lower	Upper	p
CWM-LA					
PCA1	-1.940	3.490	-8.780	4.901	ns.
PCA2	-10.366	4.754	-19.683	-1.048	**0.03**
PCA1:PCA2	1.267	3.243	-5.090	7.624	ns.
CV-LA					
PCA1	2.254	2.992	0.888	3.620	**0.00***
PCA2	-3.282	0.840	-4.938	-1.636	**0.00***
PCA1:PCA2	-0.215	0.535	-1.264	0.835	ns.
CWM-SLA					
PCA1	0.313	8.013	-15.391	16.019	ns.
PCA2	-3.085	10.743	-24.141	17.972	ns.
PCA1:PCA2	3.146	7.255	-11.073	17.365	ns.
CV-SLA					
PCA1	0.802	1.065	-1.286	2.890	ns.
PCA2	-3.2424	1.430	-6.045	-0.440	**0.02**
PCA1:PCA2	0.401	0.966	-1.493	2.294	ns.
CWM-LDMC					
PCA1	0.009	0.026	-0.043	0.060	ns.
PCA2	0.036	0.031	-0.024	0.096	ns.
PCA1:PCA2	-0.035	0.020	-0.074	0.004	ns.
CV-LDMC					
PCA1	1.7687	1.2775	-0.095	0.355	ns.
PCA2	-2.1802	1.6285	-0.350	0.067	ns.
PCA1:PCA2	-0.0185	1.0377	-0.146	0.122	ns.

CWM-LWC					
PCA1	-0.014	0.016	-0.045	0.018	ns.
PCA2	-0.016	0.020	-0.056	0.023	ns.
PCA1:PCA2	0.008	0.011	-0.014	0.030	ns.
CV-LWC					
PCA1	2.098	0.961	0.214	3.982	**0.03**
PCA2	-3.144	1.185	-5.466	-0.821	**0.01**
PCA1:PCA2	0.133	0.764	-1.364	1.630	ns.
FRic					
PCA1	0.026	0.012	0.003	0.050	**0.03**
PCA2	0.032	0.013	0.006	0.058	**0.01**
PCA1:PCA2	0.002	0.010	-0.017	0.021	ns.
FRed					
PCA1	-0.054	0.013	-0.080	-0.028	**0.00**
PCA2	0.030	0.016	-0.002	0.061	ns.
PCA1:PCA2	0.003	0.010	-0.017	0.02	ns.
SESRao					
			95% CI		
Model factors	β	SE	Lower	Upper	p
PCA1	0.181	0.086	0.013	0.350	**0.01**
PCA2	-0.140	0.118	-0.372	0.092	ns.
PCA1:PCA2	-0.074	0.081	-0.234	0.085	ns.

Figure legends

Figure 1. The standardized effect size of the mean pairwise distance (SESMPD) of leaf economic spectrum traits in 22 local fern assemblages in Atlantic forest remnants in northeastern Brazil. SESMPD <0 indicates trait convergence whereas SESMPD >0 indicates trait divergence. *p ≤ 0.05.

Figures



Acknowledgments

We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, National Council for Scientific and Technological Development) for the doctorate scholarship of LC, the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) for the doctorate 'sandwich' internship (process 88881.189293/2018-01), the Laboratório de Química do Solo of the Universidade Federal Rural de Pernambuco for supporting soil analysis, and Cucau and Trapiche Mills for logistic support during the fieldwork.

Disclosure statements

No potential conflict of interest was reported by the authors

Funding

This study was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) under the Finance Code 001.

References

Abrahão, A., Costa, P. D. B., Lambers, H., Andrade, S. A. L., Sawaya, A. C. H. F., Ryan, M. H., & Oliveira, R. S. (2019). Soil types select for plants with matching nutrient-acquisition and-use traits in hyperdiverse and severely nutrient-impoverished campos rupestres and cerrado in Central *Journal of Ecolgy*, 107, 1302–1316. https://doi.org/10.1111/1365-2745.13111

Adler, P. B., Ellner, S. P., & Levine, J. M. (2010). Coexistence of perennial plants: an embarrassment of niches. *Ecology Letters*, 13, 1019–1029. https://doi.org/10.1111/j.1461-0248.2010.01496.x

Borrelli, P., Robinson, D. A., Fleischer, L. R., Lugato, E., Ballabio, C., Alewell, C., … Panagos, P. (2017). An assessment of the global impact of 21st century land use change on soil erosion. *Nature Communications*, 8. https://doi.org/10.1038/s41467-017-02142-7

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., ... Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature Ecology* & *Evolution*, 2, 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Butterfield, B. J., & Suding, K. N. (2013). Single-trait functional indices outperform multi- trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology*, 101, 9–17. https://doi.org/10.1111/1365-2745.12013

Cadotte, M. W. (2011). The new diversity: management gains through insights into the functional diversity of communities. *Journal of Applied Ecology*, 48, 1067–1069. https://doi.org/10.1111/j.1365-2664.2011.02056.x

Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PloS One*, 4, e5695. https://doi.org/10.1371/journal.pone.0005695

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. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Carvajal-Hernández, C. I., Gómez-Díaz, J. A., Kessler, M., & Krömer, T. (2018). Influence of elevation and habitat disturbance on the functional diversity of ferns and lycophytes. *Plant Ecology and Diversity*, 11, 335–347. https://doi.org/10.1080/17550874.2018.1484526

Cavender-Bares, J., Keen, A., & Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on spatial and taxonomic scale. *Ecology*, 87: S109–S122. https://doi.org/10.1890/0012-9658%282006%2987%5B109%3APSOFPC%5D2.0.CO%3B2

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., … Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335–380. https://doi.org/10.1071/BT02124

Cornell, H. V., & Lawton, J. H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, 61, 1–12. . https://doi.org/10.2307/5503

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. https://doi.org/10.1890/07-1134.1

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87, 1465–1471. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Costa, F. R., Magnusson, W. E., & Luizao, R. C. (2005). Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *Journal of Ecology*, 93, 863–878. https://doi.org/10.1111/j.1365-2745.2005.01020.x

de Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J. C., Macek, P., … Lavorel, S. (2009). Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science*, 20, 475–486. https://doi.org/10.1111/j.1654-1103.2009.01042.x

de Bello F, Lavergne S, Meynard CN, Lepš J, & Thuiller W. (2010). The partitioning of diversity: showing Theseus a way out of the labyrinth. *Journal of Vegetation Science*, 21, 992–1000. https://doi.org/10.1111/j.1654-1103.2010.01195.x

de Bello, F., Vandewalle, M., Reitalu, T., Lepš, J., Prentice, H. C., Lavorel, S., … Vesk, P. (2013). Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology*, 101, 237–1244. https://doi.org/10.1111/1365-2745.12139

Diamond, J. M. (1975). Assembly rules of species communities. *Ecology and Evolution of Communities* (pp. 342–444). Cambridge: Harvard University Press.

Díaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proccedings of the National Academy of Sciences of the United State of America*, 104, 20684–20689. https://doi.org/10.1073/pnas.0704716104

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. https://doi.org/10.1038/nature16489

Eisenlohr, P. V., Oliveira-Filho, A. T., & Prado, J. (2015). The Brazilian Atlantic Forest: new findings, challenges and prospects in a shrinking hotspot. *Biodiversity and Conservation*, 24, 2129–2133. https://doi.org/10.1007/s10531-015-0995-4

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., … De Clerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12, 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Fonseca, C. R., & Ganade, G. (2001). Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology*, 89, 118–125. https://doi.org/10.1046/j.1365-2745.2001.00528.x

Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, 83, 2091–2096. https://doi.org/10.1890/0012-9658(2002)083[2091:SCOAMA]2.0.CO;2

Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, 17, 255–260. https://doi.org/10.1111/j.1654-1103.2006.tb02444.x

Hodgson, J. G., Montserrat-Martí, G., Charles, M., Jones, G., Wilson, P., Shipley, B., … Royo Pla, F. (2011). Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Annals of Bottany*, 108, 1337–1345. https://doi.org/10.1093/aob/mcr225

Jones, M. M., Tuomisto, H., Clark, D. B, & Olivas, P. (2006). Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. Journal of Ecology, 94, 181–195. https://doi.org/10.1111/j.1365-2745.2005.01071.x

Kang, S., Niu, J., Zhang, Q., Li, D., Ren, H., Ren, J., … Dong, J. (2017). Environmental filtering does not necessarily prevent trait divergence: a case study of the Xilin River Basin in Inner Mongolia, China. *Journal of Plant Ecology*, 10, 497–509. https://doi.org/10.1093/jpe/rtw050

Karst, J., Gilbert, B., & Lechowicz, M. J. (2005). Fern community assembly: the roles of chance and the environment at local and intermediate scales. *Ecology*, 86, 2473–2486. https://doi.org/10.1890/04-1420

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., … Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463 –1464. https://doi.org/10.1093/bioinformatics/btq166

Kent, M., & Coker, P. (1994). Vegetation Description and Analysis: A Practical Approach. Chichester: John Wiley and Sons.

Kessler, M., Salazar, L., Homeier, J., & Kluge, J. (2014). Species richness-productivity relationships of tropical terrestrial ferns at regional and local scales. *Journal of Ecology*, 102, 1623–1633. https://doi.org/10.1111/1365-2745.12299

Kluge, J., & Kessler, M. (2011). Phylogenetic diversity, trait diversity and niches: species assembly of ferns along a tropical elevational gradient. *Journal of Biogeography*, 38, 394–405. https://doi.org/10.1111/j.1365-2699.2010.02433.x

Kneitel, J. M., & Chase, J. M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, 7, 69–80. https://doi.org/10.1046/j.1461-0248.2003.00551.x

Kraft, N. J., & Ackerly, D. D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographys*, 80, 401–422. https://doi.org/10.1890/09-1672.1

Kraft, N. J., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322, 580–582. https://doi.org/10.1126/science.1160662

Laughlin, D. C., & Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends Ecology & Evolution*, 30, 487 –496. https://doi.org/10.1016/j.tree.2015.06.003

Lavorel, S., & Garnier, É. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Le Bagousse-Pinguet,Y., Gross, N., Maestre, F. T., Maire, V., de Bello, F., Fonseca, C. R., ... Liancourt, P. (2017). Testing the environmental filtering concept in global drylands. *Journal of Ecology*, 105, 1058 –1069. https://doi.org/10.1111/1365-2745.12735

Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, 91, 386–398. https://doi.org/10.1890/08-1449.1

Lehtonen, S., Jones, M. M., Zuquim, G., Prado, J., & Tuomisto, H. (2015). Phylogenetic relatedness within Neotropical fern communities increases with soil fertility. *Global Ecology and Biogeography*, 24, 695–705. https://doi.org/10.1111/geb.12294

Lohbeck, M., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J. A., Poorter, L., & Bongers, F. (2015). Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. *PloS One*, 10, e0123741. https://doi.org/10.1371/journal.pone.0123741

Mason, N. W., de Bello, F., Doležal, J., & Lepš, J. (2011). Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, 99, 788–796. https://doi.org/10.1111/j.1365-2745.2011.01801.x

Mason, N. W. H., Lanoiselee, C., Mouillot, D., Irz, P., & Argillier, C. (2007). Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia*, 153, 451–452. https://doi.org/10.1007/s00442-007-0727-x

Mason, N. W. H., Richardson, S. J., Peltzer, D. A., Wardle, D. A., de Bello, F., & Allen, R. B. (2012). Changes in co-existence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *Journal of Ecology*, 100, 678–689. https://doi.org/10.1111/j.1365-2745.2012.01965.x

Mason, N. W. H., de Bello, F., Mouillot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24, 794–806. https://doi.org/10.1111/jvs.12013

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, 96, 884–893. https://doi.org/10.1111/j.1365-2745.2008.01395.x

Moraes, D. A., Cavalin, P. O., Moro, R. S., Oliveira, R. A., Carmo, M. R., & Marques, M. C. (2016). Edaphic filters and the functional structure of plant assemblages in grasslands in southern Brazil. *Journal of Vegetation Science*, 27, 100 –110. https://doi.org/10.1111/jvs.12331

Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, 3, 743 –756. https://doi.org/10.1111/j.2041-210X.2012.00196.x

Niinemets, Ü., Portsmuth, A., Tena, D., Tobias, M., Matesanz, S., & Valladares, F. (2007). Do we underestimate the importance of leaf size in plant economics? Disproportional scaling of support costs within the spectrum of leaf physiognomy. *Annals of Botany*, 100, 283–303. https://doi.org/10.1093/aob/mcm107

Noben, S., Testo,, W., Karger, D. N., Kluge, J., Salazar, L., Lehnert, M., Quandt, D., Kessler, M. (in review). Environment and species identity determine abundances of ferns along elevational gradients. *Journal of Plant Ecology*.

Ogburn, R, & Edwards, E. (2012). Quantifying succulence: a rapid, physiologically meaningful metric of plant water storage. *Plant, Cell & Environment*, 35, 1533–1542. https://doi.org/10.1111/j.1365-3040.2012.02503.x.

Page, C. N. (2002). Ecological strategies in fern evolution: a neopteridological overview. *Review of Palaeobotany and Palynology*, 119, 1–33. https://doi.org/10.1016/S0034-6667(01)00127-0

Pereira, A. F. N., Silva, I. A. A., Santiago, A. C. P., & Barros, I. C. L. (2014). Efeito de borda sobre a comunidade de samambaias em fragmento de Floresta Atlântica (Bonito, Pernambuco, Brasil). *Interciência*, 39, 281–287.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. … , Cornelissen, J. H. C. (2003). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 64, 167–234. https://doi.org/10.1071/BT12225

Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, 76, 977–985. https://doi.org/10.1111/j.1365-2656.2007.01271.x

Poorter, L., & Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, 87, 1733–1743. https://doi.org/10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2

Poulsen, A. D., Tuomisto, H., & Balslev, H. (2006). Edaphic and floristic variation within a 1-ha plot of Lowland Amazonian Rain Forest. *Biotropica*, 38, 468–478. https://doi.org/10.1111/j.1744-7429.2006.00168.x

Prado, J., Sylvestre, L. D. S., Labiak, P. H., Windisch, P. G., Salino, A., … Matos, F. B. (2015). Diversity of ferns and lycophytes in Brazil. *Rodriguésia*, 66, 1073–1083. http://dx.doi.org/10.1590/2175-7860201566410

R Development Core Team. (2012). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P. B. (2014). The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, 102, 275–301. https://doi.org/10.1111/1365-2745.12211

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Richard, M., Bernard, T., & Bell, G. (2000). Environmental heterogeneity and the spatial structure of fern species diversity in one hectare of old-growth forest. *Ecography*, 23, 231–245. https://doi.org/10.1111/j.1600-0587.2000.tb00279.x

Sharpe, J. M., Mehltreter, K., & Walker, L. R. (2010). Ecological importance of ferns. *Fern ecology* (pp. 1–21). Cambridge: Cambridge University Press.

Silva, I. A. A., Pereira, A. F. N., & Barros, I. C. L. (2014). Fragmentation and loss of habitat: consequences for the fern communities in Atlantic forest remnants in Alagoas, north-eastern Brazil. *Plant Ecology & Diversity*, 7, 509–517. https://doi.org/10.1080/17550874.2013.862750

Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M. F., Joseph, J. A., & Dolphin, K. (2006). Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proccedings of the Royal Society B, Biological Sciences*, 273, 39–44. https://doi.org/10.1098/rspb.2005.3288

Sterck, F., Markesteijn, L., Schieving, F., & Poorter, L. (2011). Functional traits determine trade-offs and niches in a tropical forest community. *Proccedings of the National Academy of Sciences of the United State of America*, 108, 20627–20632. 10.1073/pnas.1106950108

Stubbs, W. J., & Wilson, J. B. (2004). Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, 92, 557–567. https://doi.org/10.1111/j.0022-0477.2004.00898.x

Terborgh, J., Pitman, N., Silman, M., Schichter, H., Núñez, P. (2002). Maintenance of tree diversity in tropical forests (pp. 1-17). *Seed dispersal and frugivory: Ecology, evolution and conservation*. New York (NY): CABI Publishing.

Testo, W., & Sundue, M. (2016). A 4000-species dataset provides new insight into the evolution of ferns. *Molecular Phylogenetics and Evolution*, 105, 200–211. https://doi.org/10.1016/j.ympev.2016.09.003

Tuomisto, H., & Poulsen, A. (1996). Influence of edaphic specialization on the distribution of pteridophytes in neotropical forests. *Journal of Biogeography*, 23:283–293. https://doi.org/10.1046/j.1365-2699.1996.00044.x

Tuomisto, H., Ruokolainen, K., Poulsen, A. D., Moran, R. C., Quintana, C., Cañas, G., & Celi, J. (2002). Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuní National Park, Ecuadorian Amazonia. *Biotropica*, 34, 516–533. https://doi.org/10.1111/j.1744-7429.2002.tb00571.x

Viani, R. A., Rodrigues, R. R., Dawson, T. E., Lambers, H., & Oliveira, R. S. (2014). Soil pH accounts for differences in species distribution and leaf nutrient concentrations of Brazilian woodland savannah and seasonally dry forest species. *Perspectives in Plant Ecology, Evolution and Systematics*, 16, 64–74. 10.1016/j.ppees.2014.02.001

Webb, C. O., Ackerly, D. D., Mcpeek, M. A, & Donoghue, M J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Westoby, M. (1998). A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213–227. https://doi.org/10.1023/A:1004327224729

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Vilar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827. https://doi.org/10.1038/nature02403

Yachi, S., & Loreau, M. (2007). Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecology Letters*, 10, 54–62. https://doi.org/10.1111/j.1461-0248.2006.00994.x

Zhang, H., Zhu, S., John, R., Li, R., Liu, H., & Ye, Q. (2017). Habitat filtering and exclusion of weak competitors jointly explain fern species assemblage along a light and water gradient. *Scientific Reports*, 7, 298. https://doi.org/10.1038/s41598-017-00429-9

Zuquim, G., Tuomisto, H., Jones, M., Prado, J., Figueiredo, F. O. G., Moulatlet, G. M., & Emilio, T. (2014). Predicting environmental gradients with fern species composition in Brazilian Amazonia. *Journal of Vegetation Science*, 25, 1195 –1207. https://doi.org/10.1111/jvs.12174

Table S1: Local environmental variables measured for 22 plots in Atlantic forest remnants in northeastern Brazil. LL: Lowland Forest remnants in Rio Formoso district, Pernambuco, Brazil; SB: Submontane forest remnants in Bonito district, Pernambuco, Brazil; SM: Submontane remnants in São Vicente Férrer district, Pernambuco, Brazil. Rock: rock coverage; NT: number of trees; BA: basal area; EB: exchangeable bases (cmolc/dm³); CEC: cation-exchange capacity; BS: base saturation; AlS: aluminum saturation. Values were log10+1 transformed with exception to values expressed in percentage, which were root square transformed.

Plot	Rock (%)	NT	BA (m²)	Soil texture (%)			pH	Soil nutrients (mg/dm³)						EB	CEC (t)	BS (%)	AlS (%)
				Sand	Silt	Clay		Al	Ca	Mg	P	K	Na				
1^{LL}	7.071	1.491	0.622	9.077	3.873	1.617	0.791	2.345	2.692	2.288	1.310	2.001	1.864	0.634	0.830	7.979	6.028
2^{LL}	8.367	1.279	2.339	7.987	3.535	4.869	0.715	2.462	2.961	2.121	0.890	2.481	1.782	0.808	0.984	8.163	5.777
3^{LL}	0	1.230	1.389	7.932	3.535	4.957	0.693	2.578	2.886	2.388	1.151	2.227	1.832	0.798	1.021	7.737	6.335
4^{LL}	0	1.279	1.579	8.723	3.535	3.378	0.704	2.448	2.729	2.508	1.006	2.128	1.776	0.752	0.943	8.030	5.959
5^{LL}	6.708	0.778	1.277	9.324	2.236	2.840	0.785	1.802	2.451	2.293	0.809	2.061	1.516	0.521	0.604	9.081	4.188
6^{LL}	6.708	0	0	9.262	2.121	3.116	0.809	1.879	2.762	2.338	0.667	2.396	1.588	0.725	0.789	9.292	3.696
7^{LL}	5.477	0.778	1.658	8.264	3.082	4.711	0.770	1.722	2.988	2.615	1.294	2.357	1.477	0.946	0.973	9.683	2.496
8^{SB}	0	1.230	1.472	8.215	3.535	4.473	0.658	2.026	2.368	2.005	1.000	1.918	1.454	0.344	0.530	8.072	5.902
9^{SB}	0	1.362	1.786	7.858	3.535	5.074	0.689	2.816	2.392	2.162	0.851	2.005	1.613	0.428	0.998	5.190	8.548
10^{SB}	0	0.477	1.618	7.904	2.236	5.703	0.674	2.769	2.092	2.711	1.346	2.407	2.183	0.740	1.080	6.759	7.370
11^{SB}	3.162	1.146	1.808	8.835	2.236	4.116	0.681	2.511	2.833	2.324	1.445	2.309	1.768	0.752	0.966	7.814	6.239
12^{SB}	0	1	2.422	7.433	2.236	6.304	0.629	2.112	2.288	2.298	0.972	2.271	1.669	0.489	0.655	8.257	5.641
13^{SB}	4.123	1	1.781	7.607	3.535	5.444	0.735	2.473	2.647	2.288	0.498	2.104	1.548	0.617	0.871	7.457	6.662
14^{SB}	0	1.204	1.274	7.614	3.535	5.434	0.767	2.696	2.840	2.473	0.883	2.155	1.720	0.797	1.071	7.288	6.846
15^{SB}	0	0.778	2.711	7.927	3.082	5.260	0.688	2.630	2.697	2.391	0.208	2.205	1.785	0.692	0.985	7.134	7.007
16^{SM}	0	1.204	1.895	7.656	4.183	4.886	0.717	2.665	2.786	2.804	0.366	2.276	1.765	0.943	1.143	7.940	6.079
17^{SM}	0	0.845	2.449	7.925	3.873	4.710	0.651	2.843	2.432	2.510	0.913	2.172	1.724	0.642	1.084	6.016	7.988
18^{SM}	0	0.778	2.000	7.409	4.183	5.253	0.657	2.695	2.789	2.066	0.879	2.294	1.516	0.656	1.002	6.716	7.409
19^{SM}	0	0.903	1.820	7.622	2.236	6.075	0.647	2.884	2.763	2.291	1.023	2.320	1.718	0.702	1.132	6.096	7.927
20^{SM}	0	0.845	2.332	8.112	3.535	4.658	0.739	1.740	2.304	2.734	1.044	2.422	1.276	0.788	0.829	9.537	3.008
21^{SM}	5.477	0.954	1.948	7.869	3.873	4.803	0.753	1.740	2.330	2.676	0.803	2.537	1.913	0.767	0.811	9.515	3.076

Plot	Rock (%)	NT	BA (m²)	Soil texture (%)			pH	Soil nutrients (mg/dm³)						EB	CEC (t)	BS (%)	AlS (%)
				Sand	Silt	Clay		Al	Ca	Mg	P	K	Na				

22^{SM}	6.708	0.954	1.996	7.668	3.535	5.356	0.752	2.028	2.091	2.694	0.453	2.303	1.797	0.716	0.805	9.023	4.312

Table S2: Functional structure included community-weighted means (CWM) and coefficient of variations (CV%) of the leaf traits: leaf area (mm^2 – LA), specific leaf area (mm^2/mg – SLA), leaf dry matter content ($mg\ g^{-1}$ – LDMC) and leaf water content (% – LWC); and functional diversity indexes: functional richness (FRic), functional redundancy (FRed), functional divergence (FDiv). Taxonomic structure included Species Richness (SR), Shannon diversity (H'), Pielou' evenness (J) and the two first axes of a non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity. LL: Lowland Forest remnants in Rio Formoso district; SB: Submontane forest remnants in Bonito district; SM: Submontane remnants in São Vicente Férrer district.

Plot	Site	Functional Structure											Taxonomic Structure				
		LA-CWM	LA-CV	SLA-CWM	SLA-CV	LDMC-CWM	LDMC-CV	LWC-CWM	LWC-CV	FRic	FRed	SESRao	SR	H'	J	NMDS1	NMDS2
1	LL	116.342	20.395	280.938	8.643	0.258	11.394	74.254	14.487	0.466	0.265	1.311	5	1.465	0.818	-0.71194155	-0.40917
2	LL	84.186	11.948	387.383	21.882	0.225	6.190	77.511	14.165	0.341	0.288	1.023	4	1.574	0.809	-0.48235	-0.56369
3	LL	104.455	7.915	270.104	6.195	0.268	5.077	85.004	6.717	0.072	0.506	-1.282	7	2.015	0.917	0.548141	-0.35435
4	LL	94.954	14.911	250.514	11.552	0.236	9.895	76.433	11.105	0.051	0.410	-0.803	5	1.557	0.869	0.543328	-0.55854
5	LL	90.079	31.123	220.647	26.485	0.302	29.540	69.852	28.864	0.273	0.139	0.302	4	0.686	0.426	-1.29736	-0.08677
6	LL	80.250	25.888	206.990	23.778	0.300	25.538	69.451	25.315	0.509	0.075	-0.180	6	0.527	0.254	-0.57744	-0.91256
7	LL	91.037	5.786	220.512	4.613	0.266	6.106	73.372	5.283	0.219	0.491	-1.276	10	2.192	0.914	0.084544	-0.58435
8	SBB	136.561	24.499	255.586	29.487	0.321	17.880	76.546	27.719	0.021	0.208	0.432	3	0.866	0.625	0.065182	1.701507
9	SBB	130.168	22.373	298.262	24.917	0.241	18.607	75.890	22.285	0.168	0.265	-0.326	4	0.942	0.679	0.416427	1.553813
10	SBB	88.447	7.429	255.426	10.398	0.316	11.021	83.056	10.883	0.109	0.399	-1.039	8	1.527	0.734	-0.38217	0.522485
11	SBB	138.427	21.075	179.959	9.544	0.272	14.430	72.820	14.337	0.024	0.278	0.667	3	1.002	0.912	-0.60231	0.62103
12	SBB	111.206	30.058	185.610	33.158	0.250	34.431	74.962	32.731	0.027	0.199	-1.047	3	0.572	0.521	-0.03615	0.432871
13	SBB	143.514	17.553	267.901	9.281	0.283	0.576	74.402	10.237	0.080	0.342	-0.503	3	1.265	0.913	-0.78964	-0.20797
14	SBB	44.007	21.449	91.711	33.158	0.500	37.189	49.990	31.234	0.015	0.109	0.590	3	0.476	0.433	-3.07989	-0.25277
15	SBB	130.920	16.354	291.840	21.522	0.220	17.285	81.888	19.541	0.080	0.347	-1.280	5	1.050	0.652	-0.07429	0.550409
16	SBM	73.525	14.737	197.331	10.128	0.329	10,5311$	67.151	9.776	0.203	0.427	-0.992	7	2.034	0.818	0.562387	0.157297
17	SBM	71.858	15.042	212.269	12.840	0.333	13.379	74.922	13.088	0.126	0.437	-1.142	7	1.341	0.689	0.860967	0.50558
18	SBM	75.556	18.600	261.825	12.236	0.245	14.473	75.544	14.815	0.086	0.411	-0.977	5	1.239	0.770	1.483129	-0.36012
19	SBM	117.314	17.131	252.364	12.862	0.221	12.226	78.561	13.475	0.109	0.413	-0.809	5	1.654	0.850	0.745634	-0.12311
20	SBM	107.959	30.179	297.131	20.176	0.214	20.302	80.089	20.825	0.086	0.322	-0.272	4	1.224	0.760	1.153486	-0.66703
Plot	Site	LA-CWM	LA-CV	SLA-CWM	SLA-CV	LDMC-CWM	LDMC-CV	LWC-CWM	LWC-CV	FRic	FRed	SESRao	SR	H'	J	NMDS1	NMDS2

21	SBM	26.178	22.222	320.300	25.737	0.228	23.579	78.686	26.793	0.075	0.227	-0.795	4	0.644	0.464	1.805238	-0.52989
22	SBM	112.325	24.683	271.542	27.478	0.247	27.306	76.070	27.032	0.152	0.118	-0.487	5	0.494	0.276	-0.23492	-0.43467

Table S3: List of species collected in 22 plots in Atlantic Forest remnants in northeastern Brazil. N: Number of the species; LL: Lowland Forest remnants in Rio Formoso district; SB: Submontane forest remnants in Bonito district; SM: Submontane remnants in São Vicente Férrer district. X: Presence; -: Absence.

Family/ Species	Site		
	LL	SB	SM
Anemiaceae			
Anemia hirta (L.) Sw.	X	-	-
Anemia villosa Humb. & Bonpl. ex Willd.	-	X	-
Athyriaceae			
Diplazium cristatum (Desr.) Alston	-	-	X
Blechnaceae			
Blechnum occidentale L.	X	X	X
Neoblechnum brasiliense (Desv.) Gasper & V.A.O. Dittrich	X	X	X
Salpichlaena volubilis (Kaulf.)J.Sm.	-	X	-
Telmatoblechnum serrulatum (Rich.) Perrie et al.	-	X	-
Cyatheaceae			
Alsophila sternbergii (Sternb.) D.S. Conant	X	-	-
Cyathea microdonta (Desv.) Domin	X	X	-
Cyathea phalerata Mart.	X	X	-
Cyathea praecincta (Kunze) Domin	X	-	-
Dryopteridaceae			
Ctenitis distans (Brack.) Ching	-	-	X
Cyclodium meniscioides (Willd.) C.Presl	X	X	-
Didymochlaena truncatula (Sw.) J. Sm.	-	-	X
*Elaphoglossum iguapens*e Brade	-	X	-
Polybotrya osmundacea Willd.	X	X	X
Olfersia cervina (L.) Kunze	X	-	-
Gleicheniaceae			
Gleichenella pectinata (Willd.) Ching	X	X	-
Lindsaeaceae			
Lindsaea lancea (L.) Bedd.	X	-	-
Lindsaea quadrangularis Raddi	-	X	-
Lomariopsidaceae			
Lomariopsis japurensis (Mart.) J.Sm	-	-	X
Marattiaceae			
Danaea geniculata Raddi	X	-	X
Metaxyaceae			
Metaxya parkeri (Hook. & Grev.) ex J. Sm.	X	-	-
Polypodiaceae			
Pecluma robusta (Fée) M.Kessler & A.R.Sm.	-	X	-

Family/ Species	LL	SB	SM
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	-	X	-
Serpocaulon sp.	-	X	X
Pteridaceae			
Adiantopsis radiata (L.) Fée	-	-	X
Pteridium arachnoideum (Kaulf.) Maxon	-	X	-
Saccolomataceae			
Saccoloma elegans Kaulf.	-	-	X
Tectariaceae			
Tectaria incisa Cav.	X	-	-
Triplophyllum dicksonioides (Fée) Holttum	-	X	X
Thelypteridaceae			
Goniopteris biolleyi (Christ) Pic.Serm.	-	-	X
Meniscium longifolium Desv.	-	X	X
Meniscium macrophyllum Kunze	X	-	X
Meniscium serratum Cav.	X	X	-
Steiropteris polypodioides (Raddi) Salino & T.E. Almeida	X	-	-

Table S4: Assemblages mean pair-wise distance (MPD) of co-occurring fern species based on leaf traits. MPD_{obs}: observed assemblage MPD; MPD_{null}: MPD obtained from null communities; MPD-SD_{null}: standard deviation of MPD in null communities; p-value.

Plot	MPD_{obs}	MPD_{null}	MPD-SD_{null}	SESMPD	p
1	2.113	1.679	0.534	0.812	0.080
2	1.917	1.655	0.533	0.491	0.052
3	1.294	2.056	0.466	-1.634	0.044
4	1.280	1.792	0.538	-0.951	0.018
5	1.316	1.126	0.492	0.385	0.069
6	1.107	1.243	0.467	-0.290	0.044
7	1.115	1.730	0.491	-1.252	0.058
8	1.419	1.805	0.489	-0.789	0.024
9	0.831	1.696	0.564	-1.533	0.027
10	1.109	1.656	0.597	-0.916	0.019
11	1.155	1.731	0.573	-1.005	0.015
12	1.437	1.405	0.613	0.051	0.060
13	0.554	0.890	0.411	-0.818	0.025
14	0.419	0.580	0.246	-0.651	0.029
15	1.917	1.502	0.620	0.669	0.058
16	0.327	0.732	0.294	-1.378	0.052
17	1.212	1.653	0.646	-0.682	0.028
18	0.934	0.658	0.314	0.880	0.048
19	0.550	1.279	0.414	-1.760	0.015
20	0.742	0.740	0.289	0.008	0.055
21	0.287	0.343	0.119	-0.467	0.036
22	1.575	2.162	0.449	-1.307	0.084

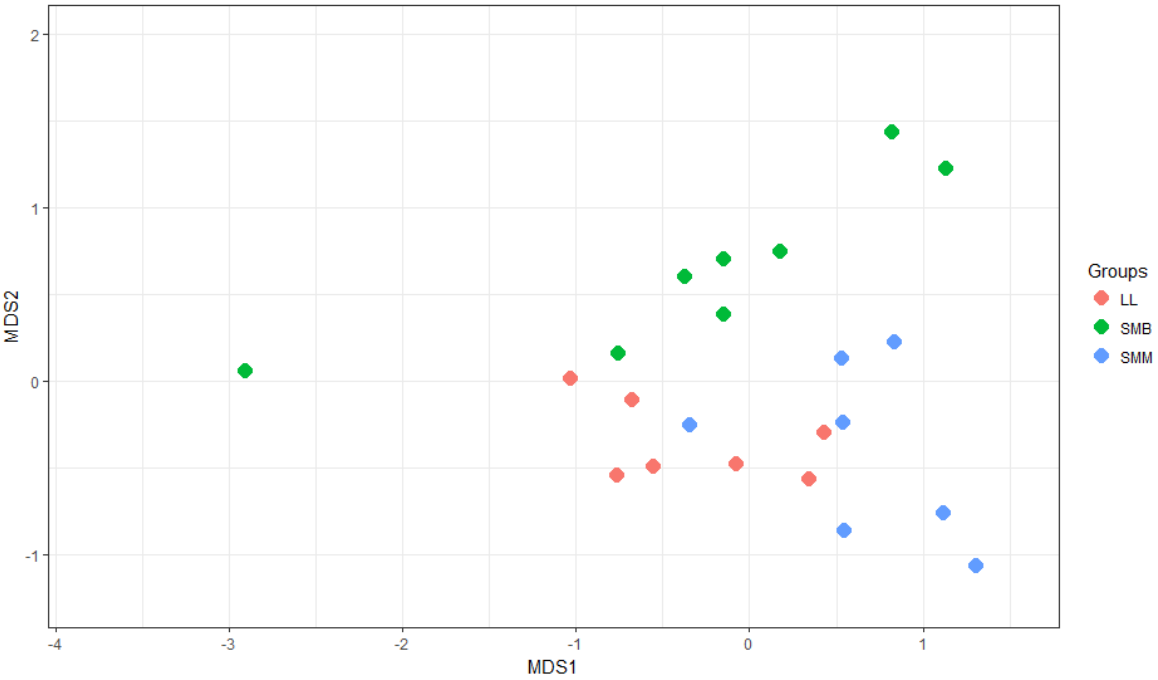


Figure S1: Ordination diagram using nonmetric multidimensional scaling (NMDS) of the floristic patterns of fern assemblages in 22 plots in Atlantic forest remnants in northeastern Brazil. Stress = 0.1044. LL: Lowland Forest remnants in Rio Formoso district; SB: Submontane forest remnants in Bonito district; SM: Submontane remnants in São Vicente Férrer district.

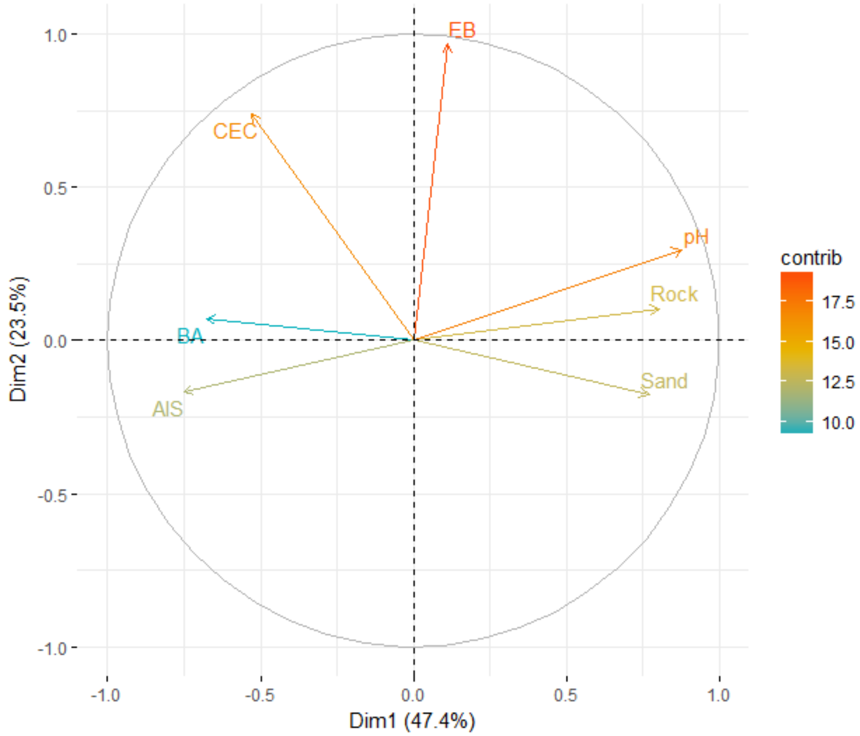


Figure S2: Principal component analysis results of local environmental conditions from 22 plots in Atlantic forest remnants in northeastern Brazil. EB: exchangeable bases; CEC: cation-exchange capacity; BA: basal area; AlS; aluminum saturation; Sand: sand content; Rock: rock coverage; pH: hydrogen potential. Contrib.: Contribution (%) of the variable to the first two axes.

6 THE JOINT EFFECT OF LOCAL AND BROADER ENVIRONMENTAL FACTORS SHAPES FUNCTIONAL BETA DIVERSITY AMONG FERN ASSEMBLAGES IN THE NOVEL BRAZILIAN ATLANTIC FOREST

MANUSCRITO A SUBMETIDO AO PERIÓDICO ECOLOGY

The joint effect of local and broader environmental factors shapes functional beta diversity among fern assemblages in the novel Brazilian Atlantic Forest

Lucas Erickson Nascimento da Costa[1*]; Rafael de Paiva Farias[1]; Michael Kessler[2]; Iva Carneiro Leão Barros[1]

[1] Departamento de Botânica, Universidade Federal de Pernambuco. Avenida Professor Moraes Rêgo, 50560-901, Recife, PE, Brasil.

[2] Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland.

* lucasbiologicasufpe@hotmail.com

Abstract

Studies addressing beta diversity patterns from functional perspective should be bring new perspectives towards the understanding of the mechanism maintaining biodiversity across scales, as well as the degree of species specialization among habitats, and responses of the species to environmental filters. In this study, we determined the role of spatial processes and local and broader scale environmental factors on functional beta diversity of ferns from Tropical Forests. As we know that fern taxonomic diversity is driven by edaphic gradient s at a local scale, we hypothesized this gradient also driver functional beta diversity to group. For this purpose, we conducted sampling of ferns and environmental variables in 22 plots in three Atlantic forest areas, Brazil. Our results showed a strong individual and combined effect of local and broad scale environmental variables on functional beta diversity, with no significant effect of purely spatial processes. Soil pH and annual temperature determined the functional beta diversity structuring to ferns. Thus, we may indicate that those effects in the taxonomic structure are the outcome of the pronounced shifts in the functional patterns among fern assemblages mediated by both local and broad scale environmental.

Keywords: environmental filtering, spatial scale, functional trait turnover; herbaceous plants, pteridophytes, soil Ph.

INTRODUCTION

Beta diversity patterns are often evoked in order to investigate the ecological processes shaping biodiversity distributional patterns (Qian et al. 2005; Gabriel et al. 2006). Beta diversity, as most of ecological processes, are scale-dependent (Whittaker 1972), due the contribution of different local and regional processes (Gabriel et al. 2006; Swenson et al. 2009; Boschilia et al. 2016). At large scales (i.e., regional), climate, as well as, altitude and latitude gradients (which also harbors associated climate trends) are widely recognized as meaningful regional drivers (Cornwell, Schwilk & Ackerly 2006; Cavender-Bares et al. 2009), while local edaphic conditions, environmental heterogeneity and biotic interactions (e.g., competition) were identified as key drivers of fine-scale beta diversity patterns (Cavender-Bares et al. 2009).

Yet, climate is also able to shape fine-scale beta diversity patterns (Alahuhta et al. 2018; Zhang et al. 2018; Bertuzzi et al. 2019), since plants might differ in the responses to environmental gradients according to climate conditions (Zhang et al. 2018; Bertuzzi et al. 2019). On the other hand, the effects of local environmental variables on beta diversity may be scalled up to coarse scales (Alahuhta et al. 2017). Furthermore, both local and broad scale processes can interact with each other and with spatial processes due to the natural spatial structure displayed by environmental gradients (Legendre & Legendre 1998), as well as by dispersion limitations among species (Hubbell 2001; Alahuhta et al. 2017). However, occasionally, these different processes might create similar patterns (Laliberté et al. 2009).

Thus, it has been suggested the influence of environmental filtering and spatial processes should be investigated simultaneously in order to identify the relative contribution of each processes (e.g., Duivenvoorden et al. 2002; Borcard et al., 2004; Vellend 2010). Although disentangle the impacts of different process driving beta diversity across scales might be challenging (Gilbert & Lechowicz 2004; Laliberté et al. 2009), the outcomes seem to be worth it. In this sense, revealing whether beta diversity patterns are explained by environment, spatial processes and space, or by the interplaying of both gives important insights about the role of environmental filtering and dispersal processes in the maintaining of biodiversity across scales, with significant information to more effective and predictive conservation actions (McGill et al. 2006; Kraft et al. 2011), especially in the current scenario of biodiversity erosion (Cardinale et al. 2012) and climate change (IPCC 2014).

Most of the studies of beta diversity were focused on a taxonomic perspective, i.e. species identity (e.g., Duivenvoorden et al. 2002; Cottenie 2005; Karst et al. 2005; Jones et al. 2008; Bishop et al. 2015) using a wide and diversity set of measurements (Anderson et al. 2011). Despite the importance of understanding species distribution and its main drivers, it has been widely defunded that interpretations of general ecological patterns from a taxonomic perspective might be limited (Bishop et al. 2015), since species identities do not provide significant insights towards their ecologies, making single taxonomic approaches less informative (Whittaker, Willis & Field, 2001; McGill et al. 2006; Bishop et al. 2015). Thus, studies addressing beta diversity patterns from other biodiversity facets, as the phylogenetic and functional perspectives should be encouraged since an integrative approach might bring new perspectives towards the understanding of the mechanism maintaining biodiversity across scales (Swenson et al. 2009; Bernard-Verdier et al. 2013; Cardoso et al. 2014; Bishop et al. 2015; Carvalho et al. 2019).

Regarding the functional facet, the inclusion of functional traits (see Violle et al. 2007) on beta diversity studies can be more easily linked to the degree of species specialization among different habitats (Wang et al. 2019), to the responses of the species to environmental filters, and species feedback on ecosystem services across spatial scales (Diaz et al. 2007; Mouchet et al. 2010;

Wang et al. 2019). In the meantime, several analyses able to incorporate trait-based beta diversity approaches (i.e., functional beta diversity) were developed (e.g., Baselga & Orme 2012; Marcon & Hérault 2015). However, studies addressing functional beta diversity approaches investigating the role of environment and space, as well as, identifying key environmental variables structuring beta functional patterns remain scarce for several biological groups (but see Siefert et al. 2013; Villéger et al. 2013; Arnan et al. 2015).

With an approximate number of 10.578 species worldwide (PPG I 2016), ferns are an abundant component of tropical forest understories, where they can comprise up to 15% of the understory cover (Harms et al. 2004), with high functional importance, such as substrates to epiphytes plants (Mehltreter et al. 2005), and resource to herbivorous (Farias et al. 2018a). Previous studies denoted the outstanding role of environmental variables as climate and edaphic conditions affecting ferns diversity and structuring species turnover (i.e., beta diversity) at distinct scales (e.g., Jones et al. 2008; Duivenvoorden et al. 2002; Tuomisto et al. 2003a; Karst et al. 2005). Yet, most of these studies were developed in the Amazon forest, while other important hotspots were poorly studied, as the Brazilian Atlantic forest (but see Costa et al. 2019). The remain Brazilian Atlantic forest are composed by highly fragmented areas (Tabarelli et al. 2005), where ferns been affected by fragmentation and edge effects (Silva et al. 2014; Silva et al. 2011), rarely exceeding one hundred species by study area (see Farias et al. 2017). In a previous study from a taxonomic perspective Costa et al. (2019) highlighted the role of local edaphic conditions on ferns diversity and species composition with a pronounced turnover at the local scale which was as higher as the turnover reported for the regional scale.

Based on this previous study, we aimed to evaluate the role of spatial processes and local and broader scale environmental factors on functional beta diversity of ferns from Atlantic forest remnants. Regarding the strong edaphic control exhibited by ferns (Zuquim et al. 2014; Moulatlet et al. 2019), and since edaphic conditions may control beta diversity among different facets and scales (Bernard-Verdier et al. 2012; Wang et al. 2019), we hypothesized that local environmental filtering, via local edaphic conditions is the main driver of functional beta diversity of the fern assemblages in the across Brazilian Atlantic Forest remnants. We expected a higher strength of local scale variables, especially edaphic conditions driving functional beta diversity with no effects of purely spatial process (due to high dispersal ability of ferns, it is unlikely that limitation of dispersion were significant at the scales of study). We expected significant effects of nutrient availability will be the leading local edaphic condition increasing beta diversity among local assemblages by promoting functional divergence.

METHODS

Study area and data collection

We sampled three Atlantic forest areas located in Pernambuco state, northeastern of Brazil (Figure1). The climate was hot and wet according to the Köppen Climate Classification System, with annual temperature means ranging between 21.5C-27.4C and annual rainfall ranging between 1200-2000mm. The study areas are classified as lowland forest (Rio Formoso district - LL) and -88 340 S; 358 70 W, below 100 ma.s.l.) and submontane Forest (Bonito district - SBB and São Vicente Férrer district – SBM).

We selected these areas because they were well explored in terms of ferns inventories and sampling efforts for ecological studies (see Costa et al. 2019). This is essential for beta diversity studies due to biased responses according to sampling effort (Beck, Holloway & Schwanghart 2013). Furthermore, previous studies in the same dataset explored ferns alpha and beta taxonomic patterns (Costa et al. 2019), which allows direct comparations with other facet of the biodiversity, as denoted by Wang et al. (2015).

The data was collected from 22 plots (10m×20 m) in the three areas, which were at least 100m apart from each other. Plot establishment followed previous studies with ferns along Atlantic forest remnants (e.g., Silva et al. 2014), exploring suitable habits for ferns, as shaded microhabitats, slopes and ravines. All the fern species in the plot were counted and identified following specialized literature (Table 1, Appendix 1), with authorities' names abbreviated according to the International Plant Names Index (IPNI) available at www.ipni.org. Species vouchers were deposited at the UFP Herbarium.

Trait selection

We sampled a set of 10 meaningful functional traits including both response and effect traits, which hold whole plant responses (i.e., leaf and rhizome) in other to summarize traits that affect species performance and effect on ecosystem functioning. The rhizome type, laminar dissection and laminar morphology were categorically measured following previous studies with ferns (e.g., Kluge & Kessler 2007). Rhizome type influence the competition for space and light (Kluge & Kessler 2007), being categorized as: erect/short creeping (1), creeping (2) and tree-like (3). Laminar dissection included entire (1), once-pinnate, to pinnate-pinnatifid, (2), and twice- or more-pinnate leaves (3). This trait might reflect adaptation to harsh conditions, especially temperature and humidity fluctuations (Kramer et al. 1995), while laminar morphology indicates resource demand to reproductive events and spore dispersion (Kramer et al. 1995). We also measured the leaf area (LA), the specific leaf area (SLA) the leaf dry matter content (LDMC), the leaf water content (LWC), leaf phenol concentrations, and the leaf nitrogen (N) and phosphorous (P) concentrations. These traits are related to important trade-offs for resource acquisition, stress tolerance and ecosystem functioning (Bakker et al. 2011; Hodgson et al. 2011; Pérez-Harguindeguy et al. 2013; Finegan et al. 2015; Díaz et al. 2016). The LA, SLA LDMC and LWC were measured from fully expanded mature sterile leaves, with no traces of herbivory following Pérez-Harguindeguy et al. (2013). Traits were collected in five individuals of each species per plot. In plots with less than five individuals per species, leaves were collected in the surrounding area of the plot. Leaf N and P concentrations were measured using adapted protocols from Kjeldahl (Bremner & Mulvaney 1982), and Bezerra-Neto and Barreto (2011), respectively. Phenol concentrations were measured from 100 mg of dry leaves in 80% methanol, with a 10% Folin–Ciocalteu reagent according to Amorim et al. (2008), a spectrophotometer (Genesys 10S UVVIS, Thermo Scientific, Waltham, USA) calibrated at a wavelength of 760 nm. Due to logistic questions it was not possible to perform analysis of leaf N, P and phenol concentrations in *Meniscium longifolium*, *Lindsaea falcata* and *Alsophila sternbergii*, thus, these traits were calculated as the mean of the genus for the formers, and as the mean for the family for the latter.

Spatial structure

We used Principal Coordinates of Neighbourhood Matrix (PCNM) to evaluate spatial structure of the plots. We applied Euclidean distances on geographic distance matrix. Data truncation distance was based on the longest distance to keep data connected. PCNM vectors summarizes spatial structure, where the first PCNM vectors indicate broader distance and the latter indicate smaller scale variation (Bocard et al. 2004).

Local and broad scale environmental variables

Local environmental variables were measured at the plot level and included the number of trees, the basal area of the trees (as a proxy to understory luminosity and forest structure, rock coverage (as a proxy to habitat heterogeneity due to rock outcrops), and a set of edaphic variables (i.e., soil pH, soil contents of Ca, Mg, Al, K, P, and Na, as well as, percentages of sand, silt and clay). Basal area was calculated as: G = $\sum_{i=1}^{n} = \frac{\pi.\ DHB^2}{4}$, where G is the sum of the basal area of all individuals with DHB≥15 cm (Gama et al. 2007); π is the constant; and DBH is the diameter at breast height. Rock coverage was measured as the percentage of the plot covered by rocks following the Blaun–Blanket scale. Edaphic variables were obtained from surface soil samples (0-20 cm depth) collected in five points of the plot and mixed to a composite sample (500 g). Samples were air-dried, cleaned from roots and detritus, and homogenized. Soil pH was measured in a water solution. Concentrations of Ca, Mg and Al were extracted and determined with KCl 1 mol/L and atomic absorption spectrophotometer, respectively. Available P and exchangeable K and Na were extracted with Mehlich 1 method and determined by spectrophotometry (P), and flame photometer (K and Na). We also calculated the exchangeable bases (EB), the effective cation-exchange capacity (CEC(t)), the base saturation (BS), and Al-saturation (AlS). Soil percentage of clay, silt, and sand were determined using the pipette method. Soil analysis followed standard methods according to Embrapa (2017).

Broad scale variables were obtained from climate data from each plot extracted from the WORLDCLIM (http://www.worldclim.org/bioclim) data base at 1km spatial resolution (Fick & Hijmans 2017). We obtained values for 10 bioclimate variables (Table 1, Appendix 2) representing annual trends (e.g., annual precipitation) and limiting environmental factors (e.g., temperature of the coldest and warmest month).

Statistical analysis

In order to estimate functional beta diversity among plots, we calculated the functional beta entropy of the assemblages and transformed the beta functional entropy into functional beta diversity (βF) (Jost 2007; Marcon et al. 2014a). We constructed a distance-base functional tree by calculating the functional distance between species using the Gower distance, which allows mixed continuous and categorical ordinal traits (Podani & Schmeera 2007), and clustered species using unweighted pair group method with arithmetic mean (UPGMA) (“vegdist” and “hclust” functions in *vegan* package). The functional tree was combined with the community matrix (site-species abundance) to calc beta functional entropy weighted by “true” diversity in order 1 (“BetaEntropy” in *entropart* package), which was posteriorly converted in to true βF (Jost 2007; Tuomisto 2010) by using of deformed exponential of order q on entropy values (“expq” in *entropart*). Beta functional entropy was derived from bias-corrected and normalized according to the height of the tree (Marcon et al. 2014b). We estimated beta diversity to order 1, because orders 0 and 2 are disproportionately sensitives to rare and most common species, respectively (Jost 2007).

We selected the most meaningful environmental variables in both local and broad scales based on the contributions of the variables to principal component analysis (PCAs) (“princomp” in *factoextra*). We excluded variables with low contribution to PCA axes (≤ 0.40) or correlated ($r \geq 0.7$). Based on PCA results (Figures 1-2,Appendix 2), the most representative local variables were rock coverage, soil pH and edaphic variables (i.e., AlS, EB, K, Mg and sand content). The most meaningful environmental variables to the broad scale were the annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, and annual precipitation (Figures 1-2, Appendix 2).

We analyzed the role of spatial and local and broad scale environmental variables in two ways. Firstly, we performed a variation partition based on partial regressions (“varpart” in *vegan*) in order to partialling out the effects of spatial processes, and local and broad scale environmental variables on βF (Borcard et al. 1992). Prior to variance partitioning analysis, we tested whether local and broad scale environmental variables were correlated with spatial distance via Mantel tests. We also tested for correlations between local and broad scale between, isolating the spatial structure of these two gradients with a partial Mantel test ("mantel" and "mantel.partial" in *vegan*). Spatial distance, as well as, both the environmental distances (i.e., local and broad scale) followed Euclidian distances. All Mantel testes used 1000 randomizations. Further, we analyzed specifically the effect of spatial structure (small and larger distances) on βF with multiple regressions with forward selection on PCNM axes. To analyze specific effects of local and broad scale environmental variables on βF, we general linear mixed models (GLMM) ("glmer" in *lme4*). To the final model, βF of each assemblage was the response variable and environmental variables (both local and broad scale) were the explanatory variables. Spatial distance was added as a random effect, in order to control for spatial autocorrelation. We performed a model selection using backward-selection procedures to identify the best-fit models from the full model (i.e. including all fixed effects) using the "dredge" function in the *MuMIn* package. A null model (i.e. without fixed effects) was included in the analysis to verify if the selected model would differ from null expectations. The best-supported models were selected according to the small-sample-size corrected Akaike's information criterion (AICc) and ΔAICc values (Burnham & Anderson 2002). Best-fit models with a ΔAICc<2 were considered equally plausible and were averaged according full averages coefficients (Grueber et al. 2011). Prior to the model analysis, we calculated the variance inflation factor (VIF) for all the variables in the model in other to avoid multicollinearity ("vif" in *car*). A VIF value higher than five indicates a problematic collinearity in the model (James et al. 2014). Consequentially, we excluded maximum temperature of warmest month, minimum temperature of coldest month, due to high VIF values. All the analyses were performed in R environment (R Core Team 2015) and $p \leq 0.05$ were considered significant.

RESULTS

We sampled 37 species over the 22 assemblages and sampling sufficiency reached up to 80% of coverage for all plots (see Costa et al. 2019 for detailed floristic information). The mean βF was 3.523 ±3.542, with a coefficient of variation of 99.68, denoting an outstanding discrepancy in functional distances among fern assemblages.

Spatial structure generated nine PCNM vectors, and some vectors exhibited negative values, indicating that some plots are lightly spatially structured (Table 2, Appendix 2). When analyzed the two first and the two last PCNM vectors, it is possibly to visualize a decreasing in the scale of the spatial gradient according with the increasing in PCNM axes (Figure 1, Appendix 3). The PCA for local environmental vectors explained 50.1% of the total variation in the two first axes (PC1 = 31.7; PC2 = 18.4), while for broad scale the first two axes accounted for 91.9% of the variations (PC1 = 74.6; PC2 = 17.3%). Detailed information about PCAs is available from the supplementary material (Figures 1-2, Appendix 2).

We observed a significant contribution of both the local and broad scale environmental conditions on overall βF, with 16 and 11% explained by broad and local scale, respectively (Figure 2). We also reported the jointly effect of local and broad scale environmental factors, as well as, the effect of all factors together on βF (Figure 2). Despite the spatial structure of local and broad scale environmental gradients denoted by Mantel tests (Table 1, Appendix 4), spatial structure associated with either local or broad scale environmental gradients exhibited no significant contributions to shifts in ferns βF (Figure 2). Instead, spatially structured environmental gradients, as well as, solely spatial gradient produced negative adjusted R^2 values, indicating that these models performed worse than null expectations (Table 2 of the Appendix 5). In accordance with these results, none of the PCNM vectors presented significant effects on βF (Table 1, Appendix 4).

According to the model selection, only a single model was supported (i.e., ΔAICc<2) indicating that soil pH (local environmental variable) and annual temperature (broad scale environmental variable) affected significantly ferns βF with a positive correlation for the former and negative for the later (Table 1; Figure 3A-B). Since only these two variables were retained in the best supported model, we performed a posteriori model and evidenced the interactive effect of these variables on ferns βF (Table 1; Figure 3C).

DISCUSSION

We evidenced a strong individual and combined effect of local and broad scale environmental variables on functional beta diversity, with no significant effect of purely spatial processes, which partially corroborated our hypothesis. Local edaphic conditions were not the only drivers of ferns functional beta diversity. Instead, we denoted the effect of climatic conditions (which were correlated with local environmental variables even in the absence of spatial structure) and highlighted the joint effect of annual temperature and soil pH on functional beta diversity, via a negative and positive associations, respectively.

Regarding the relative contribution of spatial and environmental gradients (local and broad scale) to βF, previous studies reported the high contribution of environmental conditions beta diversity, followed by environment spatially structured and a small but consistent contribution of the pure spatial structure (e.g., Karst et al. 2005; Jones et al. 2008). Although these studies focused on the taxonomic component, we believe that this effect can be extrapolated to the functional component. In fact, Costa et al. (2019) analyzed the same assemblages from a taxonomic perspective (including alpha and beta components) and reported the outstand role of environmental filtering on ferns diversity, which was coupled with a high species turnover of the same magnitude on local and regional scale. Our results indicate that these effects in the taxonomic structure are the outcome of the pronounced shifts in the functional patterns among fern assemblages mediated by both local and broad scale environmental conditions. To our knowledge, this is the first study addressing the role of local and broad scale environmental variables on the βF patterns of fern assemblages, indicating that the strength of the environmental conditions on the fern assemblages is consistent across biodiversity facets.

Interestingly, we found no significant contributions of spatial processes alone or combined with the environmental structure (either local or broad scale). Spatial processes (i.e., dispersion), can act at larger scales affecting species pool and connecting metacommunities at the local scale (Vellend 2010). Tuomisto et al. (2003b) analyzing fern species turnover along Amazon forest found partial support for spatial processes at a larger scale (up to 1.400km). The non-significant effect of spatial processes reported in our study might be related to three main factors: (1) our spatial range is of approximately 250 km, which not represent a significant dispersal barrier for ferns due high dispersal ability via spores (Page 2002); (2) taxonomic and functional beta diversity do not necessary follows the same trends, since each facet might vary in different ways (De Bello et al. 2006; Carvalho et al. 2019). Yet, since species may change with no significant shifts in functional patterns (Cadotte 2001; Flynn et al. 2009), while functional patterns might change due shifts in species composition (species with different traits) or due to intraspecific variation (Auger & Shipley 2013); (3) Finally, it is important to highlight that both local and broad scale gradients where spatially structured. Thus, shifts toward functional traits might reflect the structure of different strategies (i.e., species with different traits or differences in the proportion of species exhibiting a given trait) filtered along with spatial changes in environment. In such situations, the role of purely spatial processes might be blurred (Soininen et al. 2007; Laliberté et al. 2009; but see Siefert et al. 2013).

Surprisingly, the representativity of soil pH and annual temperature were disproportional to the size of the gradients that they expressed. The soil pH was acidic among all plots, ranging between 3.26 and 5.55, while annual temperature ranged between 21.5 °C and 27.4 °C (Figures 1-2, Appendix 2). Although acid soils are related to low fertility conditions, tropical ferns were reported inhabiting acid soils (Tuomuisto et al. 2002; Moulatlet et al. 2019). The logistic response of increasing βF from a delimited acidity range indicates that only specific suit of traits is available under more acid conditions, whereas, different strategies can array under less acid soils. On the other hand, temperature has a strong influence on fern ecology, impacting species along the role life cycle. High temperatures has negative impacts on spore germination, although sensitivity vary between species (Ranal et al. 1999), on sporophyte establishment and survival, on population size and phenology, as well as, species distribution (with direct impacts on soil and air humidity and water availability) (Ranal et al. 1999; Page 2002; Silva et al. 2011; Testo & Watkins Jr 2013; Farias et al. 2018), and on functional traits (Kessler et al. 2007), as well. In synthesis, both the climate and edaphic conditions were filters to fern assemblages, due to the clear edaphic niches exhibited by ferns (Moulatlet et al. 2019), and limiting conditions imposed by temperature, species under more acid conditions and high temperatures showed a high functional convergence among between assemblages (low beta diversity), whereas, less acid conditions under lower temperatures promoted a more diverse array of strategies, denoted by the high beta diversity among these assemblages.

CONCLUSION

We evidenced a remarkable effect of the environmental filtering on functional beta diversity of ferns among Atlantic Forest remnants, via the joint effect of local and broad scale environmental variables promoting a functional reorganization of the assemblages. Our results bring new insights about the mechanisms structuring communities across scales, specifically, the coordinate effect of environmental variables on fern assemblages from different facets of biodiversity (i.e., taxonomic and functional) suggest that a strong environmental filtering is operating across scales (Mouchet et al. 2010). Moreover, since local and broad scale environment were correlated even when spatial structure was considered, the effective response of each environmental scale cannot be accurately estimate (Gilbert & Lechowicz, 2004).

Further, the disproportionality between the small range of environmental gradients and fern functional responses is impressive, especially regarding the temperature. The role of temperature as one of the main driver of diversity responses was reported to other biological groups (Burgmer et al. 2007; Arnan et al. 2015; Barton & Schmitz 2018; García et al. 2018), which support general concerns about the role of climate change on community responses and ecosystem services (Jenkins et al., 2011; García et al. 2018). Although models might diverge (IPCC 2014), optimistic and pessimist scenarios predicts, respectively, an increase above 2°C and 4°C in the mean temperature of the Earth (IPCC 2014). The temperature increase might trigger cause a ferns' functional structure towards a functional homogenization of the assemblages (Devictor et al. 2008).

Yet, besides the fact that the Brazilian Atlantic forest been pointed as one of the three biodiversity hotspots most vulnerable to climate change (Béllard et al. 2014), an overview of tropical ferns responses indicates that these plants might be a threefold losers in the future scenario of climate changes, since: (1) increasing temperature will constraint ferns from spore germination to sporophyte survival and traits responses (as discussed above); (2) these plants are sensitive to fragmentation and general changes in land use (Silva et al. 2011; 2014), which are one of the main threats to biodiversity interacting with climate changes (Sala et al. 2000); (3) and present a distributional pattern closely related to soil conditions (Moulatlet et al. 2019; Zuquim et al. 2019), which are significantly affected by anthropic activities (Borrelli et al. 2017).

ACKNOWLEGMENTS

The authors would to thanks to the Laboratório de Química do Solo of the Universidade Federal Rural de Pernambuco for the support on soil analysis; to Gilson from “Mata do Estado” in São Vicente Férrer, to the Secretary of the environment of Bonito and Trapiche and Cucaú Mill for the allowance and logistic support during the fieldwork. The first author would thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, National Council for Scientific and Technological Development) to doctorate scholarship and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) to the international internship scholarship (process 88881.189293/2018-01).

FUNDING

This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Ministério de Educação do Brasil [Finance Code 001].

REFERENCES

Alahuhta, J., Kosten, S., Akasaka, M., Auderset, D., Azzella, M. M., Bolpagni, R., ... & de Winton, M. (2017). Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. Journal of Biogeography, 44(8), 1758-1769.

Alahuhta, J., Lindholm, M., Bove, C. P., Chappuis, E., Clayton, J., de Winton, M., ... & Hoyer, M. V. (2018). Global patterns in the metacommunity structuring of lake macrophytes: regional variations and driving factors. Oecologia, 188(4), 1167-1182.

Amorim, E. L., Nascimento, J. E., Monteiro, J. M., Peixoto Sobrinho, T. J. S., Araújo, T. A., & Albuquerque, U. P. (2008). A simple and accurate procedure for the determination of tannin and flavonoid levels and some applications in ethnobotany and ethnopharmacology. Functional Ecosystems and Communities, 2(1), 88-94.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., ... & Harrison, S. P. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology letters, 14(1), 19-28.

Arnan, X., Cerdá, X., & Retana, J. (2015). Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. PeerJ, 3, e1241.

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(3), 419-428.

Bakker, M. A., Carreño-Rocabado, G., & Poorter, L. (2011). Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. Functional Ecology, 25(3), 473-483.

Barton, B. T., & Schmitz, O. J. (2018). Opposite effects of daytime and nighttime warming on top-down control of plant diversity. Ecology, 99(1), 13-20.

Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. Methods in ecology and evolution, 3(5), 808-812

Beck, J., Holloway, J. D., & Schwanghart, W. (2013). Undersampling and the measurement of beta diversity. Methods in Ecology and Evolution, 4(4), 370-382.

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., & Courchamp, F. (2014). Vulnerability of biodiversity hotspots to global change. Global Ecology and Biogeography, 23(12), 1376-1386.

Bernard-Verdier, M., Flores, O., Navas, M. L., & Garnier, E. (2013). Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. Journal of Vegetation Science, 24(5), 877-889.

Bertuzzi, T., Marques Pires, M., & Maltchik, L. (2019). Drivers of the beta diversity of aquatic plant communities along a latitudinal gradient in southern Brazilian coastal ponds. Journal of Vegetation Science, 30(2), 281-290.

Bezerra-Neto, E., Barreto, L. P. (2011) Análises químicas e bioquímicas em plantas. UFRPE, Recife.

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., & Parr, C. L. (2015). Contrasting species and functional beta diversity in montane ant assemblages. Journal of Biogeography, 42(9), 1776-1786.

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. Ecology, 73(3), 1045-1055.

Borcard, D., Legendre, P., Avois-Jacquet, C., & Tuomisto, H. (2004). Dissecting the spatial structure of ecological data at multiple scales. Ecology, 85(7), 1826-1832.

Borrelli, P., Robinson, D. A., Fleischer, L. R., Lugato, E., Ballabio, C., Alewell, C., ... & Bagarello, V. (2017). An assessment of the global impact of 21st century land use change on soil erosion. Nature communications, 8(1), 1-13.

Boschilia, S. M., de Oliveira, E. F., & Schwarzbold, A. (2016). Partitioning beta diversity of aquatic macrophyte assemblages in a large subtropical reservoir: prevalence of turnover or nestedness?. Aquatic Sciences, 78(3), 615-625.

Bremner , J. M., Mulvaney, C. S. (1982). Nitrogen total. In: Page, A. L. (ed) Methods of soil analysis, 2nd edn. Soil Science Society of America, Madison, pp 595–624.

Burgmer, T., Hillebrand, H., & Pfenninger, M. (2007). Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia, 151(1), 93-103.

Burnham, K. P., Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Ecological Modelling. Springer Science & Business Media, New York, New York, USA.

Cadotte, M. W. (2011). The new diversity: management gains through insights into the functional diversity of communities. Journal of Applied Ecology, 48(5), 1067-1069.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... & Kinzig, A. P. (2012). Biodiversity loss and its impact on humanity. Nature, 486(7401), 59-67.

Cardoso, P., Rigal, F., Carvalho, J. C., Fortelius, M., Borges, P. A., Podani, J., & Schmera, D. (2014). Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. Journal of Biogeography, 41(4), 749-761.

Carvalho, J. C., Malumbres‐Olarte, J., Arnedo, M. A., Crespo, L. C., Domenech, M., & Cardoso, P. (2019). Taxonomic divergence and functional convergence in Iberian spider forest communities: Insights from beta diversity partitioning. Journal of Biogeography.

Cavender‐Bares, J., Kozak, K. H., Fine, P. V., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. Ecology letters, 12(7), 693-715.

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait‐based test for habitat filtering: convex hull volume. Ecology, 87(6), 1465-1471.

Costa, L. E. N., Arnan, X., de Paiva Farias, R., & Barros, I. C. L. (2019). Community responses to fine-scale environmental conditions: Ferns alpha and beta diversity along Brazilian Atlantic forest remnants. Acta Oecologica, 101, 103475.

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. Ecology letters, 8(11), 1175-1182.

De Bello, F., Lepš, J., & Sebastià, M. T. (2006). Variations in species and functional plant diversity along climatic and grazing gradients. Ecography, 29(6), 801-810.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008). Functional biotic homogenization of bird communities in disturbed landscapes. Global ecology and biogeography, 17(2), 252-261.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences, 104(52), 20684-20689.

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., ... & Garnier, E. (2016). The global spectrum of plant form and function. Nature, 529(7585), 167-171.

Duivenvoorden, J. F., Svenning, J. C., & Wright, S. J. (2002). Beta diversity in tropical forests. Science, 295(5555), 636-637.

Empresa Brasileira de Pesquisa Agropecuária [EMBRAPA] (2017) Manual de métodos de análise de solos, 3rd edn. Embrapa CNPS, Rio da Janeiro.

Farias, R. P, Costa, L. E. N., Barros, I. C. L., & Mehltreter, K. (2018). Leaf Phenology of Danaea geniculata (Marattiaceae) in a submontane tropical forest, Brazil. American Fern Journal, 108(2), 35-46.

Farias, R. P., Costa, L. E. N., de Oliveira, A. F. M., Barros, I. C. L., & Mehltreter, K. (2019). Leaf defense syndromes in tropical ferns. Plant Ecology, 1-13.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International journal of climatology, 37(12), 4302-4315.

Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., ... & Licona, J. C. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. Journal of Ecology, 103(1), 191-201.

Flynn, D. F., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., ... & DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. Ecology letters, 12(1), 22-33.

Gabriel, D., Roschewitz, I., Tscharntke, T., & Thies, C. (2006). Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. Ecological applications, 16(5), 2011-2021.

Gama, J. R. V., Souza, A. L. D., Calegário, N., & Lana, G. C. (2007). Fitossociologia de duas fitocenoses de floresta ombrófila aberta no município de Codó, Estado do Maranhão. Revista Árvore, 31(3), 465-477.

García, F. C., Bestion, E., Warfield, R., & Yvon-Durocher, G. (2018). Changes in temperature alter the relationship between biodiversity and ecosystem functioning. Proceedings of the National Academy of Sciences, 115(43), 10989-10994.

Gilbert, B., & Lechowicz, M. J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences, 101(20), 7651-7656.

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. Journal of evolutionary biology, 24(4), 699-711.

Harms, K. E., Powers, J. S., & Montgomery, R. A. (2004). Variation in small sapling density, understory cover, and resource availability in four Neotropical forests. Biotropica, 36(1), 40-51.

Hodgson, J. G., Montserrat-Martí, G., Charles, M., Jones, G., Wilson, P., Shipley, B., ... & Bogard, A. (2011). Is leaf dry matter content a better predictor of soil fertility than specific leaf area?. Annals of botany, 108(7), 1337-1345.

Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton: Princeton University Press.

IPCC, 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. [barros, v.r., c.b. Field, d.j. Dokken, m.d. Mastrandrea, k.j. Mach, t.e. Bilir, m. Chatterjee, k.l. Ebi, y.o. Estrada, r.c. Genova, b. Girma, e.s. Kissel, a.n. Levy, s. Maccracken, p.r. Mastrandrea, and l.l. White (eds.)].: Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2014.

James, G., Witten, D., Hastie, T., Tibshirani, R. (2014). An Introduction to Statistical Learning: With Applications in R. Springer Publishing Company, Incorporated.

Jenkins, C. N., Sanders, N. J., Andersen, A. N., Arnan, X., Brühl, C. A., Cerda, X., ... & Gove, A. D. (2011). Global diversity in light of climate change: the case of ants. Diversity and Distributions, 17(4), 652-662.

Jones, M. M., Tuomisto, H., Borcard, D., Legendre, P., Clark, D. B., & Olivas, P. C. (2008). Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia, 155(3), 593-604.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology, 88(10), 2427-2439.

Karst, J., Gilbert, B., & Lechowicz, M. J. (2005). Fern community assembly: the roles of chance and the environment at local and intermediate scales. Ecology, 86(9), 2473-2486.

Kessler, M., Siorak, Y., Wunderlich, M., & Wegner, C. (2007). Patterns of morphological leaf traits among pteridophytes along humidity and temperature gradients in the Bolivian Andes. Functional Plant Biology, 34(11), 963-971.

Kluge, J. & Kessler, M. (2007) Morphological characteristics of fern assemblages along an elevational gradient: patterns and causes. Ecotropica, 13, 27–43.

Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., ... & Cornell, H. V. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. Science, 333(6050), 1755-1758.

Kramer, K. U., Schneller, J. J., & Wollenweber, E. (1995). Farne und Farnverwandte. G. Thieme.

Laliberté, E., Paquette, A., Legendre, P., & Bouchard, A. (2009). Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. Oecologia, 159(2), 377-388.

Legendre, P., Legendre. L. (1998). Numerical ecology (2nd edition). Amsterdam: Elsevier Science.

Marcon, E., & Hérault, B. (2015). entropart: An R package to measure and partition diversity. Journal of Statistical Software, 67(1), 1-26.

Marcon E, Scotti I, Hérault B, Rossi V, Lang G (2014a). “Generalization of the Partitioning of Shannon Diversity.” PLOS ONE, 9(3), e90289.

Marcon E, Zhang Z, Hérault B (2014b). “The Decomposition of Similarity-Based Diversity and Its Bias Correction.” HAL, hal-00989454(version 1), 1–12.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. Trends in ecology & evolution, 21(4), 178-185

Mehltreter K, Flores-Palacios A., & García-Franco J. G. (2005). Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. Journal of Tropical Ecology, 21(6), 651–660

Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24(4), 867-876.

Moulatlet, G., Zuquim, G., Tuomisto, H. (2019). The role off soils for Pteridophyte distribution in Tropical American Forests. Fern Gazette, 21(1),1-20.

Page, C. N. (2002). Ecological strategies in fern evolution: a neopteridological overview. Review of palaeobotany and palynology, 119(1-2), 1-33.

Pérez-Harguindeguy, N., Diaz, S., Gamier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... & Urcelay, C. (2013). New handbook for stand-ardised measurement of plant functional traits worldwide. Australian Journal of Botany 61: 167-234.

Podani, J., & Schmera, D. (2007). How should a dendrogram-based measure of functional diversity function? A rejoinder to Petchey and Gaston. Oikos, 116(8), 1427-1430.

PG I. (2016). A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution, 54(6), 563-603.

Qian, H., Ricklefs, R. E., & White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. Ecology Letters, 8(1), 15-22.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranal, M. A. (1999). Effects of temperature on spore germination in some fern species from semideciduous mesophytic forest. American Fern Journal, 149-158.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... & Leemans, R. (2000). Global biodiversity scenarios for the year 2100. science, 287(5459), 1770-1774.

Siefert, A., Ravenscroft, C., Weiser, M. D., & Swenson, N. G. (2013). Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. Global Ecology and Biogeography, 22(6), 682-691.

Silva, I. A. A., Pereira, A. F. N., & Barros, I. C. L. (2011). Edge effects on fern community in an Atlantic Forest remnant of Rio Formoso, PE, Brazil. Brazilian Journal of Biology, 71(2), 421-430.

Silva, I. A., Pereira, A. F. D. N., & Barros, I. C. (2014). Fragmentation and loss of habitat: consequences for the fern communities in Atlantic forest remnants in Alagoas, north-eastern Brazil. Plant Ecology & Diversity, 7(4), 509-517.

Soininen, J., McDonald, R., & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. Ecography, 30(1), 3-12.

Swenson, N. G., & Enquist, B. J. (2009). Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. Ecology, 90(8), 2161-2170.

Tabarelli, M., Pinto, L. P., Silva, J. M C., Hirota, M. M. & Bedê, L. C. (2005). Desafios e oportunidades para a conservação da biodiversidade na Mata Atlântica brasileira. Megadiversidade 1(1): 132-138Testo, W. L., & Watkins Jr, J. E. (2013). Understanding mechanisms of rarity in pteridophytes: Competition and climate change threaten the rare fern Asplenium scolopendrium var. americanum (Aspleniaceae). American Journal of Botany, 100(11), 2261-2270.

Tuomisto, H. (2010). A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography, 33(1), 2-22.

Tuomisto, H., Ruokolainen, K., Poulsen, A. D., Moran, R. C., Quintana, C., Cañas, G., & Celi, J. (2002). Distribution and diversity of pteridophytes and melastomataceae along edaphic gradients in Yasuní National Park, Ecuadorian Amazonia1. Biotropica, 34(4), 516-533.

Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003a). Dispersal, environment, and floristic variation of western Amazonian forests. Science, 299(5604), 241-244.

Tuomisto, H., Ruokolainen, K., Aguilar, M., & Sarmiento, A. (2003b). Floristic patterns along a 43-km long transect in an Amazonian rain forest. Journal of Ecology, 91(5), 743-756.

Vellend, M. (2010). Conceptual synthesis in community ecology. The Quarterly review of biology, 85(2), 183-206.

Villéger, S., Grenouillet, G., & Brosse, S. (2013). Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in E uropean fish assemblages. Global Ecology and Biogeography, 22(6), 671-681.

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(5), 882-892.

Wang, X., Wiegand, T., Swenson, N. G., Wolf, A. T., Howe, R. W., Hao, Z., ... & Yuan, Z. (2015). Mechanisms underlying local functional and phylogenetic beta diversity in two temperate forests. Ecology, 96(4), 1062-1073.

Wang, J., Chen, C., Li, J., Feng, Y., & Lu, Q. (2019). Different ecological processes determined the alpha and beta components of taxonomic, functional, and phylogenetic diversity for plant communities in dryland regions of Northwest China. PeerJ, 6, e6220.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. Taxon, 21(2-3), 213-251.

Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of biogeography, 28(4), 453-470.

Zhang, M., García Molinos, J., Zhang, X., & Xu, J. (2018). Functional and taxonomic differentiation of macrophyte assemblages across the Yangtze River floodplain under human impacts. Frontiers in plant science, 9, 387.

Zuquim, G., Tuomisto, H., Jones, M. M., Prado, J., Figueiredo, F. O., Moulatlet, G. M., ... & Emilio, T. (2014). Predicting environmental gradients with fern species composition in Brazilian Amazonia. Journal of Vegetation Science, 25(5), 1195-1207.

Zuquim, G., Costa, F. R., Tuomisto, H., Moulatlet, G. M., & Figueiredo, F. O. (2019). The importance of soils in predicting the future of plant habitat suitability in a tropical forest. Plant and Soil, 1-20.

Tables

Table 1: Results of the best-fitted model (ΔAICc < 2) and posteriori model evidencing the individual and interactive effects of local and broad scale environmental variables on functional beta diversity of the fern assemblages among Atlantic forest remnants in northeastern Brazil. β = coefficient of regression; SE = Standard error; CI = Confident intervals. Significant values (i.e., p ≤ o.o5) are highlighted in bold.

Fixed effects	β	SE	95%CI Lower	95%CI Upper	*p*-value
Intercept	25.219	6.918	11.660	38.777	**0.0000**
Annual Temperature	-12.124	3.057	-18.116	-6.132	**0.0000**
Soil pH	6.146	1.926	2.371	9.920	**0.0014**
Posteriori model					
Annual Temperature * Soil pH	-1372.962	470.121	-2375.000	470.121	**0.0105**

Figures and Captions

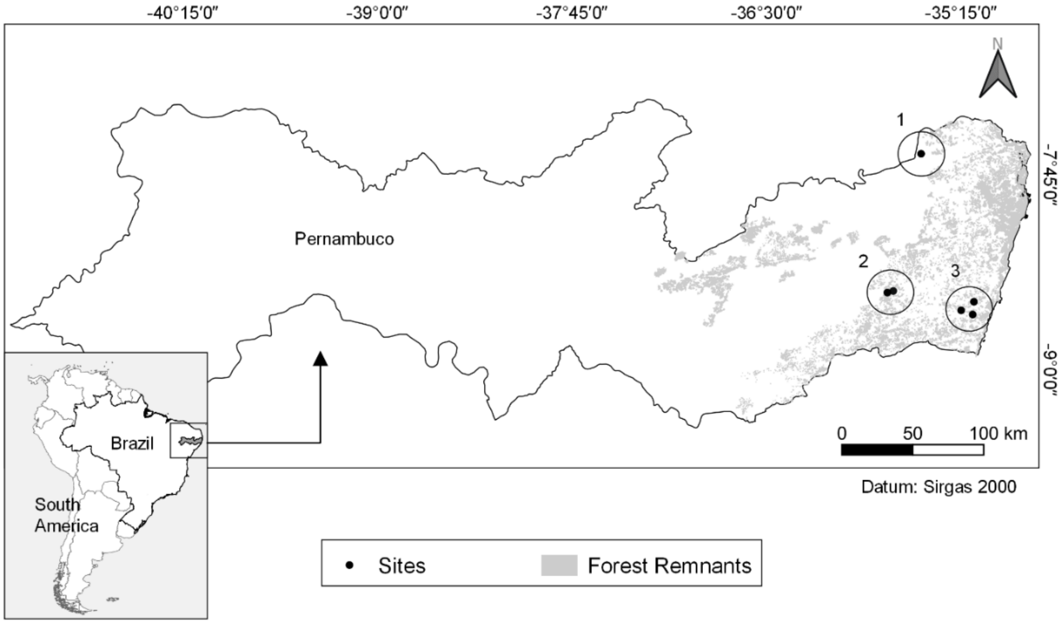


Figure 1: Study area indicating the Pernambuco state in northeastern of Brazil with the three Atlantic Forest areas: 1: São Vicente Férrer district; 2: Bonito district; 3: Rio Formoso district. Light grey patches represent the remain Atlantic forest remnants in Pernambuco state.

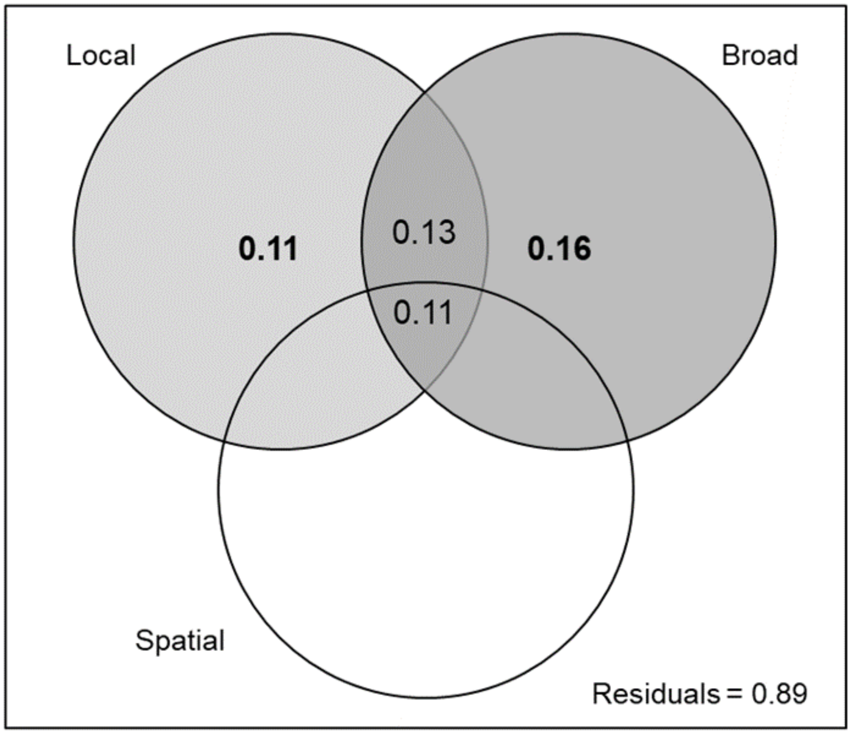


Figure 2: Variation partitioning analysis for functional beta diversity of the fern assemblages regarding the contribution of spatial structure and local and broad scale environmental variables. Values represent adjusted R^2 and negative values were not shown.

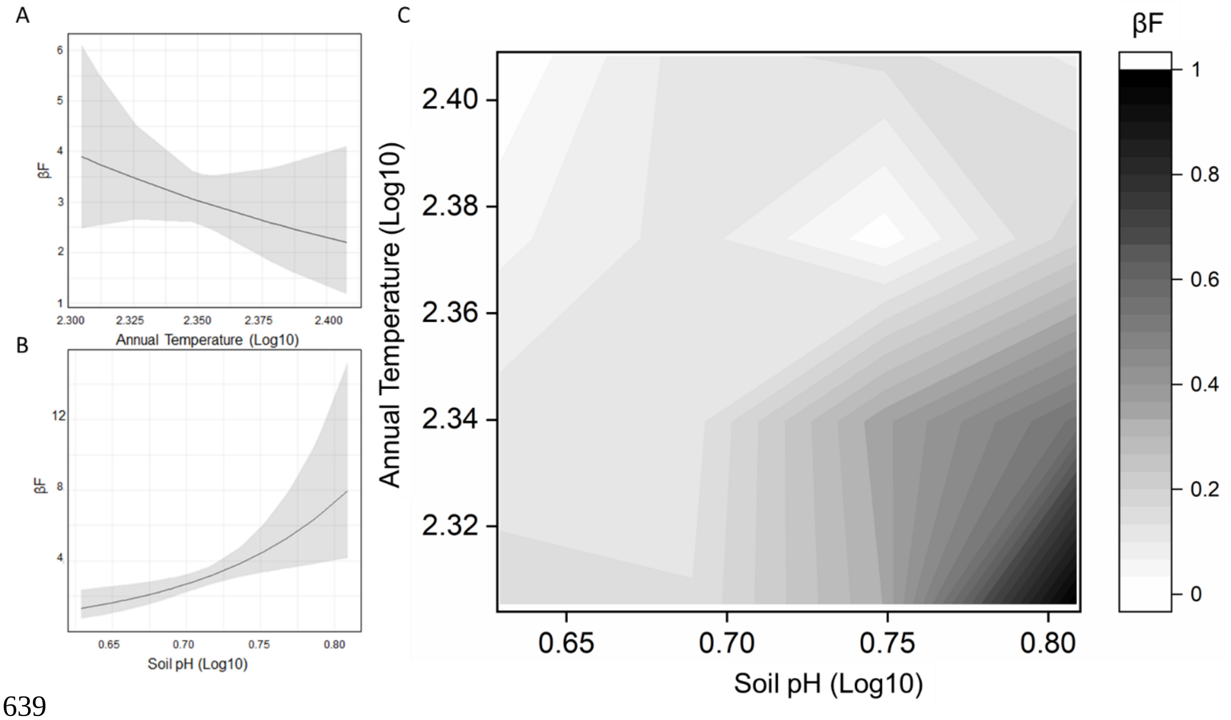


Figure 3: Influence of the individual and interactive (C) effeicts of the annual temperature (A) and soil pH (B) on functional beta (βF) diversity of the fern assemblages. The metric values and 95% confidence intervals (in grey) of individual responses (A-B) were obtained from estimates of the best-fitted model (ΔAICc < 2) from the general linear mixed effect model analysis. βF values from the posteriori interactive model was standardized between 0-1 in the countour plot.

Supplementary Material

Appendix 1

Table 1: Species list abbreviation and measured functional traits per species. Abrev: abbreviations; LA: leaf area; SLA: specific leaf area; LDMC: leaf dry matter content; N: nitrogen; P: phosphorus. R: rhizome (1- erect, short creeping; creeping; tree-like); LA: laminar dissection (0-entire; once pinate or pinnatifid; 2- twice of more pinate); LM: laminar morphology (1-monomorphic; 2- slight dimorphic; 3- dimorphic).

Species	Abrev	LA (mm^2)	SLA (mm^2/m)	LDMC (%)	LWC (%)	Leaf N (% DW)	Leaf P (g/kg DW)	Phenols (g/kg DW)	R	LD	LM
Adiantopsis radiata (L.) Fée	Arad	25.1188	199.2762	39.69274	60.30726	3.12	0.79	41.71	1	2	1
Alsophila sternbergii (Sternb.) D.S. Conant	Astern	203.73	204.1263	29.51687	70.48313	2.45	0.83	29.6	3	2	1
Anemia hirta (L.) Sw.	Ahirta	19.054	332.17	43.44379	56.55621	1.99	0.84	33.64	1	1	3
Anemia villosa Humb. & Bonpl. ex Willd.	Avilo	34.054	89.99754	52.64823	47.35177	2.03	0.83	39.79	1	1	3
Blechnum occidentale L.	Bocci	88.09071	224.1723	29.20351	70.79649	2.2	0.83	30.38	1	1	1
Ctenitis distans (Brack.) Ching	Cdist	23.04784	283.5837	32.00082	67.99918	2.57	0.77	28.8	1	1	1
Cyathea microdonta (Desv.) Domin	Cmicro	112.0588	365.7303	27.76666	72.23334	2.88	0.93	31.15	3	2	2
Cyathea phalerata Mart.	Cphale	118.4093	268.641	24.90235	75.09765	2.77	0.83	30.64	3	2	1
Cyathea praecincta (Kunze) Domin	Cprae	106.4678	215.6764	23.55921	76.44079	2.13	0.84	28.55	3	2	1
Cyclodium meniscioides (Willd.) C.Presl	Cmeni	110.4497	192.782	20.16677	79.83323	2.01	0.85	28.76	1	1	1
Danaea geniculata Raddi	Dgeni	57.71848	220.7266	22.9286	77.0714	2.63	0.82	33.03	1	1	3
Didymochlaena truncatula (Sw.) J.Sm.	Dydimo	71.2507	275.0353	23.08464	76.91536	3.21	0.89	28.3	1	2	1
Diplazium cristatum (Desr.) Alston	Dcrist	28.1881	319.9476	20.14376	79.85624	3.5	0.99	26.89	1	1	1
Elaphoglossum iguapense Brade	Elapho	113.906	107.0699	28.57773	71.42227	1.62	0.8	28.47	1	0	3
Gleichenella pectinata (Willd.) Ching	Gleich	57.533	127.7125	50.42473	49.57527	1.49	0.74	32.25	2	2	1
Goniopteris biolleyi (Christ) Pic.Serm.	Gbioll	28.60827	377.4186	27.02122	72.97878	4.09	0.89	28.18	1	1	1
Lindsaea falcata Dryand	Lfalc	56.95	219.3221	36.2214	63.7786	2.44	0.76	27.39	1	2	1
Lindsaea lancea (L.) Bedd.	Llance	42.218	177.7866	36.91406	63.08594	2.44	0.75	26.55	1	2	1
Lindsaea quadrangulares Raddi	Lquadra	110.202	207.56	36.47679	63.52321	2.43	0.77	28.23	1	2	1

Lomariopsis japurensis (Mart.) J.Sm	Ljapu	45.3463	192.0136	29.35226	70.64774	2.45	0.83	30.76	2	1	3
Species	Abrev	LA (mm²)	SLA (mm²/m)	LDMC (%)	LWC (%)	Leaf N (% DW)	Leaf P (g/kg DW)	Phenols (g/ kg DW)	R	LD	LM
Meniscium longifolium Desv.	Mlong	84.834	204.8943	33.15605	66.84395	2.24	0.85	29.85	1	1	1
Meniscium macrophyllum Kunze	Mmacrop	137.3466	284.5499	21.6569	78.3431	2.02	0.78	28.52	2	1	3
Meniscium serratum Cav.	Mserra	61.70533	259.4833	26.68215	73.31785	2.47	0.93	31.19	2	1	2
Metaxya parkeri (Hook. & Grev.) ex J. Sm.	Mpark	92.284	192.546	30.06223	69.93777	1.88	0.74	31.23	1	1	1
Neoblechnum brasiliense (Desv.) Gasper & V.A.O. Dittrich	Nbras	160.5318	243.2864	20.11783	79.88217	2.11	0.84	29.83	1	0	1
Olfersia cervina (L.) Kunze	Ocerv	102.532	212.4311	21.23579	78.76421	1.98	0.83	36.73	1	1	3
Pecluma robusta (Fée) M.Kessler & A.R.Sm.	Probusta	88.58333	178.3159	42.31901	57.68099	2.89	0.89	50.37	1	0	1
Polybotrya osmundacea Willd.	Posmun	117.0765	234.3157	25.93061	74.06939	2.32	0.76	27.7	2	2	3
Pteridium arachnoideum subsp. arachnoideum (Kaulf.) Maxon	Pterid	103.158	102.7596	33.27975	66.72025	1.67	0.85	30	2	2	1
Saccoloma elegans Kaulf.	Selega	77.37907	205.4216	31.74953	68.25047	3.18	0.83	27.95	1	1	1
Salpichlaena volubilis (Kaulf.) J.Sm.	Salpicla	131.101	173.9101	25.40925	74.59075	2.02	0.76	26.08	2	2	2
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	Scatha	125.782	260.5468	24.63638	75.36362	2.49	0.76	27.64	2	0	1
Serpocaulon sp.	Serpoca	131.202	306.3307	22.96225	77.03775	2.49	0.76	27.64	2	1	1
Steiropteris polypodioides (Raddi) Salino & T.E. Almeida	Spoly	40.57733	254.1019	33.0968	66.9032	2.25	0.83	27.78	1	1	1
Tectaria incisa Cav.	Tincisa	59.298	487.2921	18.04433	81.95567	3.22	0.99	30.83	1	1	2
Telmatoblechnum serrulatum (Rich.) Perrie et al.	Tserru	73.618	220.1703	30.7669	69.2331	1.9	0.83	32.13	1	1	2
Triplophyllum dicksonioides (Fée) Holttum	Triphlo	78.51131	270.7986	27.11119	72.88881	3.08	0.78	26.29	1	2	1

Appendix 2

Table 1: Summary of the local and broad scale enviornmental variables analysed in general linerar mixed effect models. LL: Rio Formoso district; SBM: São Vicente Féerrer district; SBB: Bonito district; Rock: soil rock coverage; EB: excheangeble bases; AlS: soil aluminum saturation; bio1: annual temperature; bio12: annual preciptation.

Plot	Área	Local scale							Broad scale	
		Rock (%)	Sand (%)	pH	Mg (mg/dm3)	K (mg/dm3)	EB (cmolc/dm3)	AlS(%)	bio1	bio12
1	LL	50	82.4	5.18	193.985	100.190	4.310	36.341	25.6	1804
2	LL	70	63.8	4.19	132.230	302.758	6.426	33.370	24.4	1280
3	LL	0	62.9	3.93	244.342	168.741	6.280	40.139	24.1	2108
4	LL	0	76.1	4.06	321.215	134.378	5.659	35.514	24.1	2108
5	LL	45	86.9	5.1	196.190	114.984	3.317	17.536	24	2015
6	LL	45	85.8	5.44	217.9955	248.777	5.315	13.659	24	2015
7	LL	30	68.3	4.89	412.0887	227.500	8.823	6.233	23.9	2020
8	SBM	0	58.6	4.21	636.902	189.033	8.774	36.959	22.7	1020
9	SBM	0	62.8	3.48	323.709	148.5106	4.391	63.811	22.7	1020
10	SBM	0	54.9	3.54	116.460	196.768	4.531	54.895	22.3	1006
11	SBM	0	58.1	3.44	195.401	209.120	5.035	62.832	22.7	1020
12	SBM	0	65.8	4.48	542.319	264.353	6.141	9.051	22.3	1006
13	SBM	30	61.9	4.66	474.878	344.790	5.855	9.460	22.3	1006
14	SBM	45	58.8	4.65	494.8459	200.756	5.200	18.584	22.5	1016
15	SBB	10	78.1	3.8	210.781	203.161	5.653	38.932	20.2	1015
16	SBB	0	55.3	3.26	198.865	186.793	3.083	31.818	20.2	1015
17	SBB	17	57.9	4.43	194.286	127.189	4.136	44.389	20.2	1015
18	SBB	0	58.0	4.85	297.475	142.769	6.261	46.875	20.2	1015
19	SBB	0	62.8	3.88	246.288	160.278	4.922	49.105	20.5	1063
20	SBB	0	67.5	3.55	101.153	82.825	2.209	34.834	20.3	1032
21	SBB	0	61.8	3.89	145.454	101.253	2.683	73.067	20.3	1032
22	SBB	0	62.5	3.72	513.649	255.532	5.496	54.317	21.2	973
	VIF:	3.830	2.557	4.432	2.858	3.728	4.150	3.150	3.371	4.872

Table 2: Code for environmental variables extracted from the Worldcilm3 at 1km spatial resolution. Reference: Fick, S.E. and Hijmans, R.J. 2017. Worldclim 2: New 1-km spatial resesolution climate surfaces for global land areas. International Journal of Climatology.

Code	**Variables**
bio1	Annual Mean Temperature
bio4	Temperature Seasonality (standard deviation *100)
bio5	Max Temperature of Warmest Month
bio6	Min Temperature of Coldest Month
bio8	Mean Temperature of Wettest Quarter
bio9	Mean Temperature of Driest Quarter
bio12	Annual Precipitation
bio13	Precipitation of Wettest Month
bio14	Precipitation of Driest Month
bio15	Precipitation Seasonality (Coefficient of Variation)

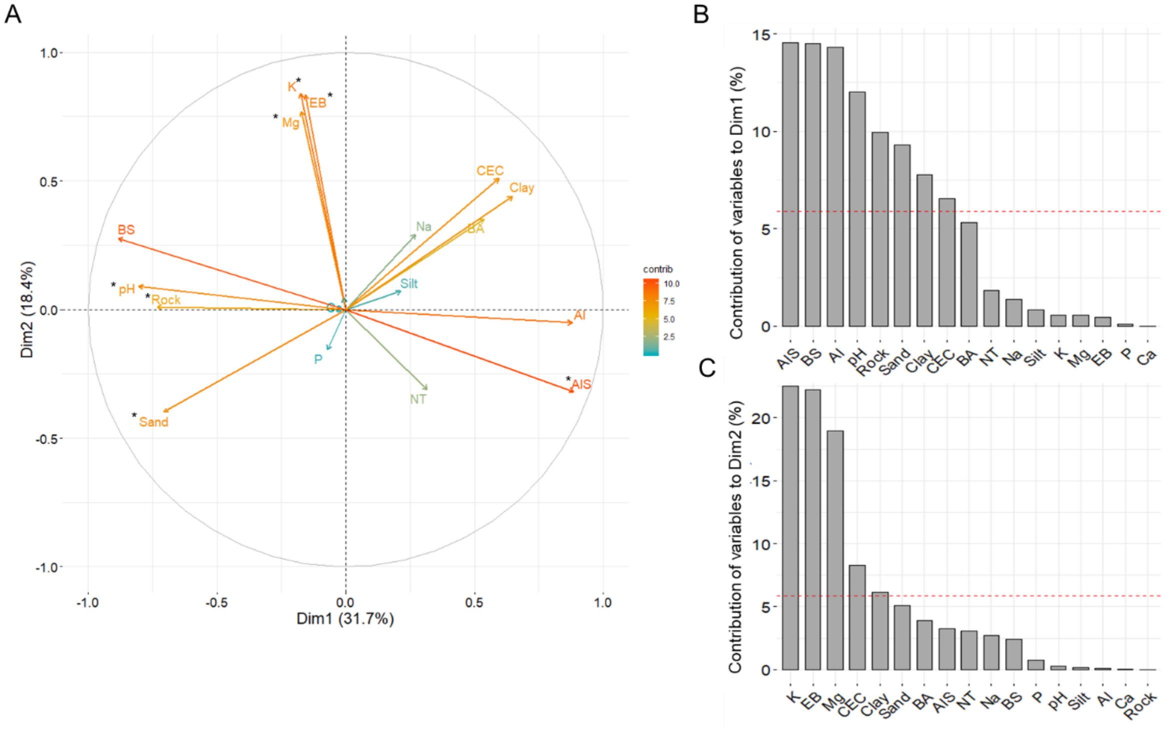


Figure 1: Results from the principal component analysis (PCA) of the local environmental variables indicating variables relationship (A) and contribution to the first (B) and second (C) axes. Contrib = sum of variables contribution to the first two PCA axes; BS: soil base sum; EB: soil exchangeable bases; CEC= soil cation exchange capacity; BA: basal area; AlS: soil aluminum saturation; NT: number of trees; *= indicate variables selected for the other analysis. Variables contribution over the dashed red line indicate significant contribution to the axis. Note that all variables were standardized prior PCA ordination.

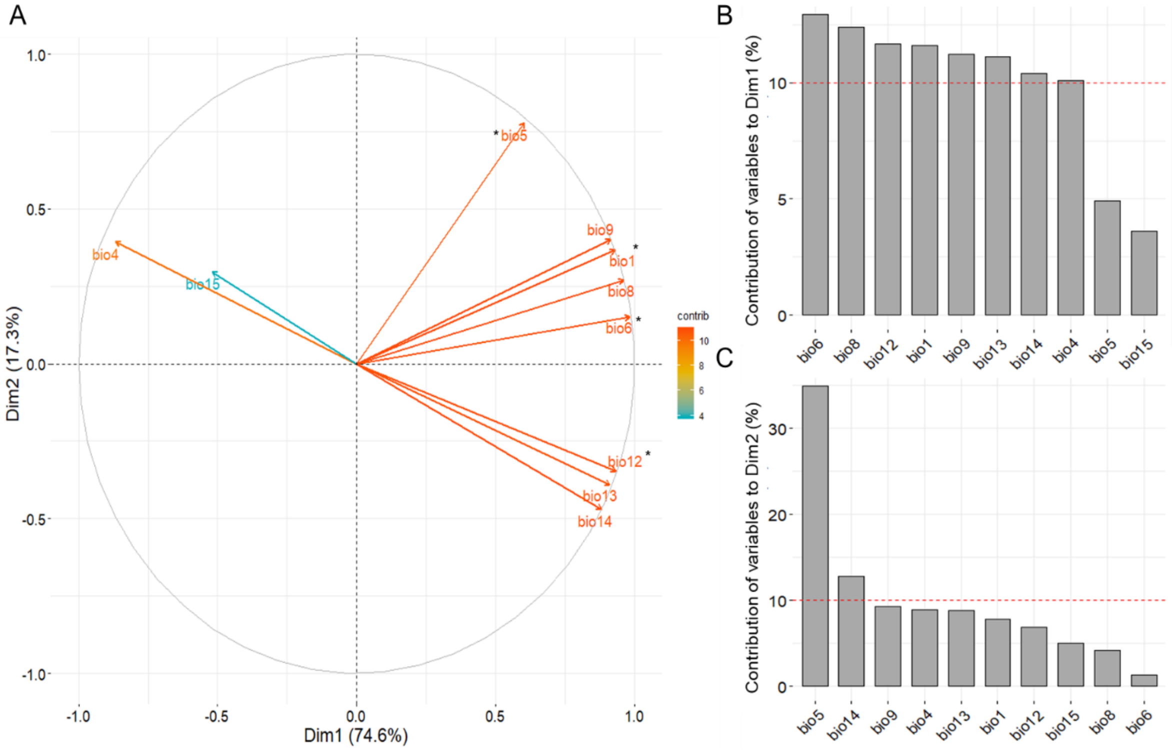


Figure 2: Results from the principal component analysis (PCA) of the broad scale environmental variables indicating variables relationship (A) and contribution to the first (B) and second (C) axes. Contrib = sum of variables contribution to the first two PCA axes; *= indicate variables selected for the other analysis. Variables contribution over the dashed red line indicate significant contribution to the axis. Note that all variables were standardized prior PCA ordination. Variables code descriptions are available in the Table 2 of this supplementary material.

Appendix 3

Table 2: Results of the multiple regressions (forward stepwise) between Principal coordinates of neighbour matrices (PCNM) based on spatial distances and functional beta diversity of fern assemblages among Atlantic Forest remnants in northeastern Brazil B = unstandardized regression; SE = standard error; β = standardized regression coefficient. Significant values (i.e., $p \leq 0.05$) are highlighted in bold. Note that only two non-significant vectors were retained after forward selection.

Factors	B	SE B	β	t	p-value
Intercept	3.475	0.730	-	9.460	**0.0000**
PCNM2	3.929	3.423	0.247	1.148	0.2653
PCNM9	-3.742	3.423	-0.236	-1.093	0.2879
Model: $F_{2,19}$= 1.256; p = 0.307; Adjusted R^2= 0.024					

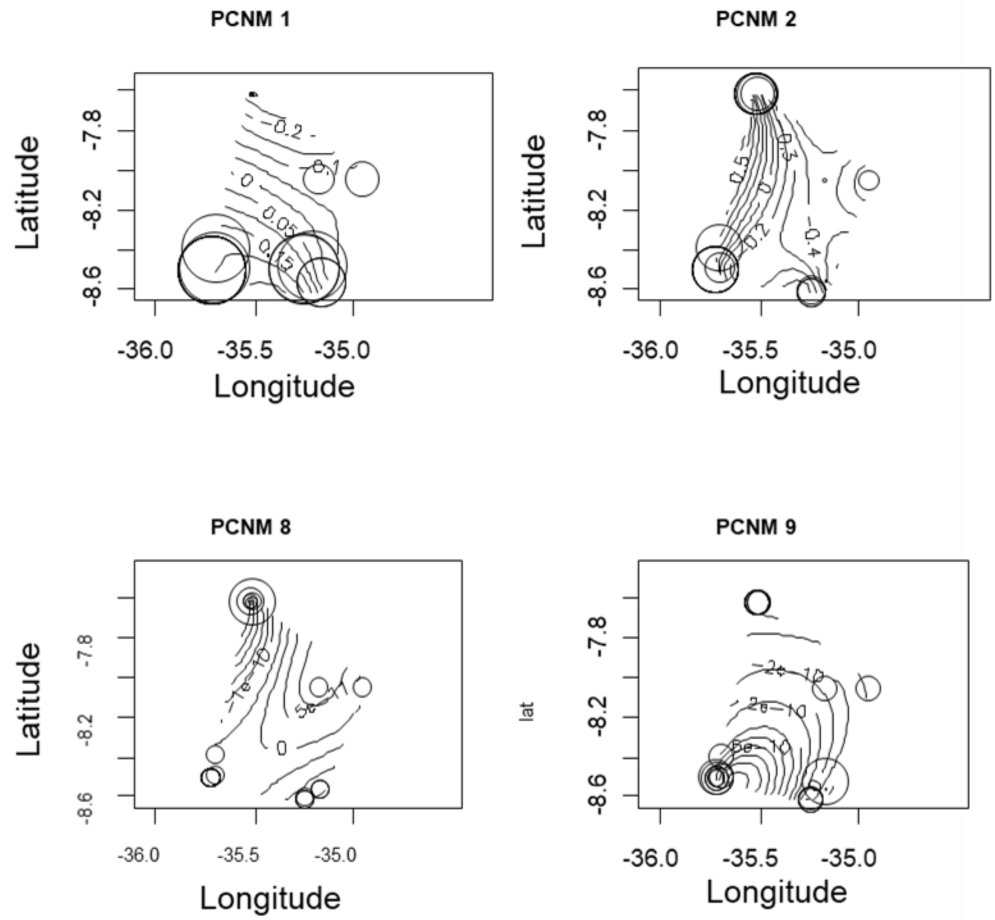


Figure 1: Spatial structure of the Principal coordinates of neighbor matrices (PCNM) vectors (two first and two latter vectors) denoting spatial structure of the sampled habitats among Atlantic Forest remnants in northeastern Brazil inhabit by fern assemblages. Circle size indicates the PCNM value indicating a decreasing in the spatial structure with increasing PCNM vectors.

Appendix 4

Table 1: Results from Mantel tests with 1000 standardizations accounting for the relationship between spatial and environmental (local and broad scale) gradients among habitats of the Atlantic Forest in northeastern Brazil inhabit by fern assemblages. Significant values (i.e., p≤ 0.05) are highlighted in bold. * = partial Mantel test.

Factors	Correlation (*r*M)	p-value
Spatial x Local environment	0.11	0.059
Spatial x Broad scale environment	0.42	**0.001**
Local x Broad scale environment	0.24	**0.023**
Local x Broad scale environment | Spatial*	0.21	**0.036**

Table 2: Results from variance partitioning based on partial regressions indicating adjusted R^2 of each factor. Note that the significance of testable individual fractions was based on redundancy analysis. Significant values (i.e., p≤ 0.05) are highlighted in bold.

Models	Df	R^2	adj. R^2	Testable
Local environment	7	0.34564	0.01846	TRUE
Broad scale environment	1	0.06573	0.01901	TRUE
Spatial	1	0.00007	-0.04993	TRUE
Local + Broad scale environment	8	0.46266	0.13199	TRUE
Local environment + Spatial	8	0.34756	-0.05394	TRUE
Broad scale environment + Spatial	2	0.09257	-0.00295	TRUE
Local + Broad scale + Spatial	9	0.4919	0.11082	TRUE
Individual fractions				
Local environment	7		**0.11377**	TRUE
Broad scale environment	1		**0.16476**	TRUE
Spatial	1		-0.02116	TRUE
Residuals			0.88918	FALSE

7 CONSIDERAÇÕES FINAIS

Essa Tese demonstrou a importância de abordagens funcionais para responder diferentes questões relacionadas à segregação de nicho, estratégias ecológicas, bem como os mecanismos estruturando as assembleias de samambaias em escala local ao longo de remanescentes de Floresta Atlântica no nordeste do Brasil.

Os atributos funcionais foram importantes para explicar a segregação de nicho nas samambaias, bem suas como às estratégias ecológicas. Em relação a coexistência de samambaias, observamos a dominância da convergência funcional, sem efeitos filogenéticos marcantes nos atributos analisados. Nossos resultados indicam que as diferentes facetas do componente taxonômicos atuam de forma independente podendo afetar desde a magnitude da variação dos atributos das assembleias até a diversidade funcional. Ainda, a diversidade beta funcional ao longo das assembleias refletiu as variações ambientais ao longo de diferentes escalas.

Finalmente, nossos resultados evidenciaram os efeitos coordenados dos filtros ambientais sobre a estrutura funcional das samambaias afetando o nicho das espécies, as estratégias ecológicas e a diversidade alpha e beta funcional padrões funcionais das assembleias. Nossos resultados indicam que samambaias podem ser importantes grupos responsivos para entender o papel das condições edáficas nas estratégias ecológicas e na coexistência de espécies na escala local.

REFERÊNCIAS

ACKERLY, D. D.; CORNWELL, W. K. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. **Ecology Letters**, 10: 135–145, 2007.

ADLER, P. B.; ELLNER, S. P.; LEVINE, J. M. Coexistence of perennial plants: an embarrassment of niches. **Ecology Letters**, 13: 1019–1029, 2010.

ANDERSON, M. J.; ELLINGSEN, K. E.; Mcardle, B. H. Multivariate dispersion as a measure of beta diversity. **Ecology Letters**, 9: 683-693, 2006.

BELLUAU, M.; SHIPLEY, B. Linking hard and soft traits: Physiology, morphology and anatomy interact to determine habitat affinities to soil water availability in herbaceous dicots. **PloS One**, 13: e0193130, 2018.

BOTTA-DUKÁT, Z. Cautionary note on calculating standardized effect size (SES) in randomization test. **Community Ecology**, 19: 77-83, (2018).

BRUELHEIDE, H.; DENGLER, J.; PURSCHKE, O.; LENOIR, J.; JIMÉNEZ-ALFARO, B.; HENNEKENS, S. M.; ...; KATTGE, J. Global trait–environment relationships of plant communities. **Nature Ecology & Evolution**, 2: 1906, 2018.

BUTTERFIELD, B. J.; SUDING, K. N. Single-trait functional indices outperform multi- trait indices in linking environmental gradients and ecosystem services in a complex landscape. **Journal of Ecology**, 101: 9–17, 2013.

CACCIANIGA, M.; LUZZARO, A.: PIERCE, S.; CERIANI, R. M.; CERABOLINI, B. The functional basis of a primary succession resolved by CSR classification. **Oikos**, 112: 10-20, 2006.

CADOTTE, M.W.; CAVENDER-BARES, J.; TILMAN, D.; OAKLEY, T. H. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. **PloS One**, 4: e5695, 2009.

CADOTTE, M. W. The new diversity: management gains through insights into the functional diversity of communities. **Journal of Applied Ecology**, 48: 1067-1069, 2011.

CADOTTE, M. W.; CARSCADDEN, K.; MIROTCHNICK, N. Beyond species: functional diversity and the maintenance of ecological processes and services. **Journal of Applied Ecology**, 48: 1079-1087, 2011.

CARREÑO-ROCABADO, G.; PEÑA-CLAROS, M.; BONGERS, F.; DÍAZ, S.; QUÉTIER, F.; CHUVIÑA, J.; POORTER, L. Land-use intensification effects on functional properties in tropical plant communities. **Ecological applications**, 26: 174-189, 2016.

CARVAJAL-HERNÁNDEZ, C. I.; GÓMEZ-DÍAZ, J. A.; KESSLER, M.; KRÖMER, T. Influence of elevation and habitat disturbance on the functional diversity of ferns and lycophytes. **Plant Ecology & Diversity**, 11: 335-347, 2018.

CARVALHO, J. C.; MALUMBRES-OLARTE, J.; ARNEDO, M. A.; CRESPO, L. C.; DOMENECH, M.; Cardoso, P. Taxonomic divergence and functional convergence in Iberian spider forest communities: Insights from beta diversity partitioning. **Journal of Biogeography**, 47: 288-300, 2019.

CAVENDER-BARES, J.; ACKERLY, D. D.; BAUM, D. A.; BAZZAZ, F. A. Phylogenetic overdispersion in Floridian oak communities. **American Naturalist**, 163:823–843, 2004.

CAVIERES, L. A.; BROOKER, R. W.; BUTTERFIELD, B. J.; COOK, B. J.; KIKVIDZE, Z.; LORTIE, C. J.; ...; ANTHELME, F. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. **Ecology Letters**, 17: 193-202, 2014.

CERABOLINI, B. E. L.; BRUSA, G.; CERIANI, R. M.; DE ANDREIS, R.; LUZZARO, A.; PIERCE, S. Can CSR classification be generally applied outside Britain? **Plant Ecology**, 210: 253–261. 2010.

CHAI, Y.; YUE, M.; WANG, M.; XU, J.; LIU, X.; ZHANG, R.; WAN, P. Plant functional traits suggest a change in novel ecological strategies for dominant species in the stages of forest succession. **Oecologia**, 180: 771-783. 2016.

CHAO, A.; CHIU, C. H.; JOST, L. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. **Annual review of ecology, evolution, and systematics**, 45: 297-324, 2014.

CIANCIARUSO, M. V.; SILVA, I. A.; BATALHA, M. A. Diversidades filogenética e funcional: novas abordagens para a Ecologia de comunidades. **Biota Neotropica**, 9: 93-103,

2009

CORNELISSEN, J. H. C.; LAVOREL, S.; GARNIER, E.; DIAZ, S.; BUCHMANN, N.; GURVICH, D. E.; ...; POORTER, H. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. **Australian Journal of Botany**, 51: 335–380, 2003.

CORNELISSEN, J. H. C.; CORNWELL, W. K. The Tree of Life in ecosystems: evolution of plant effects on carbon and nutrient cycling. **Journal of Ecology**, 102: 269–274, 2014.

CORNELL, H. V.; LAWTON, J. H. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. **Journal of Animal Ecology**, 61: 1-12, 1992.

CORNWELL, W. K.; SCHWILK, D. W.; ACKERLY, D. D. A trait-based test for habitat filtering: convex hull volume. **Ecology**, 87: 1465–1471, 2006.

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

COSTA, L. E. N.; SOUZA, K. R. M. S.; SILVA, I. A. A.; FARIAS, R. P.; BARROS, I. C. L. Florística e aspectos ecológicos de samambaias em um remanescente de Floresta Atlântica de terras baixas (Rio Formoso, Pernambuco, Brasil). **Pesquisas, Botânica**, 64: 259-271, 2013.

COUGHENOUR, M. B. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. **Annals of the Missouri Botanical Garden**, 852-863, 1985.

DE BELLO, F.; LAVERGNE, S.; MEYNARD, C. N.; LEPŠ, J.; THUILLER W. The partitioning of diversity: showing Theseus a way out of the labyrinth. **Journal of Vegetation Science**, 21: 992–1000, 2010.

DE BELLO, F.; LAVOREL, S.; LAVERGNE, S.; ALBERT, C. H.; BOULANGEAT, I.; MAZEL, F.; THUILLER, W. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. **Ecography**, 36: 393-402, 2013.

DE BELLO, F.; LEPŠ, J.; SEBASTIÀ, M. T. Variations in species and functional plant diversity along climatic and grazing gradients. **Ecography**, 29: 801-810, 2006.

DE BELLO, F.; PRICE, J. N.; MÜNKEMÜLLER, T.; LIIRA, J.; ZOBEL, M.; THUILLER, W.; ...; Zobel, K. Functional species pool framework to test for biotic effects on community assembly. **Ecology**, 93: 2263-2273, 2012.

DÍAZ, S.; CABIDO, M. Vive la différence: plant functional diversity matters to ecosystem processes. **Trends in Ecology and Evolution**, 16: 646-655, 2001.

DÍAZ, S.; HODGSON, J.; THOMPSON, K.; CABIDO, M.; CORNELISSEN, J.; JALILI, A.; MONTSERRAT-MARTÍ, G.; GRIME, J.; ZARRINKAMAR, F.; ASRI, Y. The plant traits that drive ecosystems: evidence from three continents. **Journal of Vegetation Science**, 15: 295–304, 2004.

DÍAZ, S.; KATTGE, J.; CORNELISSEN, J. H. C.; WRIGHT, I. J.; LAVOREL, S.; DRAY, S.; …; GORNÉ, L. D. The global spectrum of plant form and function. **Nature**, 529: 167–171, 2016.

DÍAZ, S.; LAVOREL, S.; DE BELLO, F.; QUÉTIER, F.; GRIGULIS, K.; ROBSON, T. M. Incorporating plant functional diversity effects in ecosystem service assessments. **Proceedings of the National Academy of Sciences of the United States of America**, 104: 20684–20689, 2007.

EISENLOHR, P. V.; OLIVEIRA-FILHO, A. T.; PRADO, J. The Brazilian Atlantic Forest: new findings, challenges and prospects in a shrinking hotspot. **Biodiversity and Conservation**, 24: 2129–2133, 2015.

FARIAS, R. P.; ARRUDA, E. C. P.; SANTIAGO, A. C. P.; ALMEIDA-CORTEZ, J. S.; CARVALHO-FERNANDES, S. P.; COSTA, L. E. N.; ...; MEHLTRETER, K. First record of galls in the tree fern *Cyathea phalerata* (Cyatheaceae) from a Tropical Rainforest in Brazil. **Brazilian Journal of Biology**, 78: 799-801, 2018.

FARIAS, R. P.; XAVIER, S. R. S. Phenology and survival of three populations of ferns in fragment of Atlantic Forest, in Paraíba, Brazil. **Biotemas**, 24: 13-20, 2011.

FLYNN, D. F. B.; GOGOL-PROKURAT, M.; NOGEIRE, T.; MOLINARI, N.; RICHERS, B.

T.; LIN, B. B.; SIMPSON, N.; MAYFIELD, M. M.; DE CLERCK, F. Loss of functional diversity under land use intensification across multiple taxa. **Ecology Letters**, 12: 22-33, 2009.

FLYNN, D. F.; MIROTCHNICK, N.; JAIN, M.; PALMER, M. I.; NAEEM, S. Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. **Ecology**, 92: 1573-1581, 2011.

FUKAMI, T.; BEZEMER, T. M.; MORTIMER, S. R.; VAN DER PUTTEN, W. H. Species divergence and trait convergence in experimental plant community assembly. **Ecology Letters**, 8; 1283–1290, 2005.

FUNK, J. L.; LARSON, J. E.; AMES, G. M.; BUTTERFIELD, B. J.; CAVENDER-BARES, J.; FIRN, J.; ...; WRIGHT, J. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. **Biological Reviews**, 92: 1156-1173, 2017.

GIRÃO, L. C.; LOPES, A. V.; TABARELLI, M.; BRUNA, E. M. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. **Plos one**, 2: e908, 2007.

GOTELLI, N. J.; MCCABE, D. J. Species co-occurrence: a meta-analysis of J. M. Diamond’s assembly rules model. **Ecology**, 83: 2091–2096, 2002.

GÖTZENBERGER, L.; DE BELLO, F.; BRÅTHEN, K. A.; DAVISON, J.; DUBUIS, A.; GUISAN, A.; ...; PELLISSIER, L. Ecological assembly rules in plant communities—approaches, patterns and prospects. **Biological reviews**, 87: 111-127, 2012.

GRIME, J. P. Vegetation classification by reference to strategies. **Nature**, 250: 26–31, 1974.

GRIME, J. P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. **The American Naturalist**, 111: 1169-1194, 1977.

GRIME, J. P. Factors limiting the contribution of pteridophytes to a local flora. **Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences**, 86: 403-421, 1985.

GRIME, J. P. **The CSR model of primary plant strategies—origins, implications and tests**. *In*: Gottlieb L. D., Jain S. K. (Eds.). Plant evolutionary biology. Dordrecht: Springer. 1988. p. 371-393.

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

GRIME, J. P. **Plant Strategies, Vegetation Processes and Ecosystem Properties**. Chichester: Wiley, 2001. 456p.

GRIME, J. P. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. **Journal of Vegetation Science**, 17: 255–260, 2006.

HARMS, K. E.; POWERS, J. S.; MONTGOMERY, R. A. Variation in small sapling density, understory cover, and resource availability in four neotropical forests. **Biotropica**, 36:40–51, 2004.

HODGSON, J.G.; WILSON, P. J.; HUNT, R.; GRIME, J. P.; THOMPSON, K. Allocating C-S-R plant functional types: a soft approach to a hard problem. **Oikos**, 85: 282-294, 1999.

HODGSON, J.G.; MONTSERRAT-MARTÍ, G.; CHARLES, M.; JONES, G.; WILSON, P.; SHIPLEY, B.; …; PLA, F. R. Is leaf dry matter content a better predictor of soil fertility than specific leaf area? **Annals of Botany**, 108: 1337–1345, 2011.

HOOPER, D.U.; CHAPIN, F. S.; EWEL, J. J.; HECTOR, A.; INCHAUSTI, P.; LAVOREL, S.; …; Wardle, D. A. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. **Ecological Monographs**, 75: 3–35, 2005.

JONES, E. J.; KRAAIJ, T.; FRITZ, H.; MOODLEY, D. A global assessment of terrestrial alien ferns (Polypodiophyta): species' traits as drivers of naturalisation and invasion. **Biological Invasions**, 21: 861-873, 2019.

KARST, A. L.; LECHOWICZ, M. J. Are correlations among foliar traits in ferns consistent with those in the seed plants? **New Phytologist**, 173: 306-312, 2007.

KESSLER, M.; SALAZAR, L.; HOMEIER, J.; KLUGE, J. Species richness-productivity relationships of tropical terrestrial ferns at regional and local scales. **Journal of Ecology**, 102: 1623–1633, 2014.

KESSLER, M.; SIORAK, Y.; WUNDERLICH, M.; WEGNER, C. Patterns of morphological leaf traits among pteridophytes along humidity and temperature gradients in the Bolivian Andes. **Functional Plant Biology**, 34: 963-971, 2007.

KLUGE, J.; KESSLER, M. Morphological characteristics of fern assemblages along an elevational gradient: patterns and causes. **Ecotropica**, 13: 27-43, 2007.

KLUGE, J.; KESSLER, M. Phylogenetic diversity, trait diversity and niches: species assembly of ferns along a tropical elevational gradient. **Journal of Biogeography**, 38: 394-405, 2011.

KNEITEL, J. M.; CHASE, J. M. Trade-offs in community ecology: linking spatial scales and species coexistence. **Ecology Letters**, 7: 69–80. 2004.

KRAFT, N. J. B.; CORNWELL, W. K.; WEBB, C. O.; ACKERLY, D. D. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. **American Naturalist**, 170: 271–283, 2007.

KRAFT, N. J.; VALENCIA, R.; ACKERLY, D. D. Functional traits and niche-based tree community assembly in an Amazonian forest. **Science,** 322: 580–582, 2008.

KURSAR, T. A.; ENGELBRECHT, B. M.; BURKE, A.; TYREE, M. T., EI OMARI, B., & GIRALDO, J. P. Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. **Functional Ecology**, 23: 93-102, 2009.

LABIAK, P. H.; Prado, J. Pteridófitas epífitas da Reserva Volta Velha, Itapoá, Santa Catarina, Brasil. **Boletim do Instituto de Botânica**, 11: 1-79, 1998.

LALIBERTÉ, E.; PAQUETTE, A.; LEGENDRE, P.; BOUCHARD, A. Assessing the scale specific importance of niches and other spatial processes on beta diversity: A case study from a Temperate Forest. **Oecologia**, 159: 377–388. 2009.

LANDEIRO, V. L.; BINI, L. M.; COSTA, F. R.; FRANKLIN, E.; NOGUEIRA, A.; DE SOUZA, J. L.; ...; MAGNUSSON, W. E. How far can we go in simplifying biomonitoring assessments? An integrated analysis of taxonomic surrogacy, taxonomic sufficiency and numerical resolution in a megadiverse region. **Ecological Indicators**, 23: 366-373, 2012.

LAURETO, L. M. O.; CIANCIARUSO, M. V.; SAMIA, D. S. M. Functional diversity: an overview of its history and applicability. **Natureza & Conservação**, 13: 112-116, 2015.

LAVOREL, S.; GARNIER, E. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. **Functional Ecology**, 16: 545–556, 2002.

LAVOREL, S.; GRIGULIS, K.; LAMARQUE, P.; COLACE, M. P.; GARDEN, D.; GIREL, J.; PELLET, G.; DOUZET, R. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. **Journal of Ecology**, 99: 135–147, 2011.

LAVOREL, S.; MCINTYRE, S.; LANDSBERG, J.; FORBES, T. D. A. Plant functional classifications: from general groups to specific groups based on response to disturbance. **Trends in Ecology & Evolution,** 12: 474–478, 1997.

LAWTON, J. H.; BROWN, V. K. **Redundancy in ecosystems**. *In*: Schulze, E. D.; Mooney, H. A. (Eds.). Biodiversity and Ecosystem Function. Berlin Heidelberg: Springer-Verlag, 1993. p. 255–270.

LEBRIJA-TREJOS, E.; PÉREZ-GARCÍA, E. A.; MEAVE, J. A.; BONGERS, F.; POORTER L. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. **Ecology**, 91: 386–398, 2010.

LÔBO, D.; LEÃO, T.; MELO, F. P.; SANTOS, A. M.; TABARELLI, M. Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. **Diversity and Distributions**, 17: 287-296, 2011.

LOHBECK, M.; LEBRIJA-TREJOS, E.; MARTÍNEZ-RAMOS, M.; MEAVE, J. A.; POORTER, L.; BONGERS, F. Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. **PloS One**, 10: e0123741, 2015.

MAGNAGO, L. F. S.; EDWARDS, D. P.; EDWARDS, F. A.; MAGRACH, A.; MARTINS, S. V.; LAURANCE, W. F. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. **Journal of ecology**, 102: 475-485, 2014.

MARCON, E.; HÉRAULT, B. entropart: An R package to measure and partition diversity. **Journal of Statistical Software**, 67: 1-26, 2015.

MASON, N. W. H.; DE BELLO, F.; MOUILLOT, D.; PAVOINE, S.; DRAY, S. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. **Journal of Vegetation Science**, 24: 794–806, 2013.

MASON, N. W. H.; MOUILLOT, D.; LEE, W. G.; WILSON, J. B. Functional richness, functional evenness and functional divergence: the primary components of functional diversity.

Oikos, 111: 112–118, 2005.

MASON, N. W. H.; LANOISELEE, C.; MOUILLOT, D.; IRZ, P., ARGILLIER, C. Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. **Oecologia**, 153: 451–452, 2007.

MASON, N. W. H.; RICHARDSON, S. J.; PELTZER, D. A.; WARDLE, D. A.; DE BELLO, F.; ALLEN, R. B. 2012. Changes in co-existence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. **Journal of Ecology**, 100: 678–689.

MAYFIELD, M. M.; LEVINE, J. M. Opposing effects of competitive exclusion on the phylogenetic structure of communities. **Ecology Letters**, 13: 1085–1093, 2010.

MCGILL, B. J.; ENQUIST, B. J.; WEIHER, E.; WESTOBY, M. Rebuilding community ecology from functional traits. **Trends in Ecology and Evolution**, 21: 178-185, 2006.

MEHLTRETER, K.; FLORES-PALACIOS, A.; GARCÍA-FRANCO, J. G. Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. **Journal of Tropical Ecology**, 21: 651–660, 2005.

MOKANY, K.; ASH, J.; ROXBURGH, S. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. **Journal of Ecology**, 96: 884–893, 2008.

MOUCHET, M. A.; VILLÉGER, S.; MASON, N. W. H.; MOUILLOT, D. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. **Functional Ecology**, 24: 867–876, 2010.

MÜNKEMÜLLER, T.; DE BELLO, F.; MEYNARD, C. N.; GRAVEL, D.; LAVERGNE, S.; MOUILLOT, D.; ...; THUILLER, W. From diversity indices to community assembly processes: a test with simulated data. **Ecography**, 35: 468-480, 2012.

MYERS, N.; MITTERMEIER, R. A.; MITTERMEIER, C. G.; DA FONSECA, G. A.; KENT, J. Biodiversity hotspots for conservation priorities. **Nature**, 403: 853–858, 2000.

NAEEM S. Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. **Ecology**, 83: 2925–2935, 2002.

NEGREIROS, D.; LE STRADIC, S.; FERNANDES, G. W.; RENNÓ, H. C. CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. **Plant Ecology**, 215: 379-388, 2014.

NIINEMETS, Ü.; PORTSMUTH, A.; TENA, D.; TOBIAS, M.; MATESANZ, S.; VALLADARES, F. Do we underestimate the importance of leaf size in plant economics? Disproportional scaling of support costs within the spectrum of leaf physiognomy. **Annals of Botany**, 100: 283–303, 2007.

OLIVEIRA, M. A.; GRILLO, A. S.; TABARELLI, M. Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. **Oryx**, 38: 389-394, 2004.

PAGE, C. N. Ecological strategies in fern evolution: a neopteridological overview. **Review of Palaeobotany and Palynology**, 119: 1–33, 2002.

PAVOINE, S.; BONSALL, M. B. Measuring biodiversity to explain community assembly: a unified approach. **Biological Reviews**, 86: 792-812, 2011.

PEREIRA, A. F. N.; BARROS, I. C. L.; SANTIAGO, A. C. P.; SILVA, I. A. A. Florística e distribuição geográfica das samambaias e licófitas da Reserva Gurjaú, Pernambuco, Brasil. **Rodriguésia**, 62: 001-010, 2011.

PETCHEY, O. L.; EVANS, K. L.; FISHBURN, I. S.; GASTON, K. J. Low functional diversity and no redundancy in British avian assemblages. **Journal of Animal Ecology**, 76: 977–985, 2007.

PETCHEY, O. L.; GASTON, K. J. Extinction and the loss of functional diversity. **Proceedings of the Royal Society of London. Series B: Biological Sciences**, 269: 1721–1727, 2002.

PETCHEY, O. L.; GASTON, K. J. Functional diversity: back to basics and looking forward. **Ecology Letters**, 9: 741–758, 2006.

PIANKA, E. R. On r-and K-selection. **The American Naturalist**, 104: 592-597, 1970.

PIERCE, S.; BRUSA, G.; VAGGE, I.; CERABOLINI, B. E. 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, 2013.

PIERCE, S.; BRUSA, G.; SARTORI, M.; CERABOLINI, B. E. L. Combined use of leaf size and economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive strategies. **Annals of Botany**, 109: 1047–1053, 2012.

PIERCE, S.; NEGREIROS, D.; CERABOLINI, B. E.; KATTGE, J.; DÍAZ, S.; KLEYER, M.; …; TAMPUCCI, D. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. **Functional Ecology**, 31: 444-457.

PONTES, L. D. S.; SOUSSANA, J. F.; LOUAULT, F.; ANDUEZA, D.; CARRERE, P. Leaf traits affect the above-ground productivity and quality of pasture grasses. **Functional Ecology**, 21: 844-853, 2007.

POORTER, L.; BONGERS, F. Leaf traits are good predictors of plant performance across 53 rain forest species. **Ecology**, 87:1733–1743, 2006.

PRÉVOSTO, B.; KUITERS, L.; BERNHARDT-RÖMERMANN, M.; DÖLLE, M.; SCHMIDT, W.; HOFFMANN, M.; ...; KLOTZ, S. Impacts of land abandonment on vegetation: successional pathways in European habitats. **Folia Geobotanica**, 46: 303-325, 2011.

RAUNKIAER, C. **The Life Forms of Plants and Statistical Plant Geography**. Oxford: Clarendon Press, 1934. 729p.

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

REISS, J.; BRIDLE, J. R.; MONTOYA, J. M.; WOODWARD, G. Emerging horizons in biodiversity and ecosystem functioning research. **Trends in Ecology and Evolution**, 24: 505–514, 2009.

RIBEIRO, M. C.; MARTENSEN, A. C.; METZGER, J. P.; TABARELLI, M.; SCARANO, F.; FORTIN, M. J. The Brazilian Atlantic Forest: a shrinking biodiversity hotspot. In: **Biodiversity hotspots** (pp. 405-434). Springer, Berlin, Heidelberg, 2011.

RIBEIRO, M. C.; METZGER, J. P.; MARTENSEN, A. C.; PONZONI, F. J.; HIROTA, M. M. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, 142: 1141-1153, 2009.

RICKLEFS, R. E. Disintegration of the ecological community. **American Naturalist**, 172(6):

741-750, 2008.

RICOTTA, C.; SZEIDL, L. Diversity partitioning of Rao’s quadratic entropy. **Theoretical Population Biology**, 76: 299-302, 2009.

ROCHA-URIARTT, L.; BECKER, D. F.; GRAEFF, V.; KOCH, N. M.; SCHMITT, J. L. Functional patterns and species diversity of epiphytic vascular spore-producing plants in riparian forests with different vegetation structure from southern Brazil. **Plant Ecology and Evolution**, 149: 261-271, 2016.

ROSADO, B. H.; DE MATTOS, E. A On the relative importance of CSR ecological strategies and integrative traits to explain species dominance at local scales. **Functional Ecology**, 31: 1969-1974, 2017.

ROSCHER, C.; SCHUMACHER, J.; GUBSCH, M.; LIPOWSKY, A.; WEIGELT, A.; BUCHMANN, N.; ...; SCHULZE, E. D. Using plant functional traits to explain diversity–productivity relationships. **PloS One**, 7: e36760, 2012.

ROSENFELD, J. S. Functional redundancy in ecology and conservation. **Oikos**, 98: 156-162, 2002.

SALOVAARA, K. J.; CÁRDENAS, G. G.; TUOMISTO, H. Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. **Ecography**, 27: 689-700, 2004.

SANTIAGO, A. C. P.; BARROS, I. C. L.; SYLVESTRE, L. S. Pteridófitas Ocorrentes em três Fragmentos Florestais de um Brejo de Altitude (Bonito, Pernambuco, Brasil). **Acta Botanica Brasílica**,18: 781-792, 2004.

SANTIAGO, A. C. P.; SOUSA, M. A.; SOUSA SANTANA, E.; BARROS, I. C. L. Samambaias e licófitas da Mata do Buraquinho, Paraíba, Brasil. **Biotemas**, 27: 9-18, 2014.

SANTOS, B. A.; PERES, C. A.; OLIVEIRA, M. A.; GRILLO, A.; ALVES-COSTA, C. P.; TABARELLI, M. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. **Biological Conservation**, 141: 249-260, 2008.

SCARANO, F. R.; Ceotto, P. Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. **Biodiversity and Conservation**, 24: 2319-2331, 2015.

SCHELLENBERGER COSTA, D.; GERSCHLAUER, F.; PABST, H.; KÜHNEL, A.; HUWE, B.; KIESE, R.; ...; KLEYER, M. Community-weighted means and functional dispersion of plant functional traits along environmental gradients on Mount Kilimanjaro. **Journal of Vegetation Science**, 28: 684-695, 2017.

SCHMIDT, J.; FASSNACHT, F. E.; LAUSCH, A.; SCHMIDTLEIN, S. 2017. Assessing the functional signature of heathland landscapes via hyperspectral remote sensing. **Ecological Indicators**, 73: 505-512.

SERAL, A.; MURCIANO, A.; MOLINO, S.; DE LA FUENTE, P. Functional ecology of fronds in Iberian saxicolous ferns. **Acta Botánica Malacitana**, 42: 101-110, 2017.

SHARPE, J. M.; MEHLTRETER, K.; WALKER, L. R. **Ecological importance of ferns**. *In*: Mehltreter, K.; Walker, L. R.; Sharpe, J. M. (Eds.). Fern ecology. 1st ed. Cambridge: Cambridge University Press, 2010. p. 1–21.

SILVA, I. A. A.; PEREIRA, A. F. N.; BARROS, I. C. L. Edge effects on fern community in an Atlantic Forest remnant of Rio Formoso, PE, Brazil. **Brazilian Journal of Biology**, 71: 421-430, 2011.

SILVA, I. A.; PEREIRA, A. F. D. N.; Barros, I. C. Fragmentation and loss of habitat: consequences for the fern communities in Atlantic forest remnants in Alagoas, north-eastern Brazil. **Plant Ecology & Diversity**, 7: 509-517, 2014.

SILVA, M. M.; FARIAS, R. P.; COSTA, L. E. N.; Barros, I. C. L. Leaf phenological traits of the tree fern Cyathea praecincta (Cyatheaceae) in a Brazilian lowland tropical forest. **Australian Journal of Botany**, 66: 618-627, 2019.

SOININEN, J.; HEINO, J.; WANG, J. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. **Global Ecology and Biogeography**, 27: 96-109, 2018.

STERCK, F., MARKESTEIJN L, SCHIEVING F, POORTER L. Functional traits determine trade-offs and niches in a tropical forest community. **Proceedings of the National Academy of Sciences**, 108: 20627–20632, 2011.

STUBBS, W.J.; WILSON, J. B. Evidence for limiting similarity in a sand dune community.

Journal of Ecology, 92: 557–567. 2004.

SWENSON, N. G.; ANGLADA-CORDERO, P.; BARONE, J. A. Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. **Proceedings of the Royal Society B: Biological Sciences**, 278: 877-884, 2011.

TABARELLI, M.; SIQUEIRA FILHO, J. D.; SANTOS, A. M. M. A Floresta Atlântica ao norte do rio São Francisco. **Diversidade biológica e conservação da floresta Atlântica ao norte do Rio São Francisco**, 25-37, 2006.

TERBORGH, J.; PITMAN, N.; SILMAN, M.; SCHICHTER, H.; NÚÑEZ P. **Maintenance of tree diversity in tropical forests.** *In*: Levey, D. J.; Silva, W. R.; Galetti, M. (Edts). Seed dispersal and frugivory: Ecology, evolution and conservation. New York: CABI Publishing, 2002. p. 1-17.

TILMAN, D. **Functional diversity**. *In*: Levin, S. A. (Eds.). Encyclopedia of biodiversity. San Diego: Academic Press, 2001. p. 109-120.

TOSENS, T.; NISHIDA, K.; GAGO, J.; COOPMAN, R. E.; CABRERA, H. M.; CARRIQUÍ, M.; ...; TALTS, E. The photosynthetic capacity in 35 ferns and fern allies: mesophyll CO2 diffusion as a key trait. **New Phytologist**, 209: 1576-1590, 2016.

TUOMISTO, H.; POULSEN, A. Influence of edaphic specialization on the distribution of pteridophytes in neotropical forests. **Journal of Biogeography**, 23: 283-293, 1996.

VELLEND, M. Conceptual synthesis in community ecology. **The quarterly Review of Biology**, 85: 183-206. 2010.

VILLÉGER, S.; GRENOUILLET, G.; Brosse, S. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. **Global Ecology and Biogeography**, 22: 671-681, 2013.

VILLÉGER, S.; MASON, N. W. H.; MOUILLOT, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. **Ecology**, 89: 2290–2301, 2008.

VILLÉGER, S.; NOVACK-GOTTSHALL, P. M.; MOUILLOT, D. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. **Ecology Letters**, 14: 561-568, 2011.

VILLÉGER, S.; RAMOS MIRANDA, J.; FLORES HERNANDEZ, D.; MOUILLOT, D. Low functional β-diversity despite high taxonomic β-diversity among tropical estuarine fish communities. **PLoS ONE**, 7: e40679, 2012.

VIOLLE, C.; NAVAS, M. L.; VILE, D.; KAZAKOU, E.; FORTUNEL, C.; HUMMEL, I.; GARNIER, E. Let the concept of trait be functional! **Oikos**, 116: 882-892, 2007.

WEBB, C. O.; ACKERLY, D. D.; MCPEEK, M. A.; DONOGHUE, M. J. Phylogenies and community ecology. **Annual Review of Ecology, Evolution, and Systematics**, 33: 475–505, 2002.

WEIHER, E.; KEDDY, P. A. **Ecological Assembly Rules: Perspectives, Advances, Retreats**. Cambridge: Cambridge Univ. Press, 1999. 432p.

WESTOBY, M. A leaf–height–seed (LHS) plant ecology strategy scheme. **Plant Soil**, 199: 213–227, 1998.

WESTOBY, M.; WRIGHT, I. J. Land-plant ecology on the basis of functional traits. **Trends in Ecology and Evolution**, 21: 261–268, 2006.

WIDENFALK, L. A.; BENGTSSON, J.; BERGGREN, Å.; ZWIGGELAAR, K.; SPIJKMAN, E.; HUYER-BRUGMAN, F.; BERG, M. P. Spatially structured environmental filtering of collembolan traits in late successional salt marsh vegetation. **Oecologia**, 179: 537-549, 2015.

WIENS, J. J.; GRAHAM, C. H. Niche conservativism: integrating evolution, ecology, and conservation biology. **Annual Review of Ecology, Evolution, and Systematics**, 36: 519–539, 2005.

WINDISCH, P. G. Fern conservation in Brazil. **Fern Gazette,** 16: 295-300, 2002.

WRIGHT, I. J.; REICH, P. B.; WESTOBY, M.; ACKERLY, D. D.; BARUCH, Z.; BONGERS, F.; ...; FLEXAS, J. The worldwide leaf economics spectrum. **Nature**, 428: 821–827, 2004.

XAVIER, S. R.; BARROS, I. C. L., 2003. Pteridófitas ocorrentes em fragmentos de Floresta Serrana no estado de Pernambuco, Brasil. **Rodriguésia**, 54: 13-21.

YACHI, S.; LOREAU, M. Does complementary resource use enhance ecosystem functioning?

A model of light competition in plant communities. **Ecology Letters**, 10: 54–62, 2007.

ZHANG, H.; ZHU, S.; JOHN, R.; LI, R.; LIU, H.; YE, Q. Habitat filtering and exclusion of weak competitors jointly explain fern species assemblage along a light and water gradient. **Scientific reports**, 7: 298, 2017.

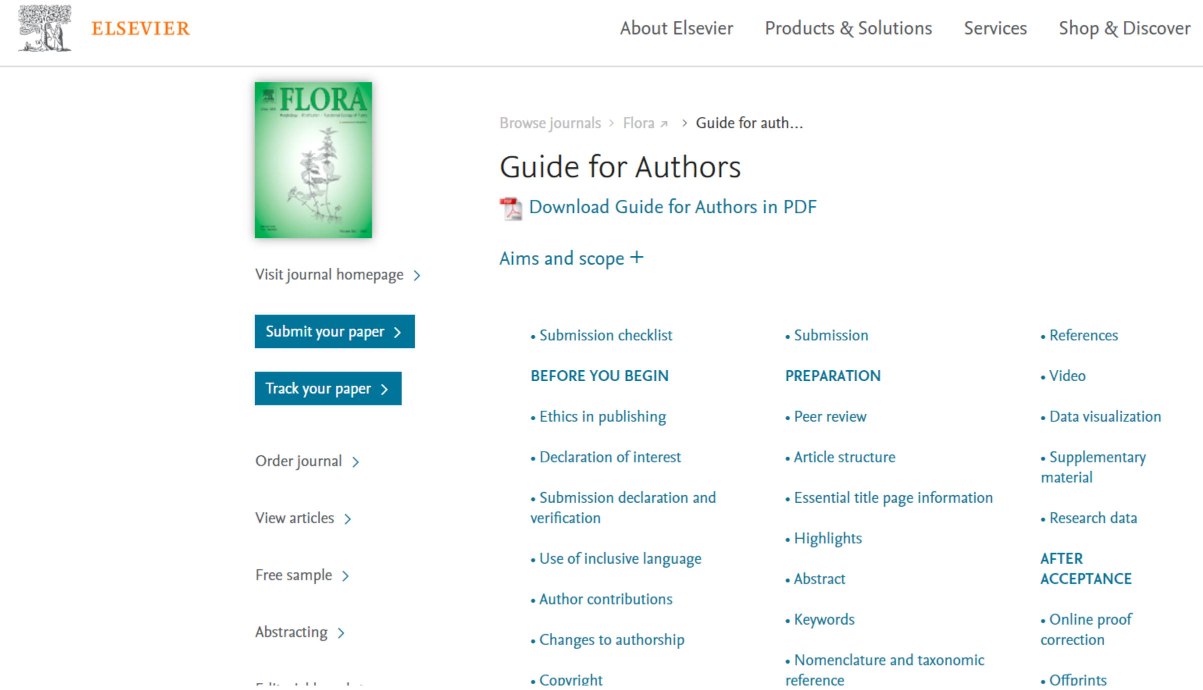
ZUQUIM, G. et al. Predicting environmental gradients with fern species composition in Brazilian Amazonia. **Journal of Vegetation Science**, 25: 1195-1207, 2014.

ANEXO A - Normas para publicação no periódico Flora

Disponível em:

https://www.elsevier.com/journals/flora/0367-2530/guide-for-authors

Acesso em 04/02/2019



ELSEVIER

About Elsevier Products & Solutions Services Shop & Discover

Browse journals > Flora > Guide for auth...

Guide for Authors

Download Guide for Authors in PDF

Aims and scope +

- Submission checklist

BEFORE YOU BEGIN

- Ethics in publishing
- Declaration of interest
- Submission declaration and verification
- Use of inclusive language
- Author contributions
- Changes to authorship
- Copyright
- Submission

PREPARATION

- Peer review
- Article structure
- Essential title page information
- Highlights
- Abstract
- Keywords
- Nomenclature and taxonomic reference
- References
- Video
- Data visualization
- Supplementary material
- Research data

AFTER ACCEPTANCE

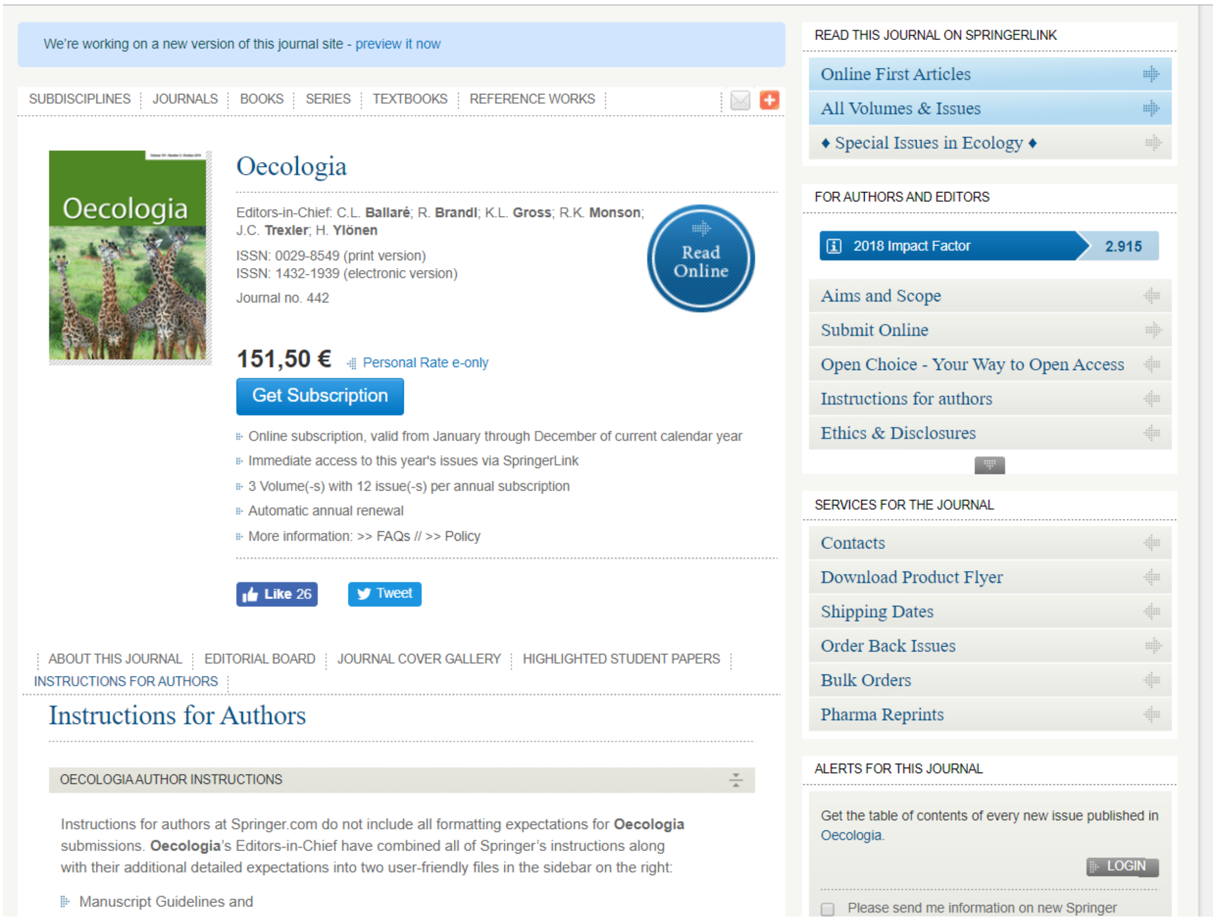
- Online proof correction
- Offprints

ANEXO B - Normas para publicação no periódico Oecologia

Disponível em:

https://www.springer.com/life+sciences/ecology/journal/442?detailsPage=pltci_1989608

Acesso em 04/02/2019



We're working on a new version of this journal site - preview it now

Oecologia

Editors-in-Chief: C.L. **Ballaré**; R. **Brandl**; K.L. **Gross**; R.K. **Monson**; J.C. **Trexler**; H. **Ylönen**

ISSN: 0029-8549 (print version)
ISSN: 1432-1939 (electronic version)

Journal no. 442

151,50 € Personal Rate e-only

- Online subscription, valid from January through December of current calendar year
- Immediate access to this year's issues via SpringerLink
- 3 Volume(-s) with 12 issue(-s) per annual subscription
- Automatic annual renewal
- More information: >> FAQs // >> Policy

Instructions for Authors

OECOLOGIA AUTHOR INSTRUCTIONS

Instructions for authors at Springer.com do not include all formatting expectations for **Oecologia** submissions. **Oecologia**'s Editors-in-Chief have combined all of Springer's instructions along with their additional detailed expectations into two user-friendly files in the sidebar on the right:

- Manuscript Guidelines and

2018 Impact Factor 2.915

Get the table of contents of every new issue published in Oecologia.

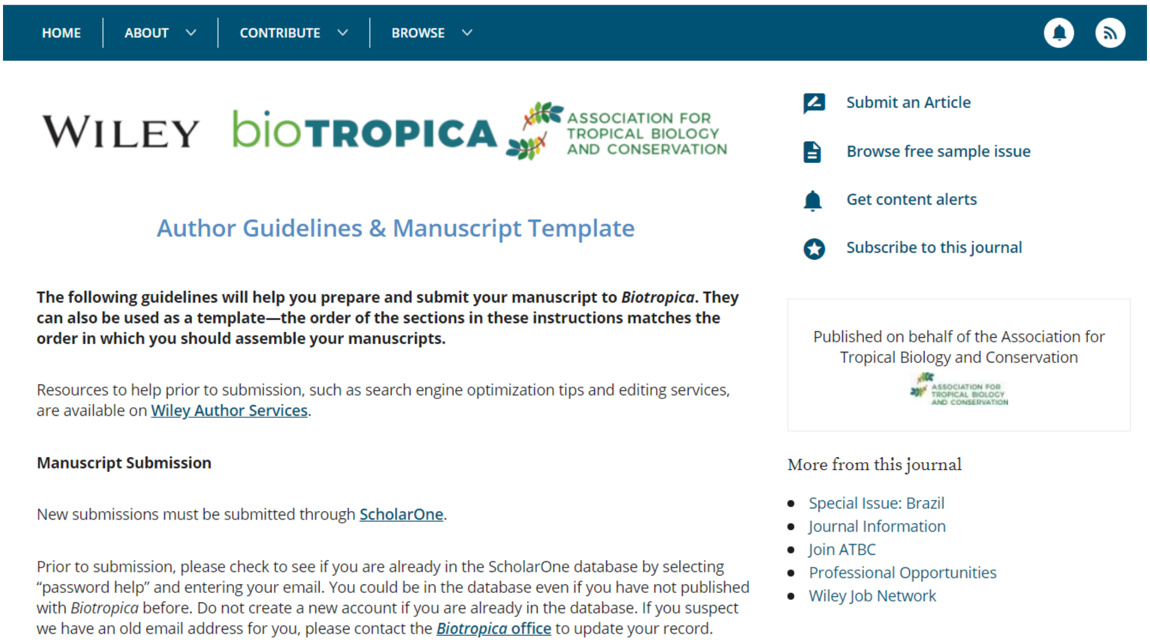
☐ Please send me information on new Springer

ANEXO C - Normas para publicação no periódico Biotropica

Disponível em:

https://onlinelibrary.wiley.com/page/journal/17447429/homepage/forauthors.html

Acesso em 04/02/2019



Author Guidelines & Manuscript Template

The following guidelines will help you prepare and submit your manuscript to *Biotropica*. They can also be used as a template—the order of the sections in these instructions matches the order in which you should assemble your manuscripts.

Resources to help prior to submission, such as search engine optimization tips and editing services, are available on Wiley Author Services.

Manuscript Submission

New submissions must be submitted through ScholarOne.

Prior to submission, please check to see if you are already in the ScholarOne database by selecting “password help” and entering your email. You could be in the database even if you have not published with *Biotropica* before. Do not create a new account if you are already in the database. If you suspect we have an old email address for you, please contact the *Biotropica* office to update your record.

Published on behalf of the Association for Tropical Biology and Conservation

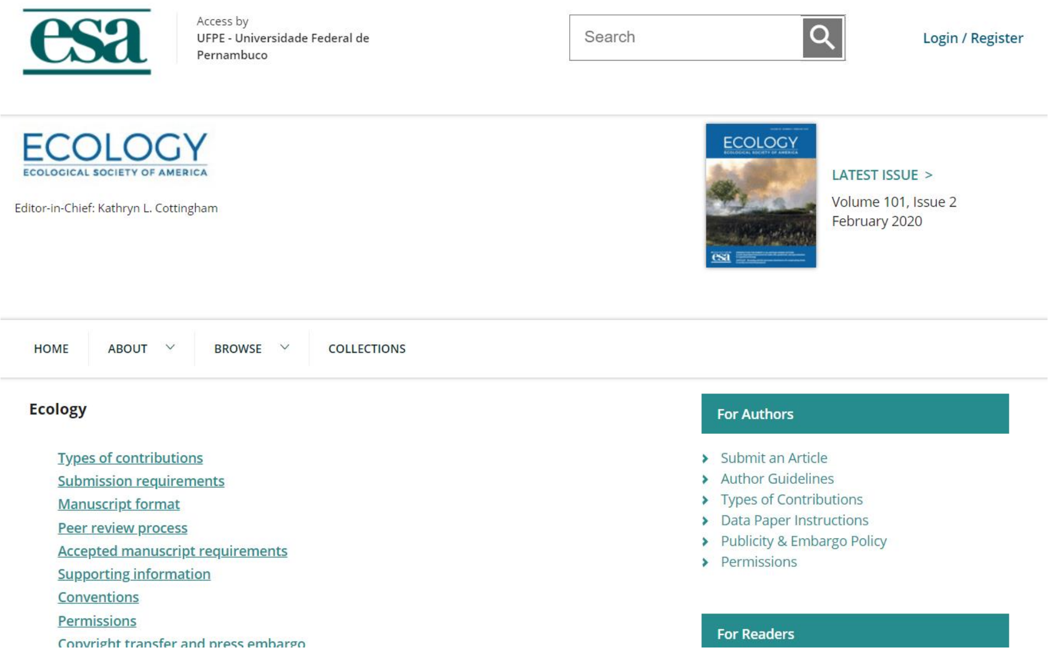
More from this journal

- Special Issue: Brazil
- Journal Information
- Join ATBC
- Professional Opportunities
- Wiley Job Network

ANEXO D - Normas para publicação no periódico Ecology

Disponível em:
https://esajournals.onlinelibrary.wiley.com/hub/journal/19399170/resources/author-guidelines-ecy

Acesso em 04/02/2019



Editor-in-Chief: Kathryn L. Cottingham

Ecology

- Types of contributions
- Submission requirements
- Manuscript format
- Peer review process
- Accepted manuscript requirements
- Supporting information
- Conventions
- Permissions
- Copyright transfer and press embargo