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BRUNO XIMENES PINHO

RESPOSTAS FUNCIONAIS DE ASSEMBLEIAS DE ÁRVORES A GRADIENTES BIOGEOGRÁFICOS, CLIMÁTICOS E DE USO-DO-SOLO EM FLORESTAS NEOTROPICAIS

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Doutor em Biologia Vegetal.

Área de concentração: Ecologia e Conservação.

Orientador: Profº Dr. Felipe P. L. Melo.
Coorientador: Profº Dr. Marcelo Tabarelli.

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BANCA EXAMINADORA

Prof. Dr. Felipe Pimentel Lopes de Melo (Orientador)
Universidade Federal de Pernambuco

Prof. Dr. Ariadna Valentina Lopes (Examinadora interna)
Universidade Federal de Pernambuco

Prof. Dr. Victor Arroyo-Rodriguez (Examinador externo)
Universidad Nacional Autónoma de México

Prof. Dr. Thiago Gonçalves (Examinador externo)
Universidade Federal Rural de Pernambuco

Dr. Bruno Filgueiras – UFPE (Examinador externo)
Universidade Federal de Pernambuco

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Usando terminologias comuns a este trabalho, posso dizer que toda a diversidade funcional que desenvolvi ao longo deste doutorado, de trabalho e de vida, não seria possível sem os diversos fragmentos, mais ou menos conectados, que compõem a diversidade de saberes que obtive ao longo desta trajetória. Fragmentos estes compostos por pessoas e lugares, que deixam marcas, mais ou menos profundas. Em analogia às estratégias ecológicas vegetais, eu diria que a importância de cada um desses elementos para a minha construção não é em nada absoluta, mas varia no espaço e tempo, a depender das condições e necessidades impostas por fatores externos, ou internos. Assim, não quero aqui citar nomes de indivíduos mais ou menos importantes neste percurso, mas apenas demonstrar a minha gratidão a todos, ou tudo, que cruzou o meu caminho neste tempo, e por confortos ou desconfortos me fez andar, sorrir, chorar, crescer... Amigos, colegas, família: um salve a todos, pois sem vocês nada disso seria possível!

“For me, trees have always been the most penetrating preachers.
I revere them when they live in tribes and families, in forests and groves.
And even more I revere them when they stand alone. They are like lonely
persons. Not like hermits who have stolen away out of some weakness,
but like great, solitary men, like Beethoven and Nietzsche. In their
highest boughs the world rustles, their roots rest in infinity; but they do
not lose themselves there, they struggle with all the force of their lives
for one thing only: to fulfil themselves according to their own laws,
to build up their own form, to represent themselves. Nothing is holier,
nothing is more exemplary than a beautiful, strong tree. When a tree is
cut down and reveals its naked death-wound to the sun, one can read its
whole history in the luminous, inscribed disk of its trunk: in the rings of
its years, its scars, all the struggle, all the suffering, all the sickness,
all the happiness and prosperity stand truly written, the narrow years and
the luxurious years, the attacks withstood, the storms endured.
And every young farmboy knows that the hardest and noblest wood
has the narrowest rings, that high on the mountains and in continuing danger
the most indestructible, the strongest, the ideal trees grow.

[…] Trees are sanctuaries. Whoever knows how to speak to them, whoever knows how to listen
to them, can learn the truth. They do not preach learning and precepts, they preach, undeterred by
particulars, the ancient law of life.”

Herman Hesse

“What speaks to the soul, escapes our measurements.”

Alexander von Humboldt

RESUMO

Florestas tropicais desempenham um papel prominente na retenção de biodiversidade e provisão de bens e serviços ecossistêmicos em escala local a global, mas são crescentemente ameaçadas pela expansão de paisagens antrópicas. Para agirmos de forma eficiente em direção a "paisagens antrópicas amigáveis à biodiversidade", nós carecemos de comparações entre biotas tropicais, para identificar a trajetória e a magnitude das mudanças, bem como as forças condicionantes. Caracteres morfo-fisiológicos adaptativos (i.e., atributos funcionais) refletem como plantas respondem a mudanças ambientais, e seus potenciais efeitos sobre processos ecossistêmicos. Em contraponto a abordagens taxonômicas tradicionais na ecologia, abordagens funcionais permitem elucidar mecanismos subjacentes a mudanças vegetacionais e gerar modelos preditivos de respostas de comunidades e ecossistemas a potenciais mudanças ambientais. Nesta perspectiva, eu exploro neste estudo, a partir de uma ampla base de dados de abundância e atributos funcionais de espécies, como o perfil funcional de assembleias de árvores em florestas neotropicais, no Brasil e no México, muda em diferentes escalas espaciais em resposta a gradientes latitudinais, fatores ambientais (e.g. climáticos) e perturbações antrópicas, agudas ou crônicas. Os resultados sugerem que (1) florestas neotropicais úmidas são substancialmente distintas funcionalmente em escala regional, sendo as florestas mais ao norte dominadas por espécies com atributos mais aquisitivos, o que em grande parte é explicado por variações climáticas; (2) Apesar das diferenças regionais, em escala de paisagem estas florestas se reorganizam em função da perda de habitat com a intensificação de uso-do-solo, tendendo a convergir para uma composição funcional típica de estágios sucessionais iniciais, embora com grande variação em termos de magnitude e escalas dos efeitos; (3) em florestas secas, a interação entre gradientes de precipitação e fertilidade de solos determina o sucesso de espécies de acordo com combinações específicas de atributos, enquanto que perturbações antrópicas crônicas parecem ter importância secundária na organização funcional de comunidades; e (4) grandes árvores emergentes em florestas tropicais úmidas desempenham funções desproporcionais e insubstituíveis no suporte a biodiversidade e provisão de serviços ambientais, mas são particularmente ameaçadas por processos que operam em escala local (e.g. extração madeireira), regional (e.g. perda e fragmentação florestal) e global (mudanças climáticas).

Palavras-chave: Atributos funcionais. funcionamento de ecossistemas. gradientes ambientais. mudanças climáticas. perda de habitat. perturbações antrópicas crônicas.

ABSTRACT

Tropical forests play a prominent role in global-scale biodiversity retention and in the provisioning of ecosystem goods and services from local to global scale, but are increasingly threatened by land-use intensification. To move towards biodiversity-friendly landscapes, we need to understand better how tropical biotas respond to environmental drivers acting at multiple spatial scales. For this, we lack comparisons between biotas, to understand inconsistences and identify generalities regarding the direction and magnitude of changes, and the underlying forces. Adaptive, or functional traits (i.e. morpho-physiological traits which impacts individual performance) reflect how plants respond to environmental changes, and their potential effects on ecosystem processes. In contrast to traditional taxonomic approaches in ecology, the use of functional traits allows for identification of underlying mechanisms driving vegetation changes, and the construction of predictive models of biological responses to potential environmental changes. In this sense, in this study I assess, from a large database of species abundance and functional traits, how the functional profile of tree assemblages in neotropical forests, across Brazil and Mexico, changes at multiple spatial scales in response to latitudinal gradients, environmental (e.g. climatic) factors and (acute or chronic) anthropogenic disturbances. The results suggest that (1) tropical rainforests regions across the Neotropics are dominated by functionally contrasting tree species, largely due to variation in climatic factors; (2) regardless of regional and land-use differences, at the landscape scale tropical rainforests "disassembly" with habitat loss due to land-use intensification, tending to converge towards a functional composition that is typical of early-successional communities, despite large variation in terms of magnitude and scale of effects across traits and regions; (3) in seasonally dry tropical forests, the interaction between gradients of rainfall and soil fertility determines the relative abundance of species according to combinations of functional traits, while chronic udisturbances have a secondary effect on community functional assembly; and (4) large emergent trees, or "mega-trees", provide disproportionate, irrepleaceble functions in supporting biodiversity and provisioning of ecosystem services across tropical rainforests, but are particularly threatened by processes operating at local (e.g. selective logging), regional (e.g. habitat loss and fragmentation) and global scale (climate changes).

Key-words: Climate change. ecosystem functioning. environmental gradients. functional traits. habitat loss. chronic anthropogenic disturbances.

SUMÁRIO

1 INTRODUÇÃO

Cada árvore tem uma história, mais ou menos breve. Mas cada *espécie* de árvore, tal qual de outros seres, representa uma história bem mais longa. E como toda história deixa marcas, a luta pela sobrevivência por que passaram seus ancestrais reflete-se hoje em cada espécie, em suas *adaptações* para crescer e sobreviver em condições das mais diversas. Diria Darwin (1858): “não sobrevive a espécie mais forte, mas a que se adapta à mudança”. E em um mundo em constante transformação, foram muitas as soluções que evoluíram em plantas, em resposta às restrições impostas por condições abióticas, ou pela interação com outros organismos. Tal diversidade de estratégias faz-se evidente nas múltiplas formas exibidas por espécies de plantas, seja em suas folhas, seus caules, raízes ou sementes. Entretanto, com exceção de um hipotético “demônio darwiniano”, que não seguiria fundamentais leis biofísicas ou evolutivas, todos os organismos enfrentam demandas conflitantes (i.e., “trade-offs”) na evolução de estratégias de crescimento, sobrevivência e reprodução. Em outras palavras, e analogamente à vida humana, é impossível se ter tudo, ou ser o melhor em tudo. E diante de tantas estratégias ecológicas ou “histórias-de-vida”, variações ambientais permitem a coexistência de espécies, em diferentes escalas espaciais ou temporais. Entender como e por que a distribuição e abundância de organismos varia no espaço e tempo é o objetivo central da ecologia e também o cerne deste estudo, tendo implicações importantes para a conservação de biodiversidade e serviços ecossistêmicos.

Desde Alexander von Humboldt (1769-1859), mudanças vegetacionais são compreendidas como respostas a condições físicas, particularmente clima e altitude. Mesmo observando espécies distintas em diferentes partes do mundo ao longo de suas viagens, Humboldt percebia semelhanças entre vegetações de acordo com a altitude, latitude ou clima a que estavam expostas. Ainda assim, tradicionalmente a ecologia tem se valido de abordagens taxonômicas, baseadas apenas na identidade, ou nome de cada espécie. Nesta perspectiva, cada espécie é única e todas são tão diferentes quanto entre si. Desconsidera-se, portanto, (dis)similaridades em suas adaptações, que devem determinar respostas mais ou menos similares a condições ambientais ou ecológicas. Apenas recentemente, a ecologia funcional, baseada em atributos de espécies ou indivíduos, tem emergido como uma abordagem com potencial de revelar padrões generalizáveis, elucidar mecanismos subjacentes a mudanças vegetacionais, e gerar modelos preditivos da resposta de espécies, comunidades e ecossistemas a mudanças ambientais.

Especificamente, padrões interespecíficos de co-variação entre atributos funcionais (*i.e.* características morfo-fisiológicas, que afetam a performance dos organismos) têm revelado *trade-offs* universais em estratégias ecológicas vegetais, distinguindo espécies ao longo de eixos contínuos de especialização funcional. Por exemplo, tecidos mais densos têm um maior custo de produção e estão associados a um crescimento lento, mas garantem uma maior durabilidade e consequentemente tolerância a escassez de recursos. Por outro lado, plantas que crescem rápido investem em tecidos de baixo custo, mas com baixa longevidade, tendendo a dominar ambientes com alta disponibilidade de recursos, onde suas altas taxas metabólicas podem ser mantidas. Assim, este e outros *trade-offs* tendem a limitar o sucesso de cada espécie e definir sua distribuição e abundância em diferentes contextos ambientais. Mais do que isso, atributos funcionais determinam também os efeitos que os organismos exercem sobre processos ecossistêmicos. Por exemplo, atributos associados a rápidas taxas de crescimento favorecem processos (e.g. decomposição, produtividade primária) mais dinâmicos, enquanto que atributos mais conservativos favorecem a estabilidade de serviços ecossistêmicos, como o armazenamento de carbono. Mais especificamente, a combinação de atributos de espécies que co-ocorrem em comunidades biológicas define seu efeito conjunto sobre os ecossistemas. Portanto, entender como comunidades se organizam funcionalmemte ao longo de gradientes ambientais é um desafio não apenas com grande relevância teórica, mas também com sérias implicações para conservação.

Florestas tropicais cobrem menos de 10% da cobertura terrestre, mas abrigam mais da metade da diversidade biológica do planeta. Além da clara relevância global para retenção de biodiversidade, florestas tropicais exercem um papel prominente na provisão de bens de subsistência e serviços ecossistêmicos essenciais para a sustentabilidade de populações humanas em escala local, regional e global. Por exemplo, elas representam um terço da produtividade primária bruta terrestre global, e estocam um quarto de todo o carbono em ecossistemas terrestres, controlando assim processos biogeoquímicos (e.g. ciclagem de nutrientes) e biogeofísicos (e.g. evapotranspiração) com impactos diretos na regulação climática regional e global. Embora designadas como um único bioma dada as suas similaridades estruturais, florestas tropicais possuem histórias biogeográficas contrastantes e diferem amplamente quanto às condições ambientais pretéritas ou contemporâneas a que têm sido expostas. Isso se reflete claramente em diferenças em termos estruturais ou de composição de espécies, sendo as florestas Neotropicais as mais extensas, diversas entre si e distintas das demais. Por exemplo, o canal do Panamá limitou historicamente a distribuição de vários grupos de plantas ao hemisfério norte ou sul, e fortes diferenças filogenéticas são também evidentes em florestas ao longo da costa Atlântica brasileira. Pouco se sabe, no entanto, como tais diferenças se traduzem em termos funcionais.

Em adição a forças naturais que desde os tempos mais remotos têm selecionado estratégias ecológicas, perturbações de origem antrópica têm imposto outras forças, reorganizando comunidades biológicas de escala local a regional. De fato, mudanças em padrões de uso-do-solo representam globalmente a principal ameaça à biodiversidade e podem comprometer a prestação de serviços ambientais. Tal ameaça é especialmente evidente em florestas tropicais, cuja cobertura tem sido gradualmente reduzida e os seus remanescentes incorporados a paisagens dominadas por matrizes antrópicas (e.g. cultivos agrícolas), com diferentes tipos e intensidades de uso-do-solo. Além da perda de cobertura florestal, a conversão de florestas tropicais leva ao isolamento dos remanescentes e à criação de bordas florestais, estas últimas envolvendo uma série de mudanças microclimáticas que tendem a alterar a composição e estrutura de assembléias de plantas. Adicionalmente, perturbações antrópicas crônicas, definidas como a extração contínua de pequenas quantidades de biomassa, também impõem pressões sobre a biodiversidade em paisagens antrópicas fragmentadas. Efeitos deletérios desses processos são amplamente reportados, mas a capacidade de remanescentes florestais em paisagens antrópicas manterem diversidade biológica e serviços ecossistêmicos é ainda muito controversa. Para entender tais inconsistências, é fundamental realizar estudos functionais envolvendo múltiplas paisagens e regiões, em diferentes contextos biogeográficos e com diferentes históricos e intensidades de uso do solo.

Em outras palavras, nós precisamos entender melhor a trajetória de mudança das biotas tropicais, a fim de agirmos de forma eficiente em direção às “paisagens antrópicas amigáveis à biodiversidade” (*sensu* Melo *et al.*, 2013). Para isto, nós carecemos de comparações entre paisagens e entre biotas para identificar a direção e a magnitude das mudanças, bem como as forças condicionantes, de forma a buscar as generalizações possíveis e necessárias à tomada de decisão de como manejar paisagens antrópicas. Nesta perspectiva, este estudo teve como objetivo avaliar como assembleias de árvores em florestas neotropicais se organizam funcionalmente em diferentes escalas espaciais ao longo de gradientes geográficos, climáticos e de uso-do-solo. Em quatro capítulos, eu demonstro que (1) regiões neotropicais úmidas apresentam assembleias de árvores funcionalmente distintas, sendo as florestas mais ao norte dominadas por espécies com atributos mais aquisitivos associados a rápidas taxas de crescimento, o que em grande parte é explicado por variações climáticas; (2) apesar das diferenças biogeográficas e de intensidade de uso-do-solo, em escala de paisagem estas florestas se reorganizam consistentemente em resposta à perda de habitat, tendendo a convergir para uma composição funcional típica de comunidades em estágios sucessionais iniciais (i.e., dominância de atributos aquisitivos e sementes pequenas), apesar de grande variação entre atributos e regiões quanto à magnitude e escala dos efeitos; (3) em florestas sazonalmente secas, a interação entre gradientes de precipitação e fertilidade de solos determina a abundância relativa de espécies de acordo com combinações específicas de atributos, enquanto que perturbações antrópicas crônicas parecem ter importância secundária na organização funcional de comunidades; por fim, em uma revisão eu demonstro que (4) grandes árvores emergentes, ou “mega-árvores” em florestas tropicais úmidas desempanham funções desproporcionais em magnitude e insubstituíveis no suporte a biodiversidade e serviços ecossistêmicos, mas são particularmente ameaçadas por processos que operam em escala local (e.g. extração seletiva de madeira), regional (perda e fragmentação florestal) e global (mudanças climáticas). Uma vez que atributos funcionais estão relacionados às respostas de espécies a mudanças ambientais e seus efeitos sobre processos ecossistêmicos, esses resultados têm profundas implicações para a previsão e mitigação do impacto de futuras mudanças ambientais sobre padrões de biodiversidade e funcionamento de ecossistemas em florestas tropicais. Espera-se, assim, contribuir na definição de abordagens capazes de conciliar conservação de biodiversidade com uso-do-solo e sustentabilidade de populações humanas em paisagens tropicais fragmentadas.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 ESTRATÉGIAS ECOLÓGICAS VEGETAIS: "TRADE-OFFS" E ATRIBUTOS FUNCIONAIS

Todos os organismos enfrentam demandas conflitantes (i.e., "trade-offs") no investimento de recursos para crescimento, sobrevivência e reprodução (Darwin, 1859). Em resposta à limitação de recursos, inúmeras histórias-de-vida e estratégias ecológicas evoluíram em plantas (Grime & Pierce 2012). Em um mesmo contexto ambiental, diferentes estratégias ecológicas podem co-ocorrer, mas o sucesso de uma espécie em diferentes contextos tende a ser limitado pela ocorrência de trade-offs (Grime 2001, Westoby & Wright 2006). Por exemplo, o investimento em grandes áreas foliares deve favorecer a competição por luz, bem como a captura de outros recursos através da rápida produção de biomassa (Grime & Pierce 2012), mas aumenta a perda de água por transpiração e assim limita a capacidade das plantas tolerarem ambientes sob estresse hídrico (Lebrija-Trejos et al. 2010, Wright et al. 2017). Desta forma, diferentes trade-offs tendem a interagir entre si e limitar o sucesso das espécies, definindo a sua distribuição e abundância em diferentes contextos (Fine et al. 2004, Muscarella & Uriarte 2016).

Análises multivariadas têm demonstrado padrões consistentes de co-variação entre atributos funcionais (i.e. características morfo-fisiológicas, que afetam a performance dos organismos; Violle et al. 2007), ao longo de eixos contínuos de variação entre espécies, que revelam trade-offs associados a múltiplas dimensões ecológicas vegetais (Westoby et al. 2002, Wright et al. 2004, 2007, Diaz et al. 2016, Pierce et al. 2017). A posição de cada espécie ao longo desses eixos contínuos de variação em atributos deve indicar sob quais condições ambientais ou ecológicas elas tendem a ter um maior sucesso (Westoby et al. 2002, Westoby & Wright 2006). Com base nesses pressupostos, atributos funcionais com variação contínua, associados a diferentes dimensões da estratégia ecológica vegetal, têm sido amplamente utilizados como descritores do nicho das espécies para explicar e prever padrões de distribuição e abundância de espécies ao longo de gradientes ambientais (Lebrija-Trejos et al. 2010, Laughlin & Messier 2015, Muscarella & Uriarte 2016, Pinho et al. 2018). Como sugerido por McGill et al. (2006), esta é uma abordagem que promete gerar modelos preditivos na ecologia de comunidades. Por exemplo, variações na estrutura de comunidades vegetais em resposta a mudanças ambientais podem ser previstas, caso haja uma relação consistente entre atributos e o sucesso das espécies em diferentes contextos ambientais e ecológicos. Todavia, tal abordagem depende de definições acuradas das dimensões ecológicas vegetais e do valor adaptativo de diferentes estratégias ecológicas em diferentes situações ambientais ou ecológicas (Westoby & Wright 2006, Funk et al. 2017).

Algumas "dimensões ecológicas" vegetais são hoje amplamente reconhecidas como padrões consistentes, que estão associadas a grandes restrições evolutivas (i.e., trade-offs). Pelo grau de generalização, essas dimensões favorecem análises vegetacionais em diferentes escalas espaciais, diferentemente de abordagens taxonômicas e de grupos funcionais, que dificultam generalizações. A dimensão ecológica vegetal melhor estudada e mais amplamente reconhecida está relacionada à estrutura e fisiologia foliar, referida como o "espectro econômico foliar" (*sensu* Wright et al. 2004). Esse espectro consiste em um contínuo, desde espécies que crescem rápido, produzindo folhas de baixo custo e com altas taxas fotossintéticas, mas que têm curto tempo de vida; até espécies que crescem lentamente e produzem folhas com um alto custo, mas que são mais resistentes a danos físicos e têm maior longevidade (Wright et al. 2004, 2007, Reich 2014). Vários atributos foliares estão fortemente correlacionados a esse eixo de variação, de forma que representam uma única dimensão da estratégia ecológica vegetal, associada a um único trade-off (Laughlin 2013). Atributos morfológicos de fácil mensuração, como a Área Específica Foliar – AEF (i.e., área foliar por massa seca), podem descrever a posição de uma espécie ao longo deste contínuo, revelando a sua estratégia de aquisição e uso de recursos. Folhas que resultam de um baixo investimento de carbono em sua construção (i.e., alta AEF) em geral são eficientes no desenvolvimento da área foliar por biomassa investida, resultando em maiores superfícies foliares para interceptação de luz (Poorter & Bongers 2006). Especificamente, a AEF resulta da variação de outros dois atributos foliares, o conteúdo de massa seca foliar (CMSF; i.e., massa seca/massa fresca) e a espessura foliar (Witkowski & Lamont 1991, mas veja Hodgson et al. 2011). Assim, pode ser estimada como o inverso do produto desses dois atributos, de forma que baixos valores de AEF, por exemplo, podem resultar tanto de alta espessura como de alta densidade foliar, ou de ambos. Plantas com alto CMSF possuem alta longevidade foliar e tendem a ser favorecidas em ambientes com baixa disponibilidade de recursos, especialmente nutrientes (Hodgson et al. 2011, Katabuchi et al. 2012, Pinho et al. 2018). Por outro lado, os extremos inferior e superior da espessura foliar devem refletir adaptações à baixa disponibilidade de luz e água, respectivamente (Hodgson et al. 2011).

De forma semelhante, trade-offs associados a estratégias de uso de recursos são também evidentes em outros órgãos vegetais. Por exemplo, árvores com alta densidade de madeira possuem vasos xilemáticos menores e menos abundantes, o que reduz o risco de falhas hidráulicas devido a cavitação, mas também reduz a eficiência hidráulica e a capacidade de armazenar água no caule (Hacke et al. 2001, Chave et al. 2009, Gleason et al. 2013). Atributos associados aos espectros econômicos foliar ou da madeira explicam processos a nível de indivíduo. Plantas com alta AEF ou baixa densidade de madeira, por exemplo, tendem a ter altas taxas de crescimento e baixas taxas de sobrevivência (Westoby et al. 2002, Poorter & Bongers 2006, Wright et al., 2010, Greenwood et al. 2017). Por isso, tem-se sugerido que que variações associadas a esses espectros devem refletir um trade-off entre crescimento e sobrevivência em toda a planta (Poorter et al. 2008, Wright et al. 2010, Reich 2014). De acordo com Poorter & Bongers (2006), o espectro econômico reflete de forma contínua a dicotomia entre plantas pioneiras e tardias. Isto porque espécies pioneiras, que demandam alta intensidade luminosa para o seu crescimento, investem em tecidos de baixo custo e curto tempo de vida (e.g. alta AEF), de forma que podem crescer rápido e assim se manter no topo do dossel, se antecipando na busca por luz. Por outro lado, espécies características de estágios sucessionais avançados, que se estabelecem no sub-bosque florestal, investem em um retorno seguro, com a produção de folhas bem protegidas (baixa AEF), de forma a compensar o alto custo de crescimento em um ambiente sob limitação de recursos (e.g. luz).

Além dos espectros econômicos, outros trade-offs em diferentes órgãos vegetais ou na planta como um todo definem as estratégias ecológicas vegetais e o sucesso de cada espécie em diferentes contextos ambientais. Por exemplo, sementes grandes garantem maior tolerância e dominância de plântulas sob estresses abióticos, mas são produzidas em menor quantidade, enquanto que a produção de numerosas sementes pequenas favorece a colonização de ambientes menos restritivos (i.e., “tolerance-fecundity trade-off”, *sensu* Muller-Landau 2010). Adicionalmente, a altura máxima alcançada por árvores, assim como o tamanho de seus órgãos (e.g. folhas) favorece a dominância competitiva, mas reduz sua tolerância a estresses abióticos (Grime & Pierce 2012, Pierce et al. 2017, Wright et al. 2017). Outras características caulinares (Chave et al. 2009), radiculares (Eshel & Beeckman 2013) e da planta inteira podem ainda refletir outros trade-offs (veja Pérez-Harguindeguy et al. 2013). Em conjunto, atributos de diferentes dimensões ecológicas tendem a determinar o sucesso de uma espécie em um determinado contexto ambiental e ecológico (Grime & Pierce 2012, Laughlin & Messier 2015, Muscarella & Uriarte 2016, Pierce et al. 2017).

Em escala global, tem-se demonstrado duas dimensões funcionais (i.e., eixos de co-variação de atributos) ubíquas em plantas: a primeira está relacionada ao tamanho da planta como um todo (i.e., altura máxima) e dos seus órgãos (área foliar, massa da semente), enquanto que a outra reflete variações em estratégias de uso de recursos, com a co-variação de atributos relacionados aos espectros econômicos da folha e da madeira (Diaz et al. 2016, Pierce et al. 2017). Entretanto, padrões de co-variação entre atributos funcionais podem variar fortemente em direção e magnitude entre formas-de-vida ou ecossistemas (Wright et al. 2001, Wright & Sutton-Grier 2012, Diaz et al. 2016). Assim, análises de padrões de co-variação de atributos em escala global podem mascarar importantes padrões nesses componentes (i.e., formas-de-vida e ecossistemas) isoladamente. Por exemplo, grande parte dos padrões globais de co-variação entre atributos funcionais de plantas se deve a diferenças entre árvores e outras formas de vida (Diaz et al. 2016).

2.1.1 Estratégias adaptativas vegetais: a teoria CSR, suas críticas e seus sistemas de classificação

Embora haja um crescente interesse em análises funcionais de plantas (McGill et al. 2006, Funk et al. 2017), raramente esta abordagem é aplicada no contexto de teorias de estratégias adaptativas, as quais buscam explicar como diferentes estratégias evoluíram e por que conjuntos específicos de atributos funcionais ocorrem de forma consistente em determinadas situações ambientais e ecológicas (Grime 2001, Cerabolini et al. 2010, Grime & Pierce 2012, Pierce et al. 2017). Tentando compreender como processos ecológicos e evolutivos moldam as estratégias ecológicas de espécies de plantas, Philip Grime propôs uma das mais antigas teorias de estratégias ecológicas adaptativas, a Teoria CSR (Grime 1977, 2001). Segundo ele, dois fatores externos limitam a quantidade de biomassa vegetal em qualquer habitat: estresses, que restringem a produção fotossintética das plantas a partir da limitação de recursos (i.e. luz, água e nutrientes) ou de temperaturas extremas; e distúrbios, que estão associados à destruição parcial ou total de biomassa vegetal, seja pelo homem, ou por fenômenos naturais (e.g. herbívoros, inundações, fogo). Assim, por limitarem de diferentes formas a produção de biomassa, a interação entre estresses e distúrbios, de acordo com a teoria, definiria a pressão seletiva de um determinado habitat na evolução de estratégias ecológicas vegetais (Grime et al. 2001, mas veja Grime & Pierce 2012).

Com exceção de habitats expostos a distúrbios freqüentes e fortes estresses ambientais constantes, que seriam inviáveis ao desenvolvimento vegetal, as outras três permutações entre níveis altos e baixos de estresses e distúrbios estariam associadas à evolução de três tipos principais de estratégias ecológicas em plantas, de acordo com a teoria: competidoras (“C”), que dominam ambientes com alta disponibilidade de recursos e baixa intensidade de distúrbios; tolerantes a estresses (“S”, do inglês, stress-tolerators), que ocupam ambientes estressantes com baixo nível de distúrbio; e ruderais (“R”), que mantém populações em áreas expostas a freqüentes distúrbios, sendo que com alta disponibilidade de recursos (i.e. baixo estresse). Obviamente, estas estratégias representariam extremos da especialização evolutiva de plantas, de forma que estratégias intermediárias são também evidentes, dependendo do grau de estresses e distúrbios (Grime & Pierce 2012, Pierce et al. 2017).

Mesmo reconhecendo que, em cada contexto, as plantas devem exibir adaptações específicas, Grime (2001) sugeriu, a partir da compilação de um grande número de estudos, que espécies de plantas em cada um desses grupos (i.e. C, S e R) possuem conjuntos de atributos comuns, que lhes conferem respostas similares a estresses e distúrbios em diferentes ecossistemas. Por exemplo, plantas ruderais exibem de forma consistente ciclos de vida curto, com um desenvolvimento reprodutivo precoce e prolongado, que lhes garante a manutenção de populações em ambientes expostos a distúrbios intensos e freqüentes. Esta estratégia, característica principalmente de algumas espécies herbáceas, tende a ser favorecida apenas em ambientes intermitentemente propícios ao crescimento vegetal, onde outras estratégias são desfavorecidas por não completarem seus ciclos de vida antes da ocorrência de distúrbios (Grime, 2001).

Em comparação aos habitats ocupados por plantas ruderais, os ambientes colonizados por plantas competidoras e tolerantes a estresses são caracterizados por uma baixa intensidade de distúrbios. Apesar da semelhança, diferenças claras podem ser percebidas entre esses dois grupos, dependendo da intensidade e do tipo de estresses ambientais. Em ambientes produtivos, que a princípio não restringem o crescimento vegetal, características que favorecem uma rápida e constante aquisição de recursos tendem a aumentar a habilidade competitiva e definir o sucesso das espécies. Isto inclui uma série de atributos, como grandes estaturas e áreas foliares, no caso de competição por luz. A plasticidade morfológica, que favorece o constante ajustamento das superfícies de absorção (foliar e radicular) em função de variações espaciais na disponibilidade de recursos, é uma das principais características de plantas competidoras, que lhes permite maximizar a aquisição de recursos. Esta e outras características de plantas competidoras dependem fundamentalmente de altas taxas metabólicas e de crescimento. Embora esta seja também uma característica de plantas ruderais, plantas competidoras investem fundamentalmente na maximização do crescimento vegetativo, enquanto que ruderais tendem a encurtar o desenvolvimento vegetativo e maximizar a produção de sementes (Grime 2001).

A estratégia de rápida e contínua aquisição de recursos, através do constante reajustamento espacial das superfícies de absorção, apresenta, no entanto, baixo valor adaptativo em ambientes sob estresses ambientais crônicos. Assim, em ambientes improdutivos, plantas competidoras tendem a ser eliminadas e substituídas por plantas tolerantes a estresses (Grime 2001, Grime & Pierce 2012). Os mecanismos específicos de tolerância dependem essencialmente do tipo de estresse (i.e., de luz, água ou nutrientes), mas características gerais são atribuídas a este grupo, que é considerado o mais diverso em termos morfológicos e de histórias-de-vida. Tais características incluem ciclos de vida longos, além de órgãos (e.g. folhas) resistentes e duráveis, com baixa plasticidade fenotípica, mas com mecanismos fisiológicos que permitem acumular reservas em períodos de alta disponibilidade de recursos. Assim, enquanto que plantas competidoras são adaptadas a ambientes com variações espaciais na disponibilidade de recursos, devido à depleção local gerada pela vegetação, plantas tolerantes são adaptadas a habitats intermitentemente favoráveis ao crescimento devido a variações temporais na disponibilidade de recursos, através da manutenção de baixas taxas metabólicas e da conservação de recursos em tecidos bem protegidos e duráveis (Grime 2001).

Apesar da sua coerência, a Teoria CSR logo atraiu controversa devido à carência de evidências empíricas e à dificuldade de aplicação (Tilman 1988, Westoby et al. 2002). No entanto, análises multivariadas entre atributos funcionais têm revelado de forma consistente um espaço funcional triangular (Grime et al. 1997, Cerabolini et al. 2010, Pierce et al. 2013), em concordância com os trade-offs associados ao triângulo de estratégias CSR, previsto por Grime (1979); dando espaço à proposição de diferentes métodos de classificação CSR. Basicamente, estas análises sugerem que estratégias adaptativas de plantas envolvem dois eixos principais de variação em atributos: o “espectro econômico”, que reflete um trade-off entre aquisição e conservação de recursos (Wright et al. 2004, Reich, 2014, Diaz et al. 2016); e um segundo associado ao tamanho das plantas, evidenciado também a partir de atributos relacionados a órgãos específicos, como o tamanho de folhas e sementes (Cerabolini et al., 2010; Pierce et al., 2013, 2017). Esses dois eixos estão também relacionados a características reprodutivas (Cerabolini et al., 2010) e, em conjunto, formam um espaço funcional triangular, delimitado por três estratégias extremas: plantas competidoras, que investem num rápido crescimento vegetativo em ambientes produtivos, e são altas, com folhas grandes e espectro econômico intermediário; e plantas ruderais e tolerantes a estresses, que têm estaturas menores e folhas pequenas, ocupando os dois extremos do espectro econômico foliar: ruderais com economia foliar altamente aquisitiva (e.g. alta AEF), associada a um desenvolvimento reprodutivo precoce e prolongado; e tolerantes a estresses, que investem na conservação de recursos, com tecidos densos (e.g. alto CMSF) e floração breve e infrequente (Grime et al. 1977, 1997, Pierce et al. 2013, 2017).

Hodgson et al. (1999), com base em alguns dos atributos que formam esse espaço funcional, propuseram um método de classificação, posteriormente aperfeiçoado por Cerabolini et al. (2010). Algumas restrições são, no entanto, evidentes nestes métodos, como a natureza categórica de algumas variáveis (e.g. início da floração), aplicáveis apenas em determinados contextos, e a limitação de aplicação a plantas herbáceas. Contornando essas restrições, Pierce et al. (2013) propuseram um novo método de classificação, com base apenas em atributos foliares de fácil mensuração e aplicável a plantas lenhosas, que atribui de forma contínua percentuais de estratégias C, S e R às espécies. De acordo com os autores, poucos atributos foliares capturam suficientemente os trade-offs entre estratégias CSR, sugerindo que comunidades vegetais podem ser amplamente comparadas com base em estratégias adaptativas. O sistema de classificação de Pierce et al. (2013), no entanto, foi desenvolvido com base apenas em espécies de plantas de ecossistemas da Itália. Mais recentemente, tal sistema foi ampliado e aperfeiçoado, a partir de bases de dados globais que revelaram o mesmo espaço funcional triangular associado aos trade-offs CSR (Pierce et al. 2017). Apesar do grande potencial devido à facilidade de mensuração e viabilidade de aplicação a qualquer planta vascular, o método de Pierce et al. (2017) ainda carece de testes para avaliar a coerência e eficiência na comparação entre comunidades, bem como na elucidação e previsão da resposta de comunidades a mudanças ambientais.

Pierce et al. (2017) também avaliaram a relação entre as estratégias CSR e variáveis climáticas em diferentes biomas. Apesar da concordância geral com a teoria CSR (Grime 2001), algumas inconsistências emergiram, como a associação de estratégias competitivas (C) com a sazonalidade de precipitação. Entretanto, isto pode se dever ao fato dos autores não terem incorporado variações na abundância relativa das espécies, de tal forma que, embora estratégias competitivas ocorram em ambientes com alta variação temporal na disponibilidade de recursos, elas podem ser subordinadas nas comunidades, ocorrendo apenas em manchas de habitat específicas e em baixa abundância (Pierce et al. 2017). Entender a viabilidade de aplicação deste sistema de classificação e a sua capacidade de explicar diferenças ecológicas e evolutivas entre floras é um passo com grande potencial para comparação e previsão de respostas de comunidades vegetais com base em estratégias adaptativas.

2.2 RESPOSTAS FUNCIONAIS E A ORGANIZAÇÃO DE ASSEMBLÉIAS DE PLANTAS AO LONGO DE GRADIENTES AMBIENTAIS

Dois processos de nicho têm sido sugeridos como forças opostas na estruturação de comunidades vegetais: filtros ambientais (Weiher & Keddy 1999, Kraft et al. 2008, Kraft & Ackerly 2010, Lebrija-Trejos et al. 2010) e a limitação de similaridade, ou diferenciação de nicho devido a competição entre espécies (MacArthur & Levins 1967, Stubbs & Wilson 2004). Esses processos sugerem que existem regras de montagem de comunidades, que determinam a estrutura e composição local de assembleias a partir de um conjunto regional de espécies (Weiher & Keddy 1999). A proposição de filtros ambientais como um mecanismo determinístico considera que os indivíduos que compõem uma comunidade se limitam àqueles que apresentam atributos funcionais que lhes permitem alcançar um determinado local (i.e. filtro de dispersão) e se estabelecer sob determinadas condições ambientais, i.e. filtros abióticos (Weiher & Keddy 1999, Cadotte & Tucker 2017). A hipótese de diferenciação de nicho entre espécies, por sua vez, sugere que a co-ocorrência de espécies com estratégias ecológicas similares tende a ser limitada por relações antagônicas (MacArthur & Levins 1967). No entanto, assim como filtros ambientais, processos de dominância competitiva podem também levar a reduções na diversidade funcional de comunidades (Kraft et al. 2015, Cadotte & Tucker 2017). Além de processos determinísticos, forças estocásticas, como deriva genética e limitação de dispersão, podem também influenciar padrões de comunidades (Hubbell 2001, Orrock and Watling 2010). Em escala local, interações entre espécies, particularmente competição, e processos estocásticos têm sido enfatizados como forças predominantes no processo de organização de comunidades (Hubbell 2001, Stubbs & Wilson 2004). Em escala de paisagem, filtros ambientais emergem como os principais determinantes da organização de comunidades, enquanto que processos biogeográficos e evolutivos (i.e. especiação, extinção e migração) têm maior relevância em escala regional (Lambers et al., 2012).

Partindo do pressuposto de que as espécies possuem diferentes estratégias adaptativas, abordagens e medidas tradicionais, que se baseiam apenas na identidade taxonômica das espécies, são insuficientes para explicar padrões de organização de comunidades e funcionamento de ecossistemas, visto que não consideram diferenças funcionais entre as espécies (McGill et al.

2006). A classificação de espécies em grupos funcionais pode ser útil, como forma de generalizar respostas funcionais de assembléias de plantas a diferentes situações ambientais. No entanto, estratégias ecológicas vegetais variam continuamente entre espécies (Grime 1997, Westoby et al. 2002, Wright et al. 2007, Diaz et al. 2016, Pierce et al. 2017), de forma que, além de serem dependentes de cada contexto, classificações dicotômicas e arbitrárias (e.g. pioneiras e tolerantes) desconsideram variações dentro de cada grupo e, assim, devem subestimar variações na estrutura e composição de comunidades. Logo, em contraponto a abordagens taxonômicas e à definição de grupos funcionais, a mensuração de atributos funcionais com variação contínua e relacionados a diferentes aspectos das estratégias ecológicas vegetais, tem sido enfatizada como a abordagem mais apropriada para entender e prever padrões de distribuição, abundância e coexistência de espécies em assembléias de plantas (McGill et al. 2006, Funk et al. 2017).

Por exemplo, atributos associados ao espectro econômico têm funcionado como bons descritores do nicho de espécies e da resposta de assembléias de plantas a variações na disponibilidade de recursos (veja Reich 2014). Isto porque atributos relacionados a estratégias de uso de recursos refletem um trade-off entre a capacidade de adquirir recursos e crescer rapidamente em ambientes produtivos, e de tolerar estresses conservando recursos em tecidos bem protegidos e duráveis (Poorter & Bongers 2006, Reich 2014, Pierce et al. 2017). De fato, tem-se demonstrado que comunidades sob alta disponibilidade de recursos (i.e. luz, água ou nutrientes) tendem a ser dominadas por plantas com atributos mais aquisitivos associados a altas taxas de crescimento, como alta AEF e baixo CMSF ou densidade da madeira, o oposto sendo verdadeiro no caso de ambientes sob limitação de recursos, dominados por estratégias mais conservativas (Hodgson et al. 2011, Reich 2014, Katabuchi et al. 2012, Jager et al. 2015, Greenwood et al. 2017, Pinho et al. 2018). Ao produzir folhas duráveis com alto custo sob limitação de recursos, espécies de plantas crescem lentamente, mas são favorecidas por reduzirem sua demanda metabólica de recursos, bem como a perda de recursos dada a alta longevidade dos seus tecidos (Wright et al. 2004, Chave et al. 2009, Kitajima & Poorter 2010, Grime & Pierce 2012), o que garante maiores taxas de sobrevivência (Wright et al. 2010, Reich 2014).

Atributos conferindo maior sucesso em um dado contexto favorecem maior aquisição ou retenção de recursos para crescimento e reprodução, o que deve se traduzir em aumentos de abundância ou biomassa relativa. Isto, então, deve se refletir na média dos atributos ponderada pela abundância das espécies, no nível de comunidade (i.e. do inglês, "community weighted mean –

CWM", Muscarella et al. 2017). De fato, tem-se demonstrado amplamente mudanças direcionais no CWM de atributos associados a diferentes dimensões ecológicas vegetais, ao longo de gradientes ambientais naturais ou impostos pelo homem, em escala local ou de paisagem (Westoby et al. 2002, Westoby & Wright 2006, Hodgson et al. 2011, Reich 2014, Jager et al. 2015, Carreño-Rocabado et al. 2016, Muscarella et al. 2017, Pinho et al. 2018). Mudanças no CWM de atributos associados ao espectro econômico, ao longo de gradientes de disponibilidade de recursos, são mais evidentes (veja Reich 2014), mas outros exemplos também são claros, tal como dominância de espécies de menor estatura e com sementes grandes sob menor disponibilidade de recursos (Westoby et al. 2002, Muller-Landau 2010, Marks et al. 2016, Bagousse-Pinguet et al. 2017).

Adicionalmente, a diversidade funcional de assembleias de árvores também varia amplamente ao longo de gradientes ambientais, sendo em geral menor em ambientes mais restritivos com menor disponibilidade de recursos ou condições ambientais extremas (Laliberté et al. 2010, Bernard-Verdier et al. 2012, Katabuchi et al. 2012, Mouillot et al. 2013, Pinho et al. 2018). Entretanto, a resposta de padrões de diversidade é bem menos consistente do que a de composição funcional de comunidades (Funk et al. 2017, Hatfield et al. 2018). Na verdade, diferentes índices de diversidade funcional refletem diferentes aspectos da distribuição de atributos em comunidades (Mouchet et al. 2010, Mouillot et al. 2013). Estes são basicamente relacionados ao espaço uni- ou multidimensional ocupado pelas espécies (i.e., riqueza funcional), ao quão distribuída é a abundância total ao longo do espaço funcional da comunidade (i.e., equabilidade), e ao quão opostos são os atributos de espécies dominantes (i.e., divergência funcional). Para uma melhor compreensão de diferentes aspectos da estrutura funcional de comunidades, Ricotta & Moretti (2011), como aplicado por vários autores, sugere o uso de CWM e de uma medida de divergência funcional, o "RaoQ", que representa a distância funcional média entre indivíduos em uma comunidade. Enquanto que o CWM de atributos deve expressar mudanças em dominância de estratégias funcionais, o RaoQ deve refletir padrões de convergência e divergência funcional (Ricotta & Moretti 2011).

Análises continentais ou globais de distribuição de atributos funcionais de plantas têm sido realizadas basicamente no nível de espécie, desconsiderando-se assim variações na abundância de espécies em grandes escalas espaciais (Moles et al. 2007, 2009, Swenson et al. 2012, Moles 2018). Análises globais têm revelado, por exemplo, aumentos na área foliar sob condições mais quentes e úmidas (Wright et al. 2017), diminuição na massa de sementes com o aumento da latitude (Moles et al. 2007), e maiores densidades de madeira em ambientes mais quentes em baixas latitudes (Swenson & Enquist 2007, Swenson et al. 2012). No entanto, a maioria dessas relações têm poderes de explicação muito baixos (~ $R^2 < 0.1$; Moles 2018). Ao analisar padrões globais no nível de espécie, estes estudos demonstram apenas mudanças na frequência de espécies com diferentes estratégias funcionais, uma vez que não levam em conta variações nas suas abundâncias. Apenas recentemente, Bruelheide et al. (2018) usaram uma grande base de dados global de abundância e atributos funcionais de espécies em comunidades distribuídas em diferentes ecossistemas, encontrando apenas relações fracas entre clima e a composição funcional de comunidades. Entretanto, ao analisar padrões funcionais globais incluindo diferentes formas-de-vida e ecossistemas, estudos de padrões de co-variação de atributos (Diaz et al., 2016), distribuições de espécies (Moles 2018) e composição funcional de comunidades (Bruelheide et al. 2018), podem mascarar padrões relevantes dentro de biomas e formas-de-vida.

2.3 PERTURBAÇÕES ANTRÓPICAS E PADRÕES DE DIVERSIDADE DE ASSEMBLEIAS DE ÁRVORES EM FLORESTAS TROPICAIS

A relação entre perturbações e padrões de composição e diversidade em comunidades biologias é há muito tempo investigada (Connell 1978, Huston 1979), embora em geral ainda muito controversa (Mackey & Currie 2001, Bongers et al. 2009, Huston 2014, Fletcher et al. 2018). Em florestas tropicais com baixos níveis de perturbação, processos de exclusão competitiva tendem a eliminar espécies características de estágios iniciais, enquanto que em ambientes com altos níveis de perturbação apenas espécies tolerantes a distúrbios tendem a persistir (Connell 1978, Bazzaz 1996). Em outras palavras, perturbações tendem a reiniciar o processo de sucessão localmente, gerando, em maiores escalas espaciais, heterogeneidade ambiental, e favorecendo assim a co-ocorrência de diferentes grupos ecológicos (Shea et al. 2004). Por exemplo, em ecossistemas florestais úmidos a abertura de clareiras favorece a manutenção de populações de árvores pioneiras que demandam alta luminosidade para o crescimento (Connell 1978, Bongers et al. 2009). No entanto, a expansão de perturbações antrópicas agudas (i.e., perda e fragmentação de habitats) ou crônicas (e.g. extração de madeira) tende a levar à homogeneização biológica de floras tropicais de escala local a regional (Laurance et al. 2002, 2006, Lôbo et al. 2011, Tabarelli et al. 2012, Newbold et al. 2018, Ribeiro et al. 2019). Isto porque perturbações tendem a determinar aumentos em taxas de mortalidade ou crescimento de grupos ecológicos específicos (Laurance et al. 2006, Tabarelli et al. 2012), em geral favorecendo espécies com ampla distribuição e diminuindo a riqueza e abundância de espécies com requerimentos específicos de habitat e distribuições mais restritas (Newbold et al. 2018). Isto comumente se traduz em declínios de diversidade taxômica, filogenética e funcional em diferentes escalas espaciais (Santos et al. 2008, 2010, Lopes et al. 2009, Lôbo et al. 2011, Benchimol et al. 2017, Rito et al. 2017, Ribeiro et al. 2019). No entanto, a direção e magnitude de respostas de comunidades locais deve depender da diversidade funcional do conjunto regional de espécies, visto que maior diversidade pode se traduzir como diferentes respostas potenciais de espécies a distúrbios (Haddad et al. 2008, Spasojevic et al. 2018).

Florestas tropicais são ameaçadas por uma série de perturbações antrópicas que operam em diferentes escalas espaciais (Laurance & Peres 2006, Peres et al. 2006). Essas incluem mudanças estruturais na cobertura e distribuição de habitats florestais, como desmatamento e consequente perda e fragmentação florestal, mas também ameaças menos aparentes, como extração seletiva de madeira, caça e queimadas superficiais (Peres 2001, Barlow et al. 2003, Tabarelli et al. 2004, Peres 2006). Globalmente, mudanças em padrões de uso-do-solo representam a principal ameaça à biodiversidade e podem comprometer a prestação de serviços ambientais (Sala 2000, Lewis et al. 2015). Tal ameaça é especialmente evidente em florestas tropicais úmidas, cuja cobertura tem sido gradualmente reduzida e os seus remanescentes incorporados a paisagens dominadas por matrizes antrópicas (e.g. cultivos agrícolas), com diferentes tipos e intensidades de uso-do-solo (Ribeiro et al. 2009, Laurance et al. 2014). Por outro lado, em florestas tropicais sazonalmente secas, como a Caatinga, perturbações antrópicas estão mais relacionadas ao uso de recursos naturais por populações humanas do que a mudanças em padrões de uso do solo em grandes escalas espaciais, devido a condições de pobreza que impedem empreendimentos lucrativos em larga escala (Singh 1998, Melo et al. 2017). De fato, tem-se demonstrado que remanescentes florestais na Caatinga são relativamente bem conectados (Antongiovanni et al. 2018) e variações na estrutura de paisagens têm pouco efeito sobre padrões de comunidade (Rito et al. 2017), assim como a criação de bordas florestais (Oliveira et al. 2013). Por outro lado, perturbações antrópicas crônicas tendem a reduzir diversidade taxonômica, filogenética e funcional em florestas sazonalmente secas (Ribeiro et al. 2015, 2017, Rito et al. 2017, Sfair et al. 2018).

2.3.1 Perda de habitat, fragmentação florestal e seus efeitos sobre padrões de biodiversidade em florestas tropicais

A transformação de paisagens naturais em paisagens antrópicas implica na perda e na fragmentação de habitats, na criação de bordas florestais e em outros distúrbios secundários decorrentes da presença constante de populações humanas e do manejo das áreas dedicadas às suas atividades (Fahrig 2003, Fischer & Lindenmayer 2007, Gardner et al. 2009). Como exemplos, pode-se citar a caça, extração de lenha e madeira, coleta de plantas e presença freqüente de fogo, que em geral ocorrem de forma concomitante e sinérgica com a fragmentação florestal (Peres 2001, Barlow et al. 2003, Tabarelli et al. 2004).

Os efeitos de área e isolamento de habitats sobre padrões de biodiversidade são há muito tempo reconhecidos, sendo tema central na Teoria de Biogeografia de Ilhas (TBI; MacArthur & Wilson 1967). De acordo com esta teoria, habitats menores e mais isolados em ilhas oceânicas tendem a ter maiores taxas de extinção e menores de imigração, o que determina menor riqueza de espécies (MacArthur & Wilson 1967). Isto porque ilhas menores suportam populações menores, e, portanto, mais sujeitas a extinção por endogamia ou processos estocásticos; e quanto mais isoladas, mais difícil a colonização por novas espécies. Embora a princípio desenvolvida no contexto de ilhas oceânicas, as idéias da TBI foram logo expandidas para outros ecossistemas, como florestas tropicais (Bierregaard et al. 1992, Laurance 2008), suportando desde cedo discussões sobre estratégias de conservação (Simberloff & Abele 1976). Isto parte da ideia de que populações naturais são distribuídas em manchas de habitat adequado, de forma que espécies de árvore florestais, por exemplo, devem depender da cobertura e distribuição de florestas. De fato, remanescentes florestais pequenos e/ou isolados tendem a suportar baixa diversidade de espécies localmente (Santos et al. 2008, Santo-Silva et al. 2013, Haddad et al. 2015, Newbold et al. 2015, Laurance et al. 2018). No entanto, a TBI não considera diferenças ecológicas entre espécies, que devem determinar a qualidade relativa de fragmentos de habitat (Laurance 2008). Portanto, essa tem limitada capacidade de prever grupos ecológicos mais ou menos vulneráveis, i.e., “winners and losers” (Tabarelli et al. 2012). Além disso, efeitos de borda e a composição de matrizes no entorno de ilhas não são considerados nesta teoria (MacArthur & Wilson 1967), apesar de serem reconhecidos como importantes determinantes de padrões de assembleias de árvores em florestas tropicais (Saunders et al. 1991, Laurance 2008, Driscoll et al. 2013).

Em síntese, a criação de bordas florestais implica em alterações microclimáticas, como aumento da incidência de luz, da turbulência de ventos e de extremos de temperatura e mínimos de umidade (i.e., efeitos de borda abióticos, *sensu* Murcia 1995). Paralelamente, e em parte decorrente dessas mudanças abióticas, algumas plantas pioneiras e insetos herbívoros generalistas podem proliferar em áreas de borda (Laurance et al. 2006, Santos et al., 2008; Wirth et al., 2008). Sabe-se que estes efeitos se traduzem em filtros ambientais para espécies de plantas (1) altas e com alta densidade de madeira, que consequentemente têm troncos sensíveis à turbulência de ventos (Laurance et al. 2000); (2) plântulas tolerantes a sombra, de crescimento lento e com baixa capacidade de compensar o ataque por herbívoros e patógenos (Benítez-Malvido & Lemus-Albor, 2005; Meyer et al. 2011); e (3) indivíduos sensíveis à competição com plantas pioneiras nativas (e.g. lianas) e invasoras de rápido crescimento e com reprodução freqüente e abundante (Laurance et al. 2006, 2018).

Além dos efeitos de borda agindo como filtros, a defaunação e a perda de conectividade estrutural na escala de paisagem reduzem o fluxo de sementes entre os fragmentos e várias populações de plantas experimentam limitação de dispersão à medida que suas sementes deixam de alcançar locais adequados para sua germinação e recrutamento (Melo et al. 2006, 2007, Costa et al. 2012, Santo-Silva et al. 2013). Em síntese, tão logo ocorre a fragmentação da floresta, algumas espécies pioneiras começam a proliferar nos ambientes impactados pelos efeitos de borda, como os pequenos fragmentos florestais, fragmentos de formato irregular e as bordas de grandes fragmentos florestais ou de florestas "continuas" (Tabarelli et al. 2010). Nestes "habitats tipo borda" as populações de um conjunto grande de espécies típicas de floresta (i.e., espécies dependentes de floresta madura) se tornam raras ou até mesmo extintas. O resultado acumulado destes processos sobre a natureza das assembléias de plantas pode ser observado em diferentes escalas espaciais. Na escala local, as assembléias se tornam mais pobres do ponto de vista taxonômico (redução de até 50% na riqueza média de espécies) e funcional, pois vários grupos ecológicos se tornam raros ou até mesmo ausentes (Oliveira et al. 2004, Girão et al. 2007, Melo et al. 2010). Na escala de paisagem, as assembléias se tornam mais similares taxonomicamente e funcionalmente, pois convergem em termos de composição taxonômica no nível de espécie, mas também em termos de características biológicas associadas ao crescimento e a reprodução, principalmente no que se refere a estratégias de polinização e dispersão (Michaslki et al. 2007, Santos et al. 2008, Lopes et al. 2009). Este padrão se manifesta, também, em escala regional à medida que a proliferação de pioneiras avança e a extinção de espécies sensíveis às perturbações antrópicas se acumula no tempo (Lôbo et al. 2011, Tabarelli et al. 2012).

Esta substituição permanente de grupos típicos de floresta madura por espécies colonizadoras nos habitats do tipo borda (i.e., bordas florestais e pequenos fragmentos), associado ao colapso de biomassa (Laurance et al. 1997, de Paula et al. 2011) tem sido interpretada como um processo de degeneração ou "sucessão retrogressiva" e, sem dúvida, representa uma força importante nas paisagens antrópicas (Tabarelli et al. 2008). Por exemplo, é razoável propor que a floresta Atlântica, imersa em paisagens antrópicas, esteja se reorganizando biologicamente na forma de "novos ecossistemas", com características de organização sem precedentes na história evolutiva desta biota. Por outro lado, em contextos biogeográficos específicos, como as florestas mexicanas, evidências sugerem que paisagens altamente fragmentadas podem ainda manter a integridade da biota (Arroyo-Rodriguez et al. 2009, 2012, 2013) independentemente do tamanho dos remanescentes florestais (Hernández-Ruédas et al., 2014). De fato, respostas de comunidades de plantas e animais a perda e fragmentação de habitats são claramente inconsistentes entre regiões (Vetter et al. 2011, Collins et al. 2017), provavelmente devido a diferenças regionais em padrões de uso-do-solo, e histórias biogeográficas que determinam diferenças funcionais entre conjuntos (i.e. "*pool*") regionais de espécies (Arroyo-Rodriguez et al. 2017, Colins et al. 2018, Spasojevic et al. 2018). Portanto, estudos envolvendo assembleias de árvores tropicais em múltiplos contextos biogeográficos e de uso-do-solo se fazem necessários para entender inconsistências e identificar generalidades no que concerne à resposta de assembleias de árvores a modificações de paisagens (Melo et al. 2013).

Embora os efeitos de perda e isolamento de habitats sejam claros em vários contextos (Haddad et al. 2015, Arroyo-Rodriguez et al. 2017), de acordo com a "hipótese da quantidade de habitat" (i.e. do inglês, *the habitat amount hypothesis* – HAH; *sensu* Fahrig 2013) tais efeitos se devem a um único fator: a quantida de habitat (i.e. cobertura florestal) na paisagem local, no entorno da comunidade focal. Isto porque, tendo mais floresta no entorno, devem haver mais indivíduos e espécies na paisagem local, e, portanto, maiores probabilidades de migração e menores de extinção, o que determinaria maior riqueza de espécies localmente (Fahrig 2013). De fato, área e isolamento de habitats são em geral altamente correlacionados (Tscharntke et al. 2012, Fahrig 2013). Além disso, de acordo com uma meta-análise, quando controlados os efeitos da quantidade de habitat, área e isolamento ainda têm efeitos adicionais, mas são de fato fracos (Martin 2018).

No entanto, testes empíricos e experimentais da HAH têm na verdade resultados contrastantes, incluindo tanto padrões neutros como respostas positivas e negativas da riqueza de espécies em comunidades (Hanski 2015, Haddad et al. 2017, Bueno & Peres 2019, Merckx et al. 2019). Fahrig (2013) também considera que a escala em que os efeitos de estruturas de paisagens devem se manifestar mais fortemente deve depender do grupo biológico, do contexto regional e do aspecto da comunidade considerado, embora o estudo da "escala de efeitos" ainda esteja em sua infância (Miguet et al. 2016). No caso de florestas tropicais, e particularmente de assembleias de árvores, não existem até o momento estudos abrangentes do efeito da cobertura florestal em diferentes escalas espaciais sobre padrões de comunidades.

Além disso, investigações adequadas da resposta funcional de assembleias de árvores à perda e fragmentação de habitats se fazem necessárias, visto que estudos realizados até o momento são baseados em grupos funcionais categóricos, que desconsideram, portanto, variações entre espécies em cada grupo (mas veja Magnago et al. 2014, para um exemplo com um único atributo contínuo, i.e. densidade de madeira). Por exemplo, tem-se demonstrado que plantas tolerantes a sombra, com sementes grandes e dispersas por animais de médio e grande porte, declinam em vários contextos em resposta à perda e fragmentação florestal (Santos et al. 2008, Benchimol et al. 2017, Rocha-Santos et al. 2017). No entanto, inferências a partir de padrões baseados em grupos funcionais podem tanto subestimar como superestimar efeitos, por não considerarem variações funcionais contínuas entre espécies (McGill et al. 2006). Em síntese, ainda não está claro o quão forte e consistente são os efeitos de modificações de paisagens sobre padrões de composição e diversidade funcional de assembleias de árvores em florestas tropicais (Hatfield et al. 2018).

2.4 MECANISMOS DETERMINANTES DE FUNÇÕES ECOSSISTÊMICAS

Além dos efeitos diretos de condições ambientais, variações na composição funcional de assembleias de plantas podem mediar processos ecossistêmicos (Poorter et al. 2017). Isto porque atributos funcionais determinam não apenas as respostas das espécies a estresses e perturbações, mas também seus efeitos sobre processos ecossistêmicos (Lavorel & Garnier 2002, Suding et al. 2008). Por exemplo, variações em atributos associados ao espectro de plantas e relacionados a taxas rápidas de aquisição de recursos (e.g. baixo CMSF, alto SLA) devem determinar processos mais dinâmicos (e.g. ciclagem de nutrientes, produtividade; Garnier et al. 2004, Reich 2014), enquanto que atributos associados a estratégias conservativas favorecem a estabilidade de serviços ecossistêmicos, como estoques de carbono (Poorter et al. 2017). A altura máxima alcançada por árvores está alometricamente relacionada ao seu diâmetro (King 1996) e incrementos em diâmetro determinam aumentos em escala exponencial na biomassa armazenada por árvores (Chave et al. 2005). Efeitos indiretos são também evidentes, como por exemplo a redução de estoques de carbono devido à falha de recrutamento de árvores com grandes sementes em florestas tropicais, uma vez que estas em geral também apresentam alta densidade de madeira (Bello et al. 2015).

Embora haja um crescente consenso em relação ao efeito de diferentes atributos funcionais sobre processos ecossistêmicos (Díaz et al. 2004, Garnier et al. 2004, Reich 2014), a forma como comunidades mediam variações em processos ecossistêmicos é ainda controversa (Grime 1998, Díaz et al. 2007, 2011, Finegan et al. 2014). A "hipótese da proporção de biomassa" (do inglês, "the biomass-ratio hypothesis"; *sensu* Grime 1998) prediz que processos ecossistêmicos são determinados pelas características funcionais das espécies dominantes em uma dada comunidade. Assume-se que tal dominância deve ser refletida pela média ponderada dos atributos na comunidade (i.e., CWM; Lavorel et al. 2008). Essa hipótese apresenta inúmeras evidências empíricas, em concordância com o proposto por Reich (2014), como taxas mais lentas de ciclagem de nutrientes ou menor produtividade em comunidades com maiores médias de atributos conservativos (e.g. CMSF, densidade da madeira; Garnier et al. 2004, Reich 2014), ou maior produtividade em florestas dominadas por atributos aquisitivos (e.g. maiores CWM AEF; Finegan et al., 2014). Por outro lado, há muito tempo assume-se uma relação positiva entre a riqueza, ou diversidade de espécies, e processos ecossistêmicos (Isbell et al. 2011). Tal pressuposto se fundamenta na idéia de "complementaridade funcional" (Petchey & Gaston 2006, Díaz et al. 2011), como por exemplo, maior eficiência de captura de luz em comunidades de plantas com maior diversidade de alturas (Vojtech et al. 2008). O papel da diversidade funcional sobre processos ecossistêmicos, no entanto, possui bem menos evidências do que o CWM de atributos específicos (Finegan et al. 2014).

3 RESULTADOS

3.1 ARTIGO 1

Manuscrito a ser submetido ao periódico *Global Ecology and Biogeography*

Research paper – Global Ecology and Biogeography

The functional biogeography of Neotropical rainforests: patterns of tree community specialization and its relation to climatic gradients

Bruno X. Pinho[1*], Marcelo Tabarelli[1], Gabriel Mendes[1], Victor Arroyo-Rodriguez[2], Bráulio A. Santos[3], Simon Pierce[4], Valério Pillar[5], Sandra Muller[5], Miguel Martínez[2], Madelon Lohbeck[6,7], Frans Bongers[6], Carlos A. Peres[8], Maíra Benchimol[9], Deborah Faria[9], Rodrigo Orihuela[10], Renato A.F. de Lima[11], Bettina Engelbrecht[12,13], Jos Barlow [14], [...] and Felipe P.L. Melo[1]

[1]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Brazil

[2]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico

[3]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil

[4]Department of Agricultural and Environmental Sciences, University of Milan, Milan, Italy

[5]Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[6]Forest Ecology and Forest Management group, Wageningen University, Wageningen, The Netherlands

[7]World Agroforestry Centre, Nairobi, Kenya

[8]School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, UK

[9]Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Ilhéus, Brazil

[10]Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[11]Instituto de Biociências, Universidade de São Paulo, São Paulo, Brasil

[12]Department of Plant Ecology, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Bayreuth, Germany

[13]Smithsonian Tropical Research Institute, Balboa, Republic of Panama

[14]Lancaster Environment Centre, Lancaster Univesity, United Kingdom

*Corresponding author: bxpinho@hotmail.com

Abstract

Aim: Despite being assigned to a single biome, tropical rainforests greatly differ in their past and present climatic conditions and biogeographical histories, especially in the Neotropics. However, we have limited knowledge on how and why functional trait dominance varies along biogeographical and climatic gradients across rainforests. Here we characterize the latitudinal variation in dominance of species functional traits (economic- and size-related) and adaptive (CSR) strategies across Neotropical tree assemblages, and identify key climatic drivers.

Location: Neotropics.

Taxon: Trees.

Methods: We used data from 233 forest plots across 10 regions, including >36,000 trees of 930 species. We calculated for each plot the community weighted-mean (CWM) of key functional traits and adaptative (CSR) strategies. We applied linear mixed effects models for each CWM trait/strategy with either latitude or climatic factors as predictors, accounting for within- and cross-region variation.

Results: We found that regional floras largely overlap relative to species-level trait/strategy distribution, but exhibit very distinctive functional profiles at community-level. Northern floras along the Neotropics are dominated by more competitive or ruderal (i.e. fast-growing) strategies, while ‘slow’ traits achieve greatest dominance close to equator. Although community variation along climatic gradients largely mirrored their variation along latitudinal gradients, trait dominance was in general better predicted by combination of climatic factors (17 to 79% of cross-region variation in community weighted-mean trait values), except for SLA and CSR strategies. Temperature-related variables predicted trait distribution better than precipition. Increasing potential evapo-transpitation and temperature seasonality led to increased dominance of soft tissues and small seeds. In turn, increasing mean annual precipitation (MAP) favored dominance of soft-wooded and large-leaved species, and maximum tree height decreased with increasing seasonality of both precipitation and temperature.

Main conclusions: Community-level trait-climate relationships are much stronger than previously reported patterns at the species-level. This suggest that while species spatial ranges may extend over relatively unsuitable climates, their abundances are strongly constrained by climatic factors. Our findings imply the occurrence of functionally structured tropical floras at the continental scale, which have critical implications for predictions on the impact of future climate change and human-induced disturbances on plant community composition and ecosystem functioning.

*Key-words:*CSR strategies, functional traits, latitude, precipitation, species pool, temperature.

Introduction

In an attempt to optimize growth, survival and reproduction under contrasting environmental conditions, plant species have evolved a number of solutions, which are reflected by the large trait diversity they exhibit, even within-biomes and growth-forms (Díaz et al. 2016, Pierce et al. 2017). Such diversity has partly evolved in response to varying climate, which is often considered the main driver of vegetation patterns at large spatial scales (Whittaker 1975, Moles et al. 2014, Yang et al. 2015, Wright et al. 2017). Yet functional traits are not only related to the way plants respond to changing conditions, as they also determine their effects on ecosystem functioning (Diaz et al. 2004, Suding et al. 2008). Specifically, the combination of co-occurring species traits in ecological communities defines their joint effect on ecosystems (Garnier et al. 2004, Poorter et al. 2017). Therefore, insights into how the functional composition of ecological communities varies along biogeographical and climatic gradients may advance our understanding on the effects of climate change and human-induced disturbances on ecosystem functioning. In fact, the field of ‘functional biogeography’ has recently emerged as a promising way to better understand, model and predict the impact of environmental changes on plant assemblages and ecosystem functioning across biogeographical gradients (Violle et al. 2014).

With the recent growth of global plant trait databases (e.g. Kattge et al. 2011), a large number of studies have investigated continental to global patterns of species trait variation and its relation to latitudinal and macroclimatic gradients (Moles et al. 2007, 2009; Swenson & Enquist 2007; Swenson et al. 2012; Wright et al. 2004, 2017). These have revealed some key patterns, including the increase in leaf size under hotter and wetter conditions (Wright et al. 2017), the decrease in seed mass with latitude (Moles et al. 2007), and the increase in wood density in warm sites at lower latitudes (Swenson & Enquist 2007, Swenson et al. 2012). These patterns exist because plants with traits conferring high performance in a given environment can acquire or retain a relatively high proportion of limited resources for growth and reproduction, which should translate into increased abundance or biomass. However, most of these relations have a low predictive power (~ $R^2 < 0.1$) due to the high degree of variation within regions. Moreover, these studies have addressed cross-species patterns based on species occurrence data, and therefore have not accounted for variation in abundance among functional strategies. They also do not capture local variation in species co-existence and environmental filters (i.e. community-level patterns; Bruelheide et al. 2018). Only recently, Bruelheide et al. (2018) used an unprecedented community data set including more than one million plots and a comprehensive set of traits to test for global trait-environment relationships, finding only weak support for trait-climate relationships. Nonetheless, by analyzing global data sets involving contrasting biomes and growth-forms, studies on plant trait co-variation (Diaz et al. 2016), species trait distributions (Moles et al. 2018) and community functional composition (Bruelheide et al. 2018) may mask relevant patterns within biomes and growth-forms. For instance, not only traits but also trait relationships and trait-environment relations may vary greatly in direction and/or magnitude across growth-forms and ecosystems (Wright et al. 2001, Wright & Sutton-Grier 2012, Diaz et al. 2016). Thus, by analyzing trait-environment relations within such components, we may be more able to accurately predict the response of specific vegetation types to future climate changes and human-disturbances, and adequately propose management actions.

Tropical rainforests sustain most of the Earth’s biological diversity (Groombridge & Jenkins 2002) and play a central role in the provisioning of ecosystem services, accounting for example for one third of the global terrestrial gross primary productivity (Beer et al. 2010) and one quarter of the terrestrial carbon stored in all ecosystems (Bonan 2008). Despite being assigned to a single biome, tropical rainforests greatly differ in their past and present environmental (e.g. climatic) conditions (Pyke et al. 2001, Blonder et al. 2018) and biogeographical histories (Burnham & Graham 1999, Santos et al. 2007, Hoorn et al. 2010, Cole et al. 2014). Such differences clearly result in distinct composition, structure and diversity patterns across rainforest regions, with the Neotropical region (Fig. 1) as the most extensive, diverse and distinct one (Corlett 2011). We know, for example, that many groups of plants are restricted to the Central-Northern or the South American forests, even with the formation of the

Panama land bridge 3 million years ago (Burnham & Graham 1999). Even at smaller spatial scale, profound phylogenetic differences are for example evident across forests in the Brazilian Atlantic coast, with its northeastern portion being more similar to the Amazon than to the southeastern Atlantic forest (Santos et al. 2007). We do not know, however, how such large differences across Neotropical forests translate into functional patterns of tree communities.

Briefly, community functional composition results from the joint effect of biogeographical history (Stropp et al. 2009) and environmental factors acting at different spatial scales, such as macroclimate at the regional scale (Bruelheide et al. 2018) and varying disturbances locally (Berenguer et al. 2018). In response to such multiple drivers, constraints to local variation in community functional composition should act more strongly on multivariate phenotypes (Laughlin & Messier 2015, Muscarella & Uriarte 2016), represented by co-varying traits (Diaz et al. 2016). Globally, the spectrum of plant form and function suggest the existence of two main orthogonal axes of functional specialization ubiquitous for plants, representing variation in resource-use strategies (a trade-off between rapid resource-acquisition and longevity) and the size of plants and their organs (Diaz et al. 2016). Based on these two global axes of trait co-variation, Pierce et al. (2017) built a method for calculating continuous variation in plant ecological strategies according to Grime’s competitor, stress tolerator, ruderal (CSR) theory (Grime & Pierce 2012). Theoretically, these three main strategies represent viable combination of traits that have evolved in response to varying combinations of stress and disturbance levels, which should select for competition in relatively productive and stable conditions, stress-tolerance under abiotic limitation to growth, and rapid growth and high reproductive investment under frequent disturbance, respectively (Grime & Pierce 2012). Although some effort has been made to understand the relation between CSR-strategies and climate across biomes (Pierce et al. 2017), it was not abundance-based, which may explain some of the unexpected relations found.

Furthermore, no effort has been made yet to understand community-level variation in CSR-strategies at large spatial scales.

Here we asked if it is possible to discern broad biogeographic patterns of tree community functional (traits and CSR strategies) composition across rainforests in the Neotropics, and how such patterns relate to climatic gradients. We hypothesize that (1) individual traits are related to climatic gradients at the community-level, with increasing dominance of more acquisitive and large-size traits under more productive and stable climatic conditions (i.e. higher and less seasonal temperature and rainfall); and (2) Neotropical tree communities are biogeographically structured according to combinations of traits into plant ecological (CSR) strategies.

Methods

Study sites and regions

We studied 233 rain forest sites in 10 human-modified landscapes (hereafter, regions) distributed across the Neotropics, encompassing a latitudinal interval of 45º, from the northern to the southern extremes of the Neotropical rain forest distribution (Fig. 1; see Table S1 for details on plot measurements). In fact, the region located at the southern end is just below the tropic line of Capricorn (Fig. 1). All plots were located in old-growth forests, including both continuous forests and fragments of varying size. Mean annual precipitation ranged from 1167 to 3351 mm and mean annual temperature from *c*. 17 to 27 ºC. Besides differences in their past and present environment (Pyke et al. 2001, Blonder et al. 2018) and land-use history and patterns (Table S1), the studied sites greatly differ in their biogeographical histories (Burnham & Graham 1999, Santos et al. 2007, Hoorn et al. 2010). This results from a complex history of tectonic movements and past climate changes in the Neotropics, the last leading to a recurrent expansion and contraction of forest area over time (Burnham & Graham 1999, Corlett 2011). For instance, the biota in forests from Mexico is very distinct as it is comprised of elements of both Northern and Neotropical origin (Rzedowski 1978). Moreover, palynological evidences points to faster recover from past disturbance in tropical rainforests from Central-northern America compared to those in South America, probably as a result of a higher frequency of disturbance events through time, leading to a higher degree of resilience (Cole et al. 2014).

Vegetation data

We used data on 36,080 adult trees (stems with diameter at breast height, DBH ≥ 10 cm; except for UNA where cutoff used was ≥ 15 cm) and 930 tree species from the 10 studied regions. Tree inventories within each region have been described elsewhere (Santos et al., 2008, Arroyo-Rodríguez et al., 2009; Faria et al., 2009; Orihuela et al. 2015, Arroyo-Rodríguez et al., 2013; Hernández-Ruedas et al., 2014, Benchimol & Peres, 2015, Pinho et al. 2018) and sampling strategies are summarized in Table S1. The slightly different sampling methods in each region should not affect the validity of our cross-region analyses as here we did not focus on variation in diversity patterns, but rather in tree community functional composition, which describes the relative dominance of functional traits and strategies.

Functional traits and CSR strategies

We measured in the field (following Pérez-Harguindeguy et al. 2013) and compiled from global databases (e.g. ‘TRY’; Kattge et al. 2011) a comprehensive set of traits thought to influence tree performance along climatic gradients, including both economic and size-related traits from different plant organs (leaves, stems and seeds) and the whole-plant. Our trait data covered at least 70% of the total tree abundance in each plot. When measuring leaf traits, we considered leaflets as the sample unit for compound-leaved species. The leaf (specific leaf area -

SLA and leaf dry matter content - LDMC) and stem (wood density - WD) economic traits considered are expected to reflect a trade-off between rapid resource-acquisition and growth under high resource availability, and internal conservation of resources in well protected tissues under low or seasonal resource availability (Wright et al. 2004, Chave et al. 2009). All the other traits are also related to specific trade-offs. Increasing leaf size (i.e. leaf area – LA) favors light capture and a slow heat exchange with the surrounding air, but also leads to a higher transpirational water loss, thus being related to competitive dominance specifically in wet, hot and sunny environments (Grime & Pierce 2012, Wright et al. 2017). Seed mass (SM) influences several aspects of tree regeneration strategy: larger seeds may provide competitive advantages (i.e. higher seedling performance), while smaller-seeded species have a greater seed output, and their seeds tend to present higher survival rate in the soil (see Moles 2018). Finally, maximum tree height (Hmax) is also related to competitive dominance, as larger trees tend to have greater access to light and belowground resources (Muller-Landau et al. 2006, Brum et al. 2019); but shorter trees are often more stress-tolerant (King 1990, Grime & Pierce 2012).

To define plant (CSR) strategies based on combination of traits, values of LA, LDMC and SLA were entered into the "*Stratefy*" spreadsheet developed by Pierce et al. (2017), which provide continuous C-, S- and R-scores for each species based on their position in a functional space calibrated from more than 3,000 species worldwide. Although based only on few morphological leaf traits, this method is expected to capture variation in other organ-level (e.g. wood density) and whole-plant traits (e.g. maximum height), given the co-variation patterns among such traits (Pierce et al. 2017). Specifically, 'competitors' (C-selected) are expected to dominate under relatively stable and productive habitats by investing resources in continuous vegetative growth, thus achieving a large individual and organ size, which favor resource preemption. Stress tolerators (S-selected) are expected to do better in variable and resource-poor environments by growing slowly (i.e. low metabolic resource demand) and producing dense, durable tissues (i.e. reduced loss of resources). They have greater longevity at both organ- and plant-level, and can either be small, or gradually achieve a large size over their long life-span. Ruderalists (R-selected) have evolved in an environment where disturbance is frequent, thus having a very short life-span and invest most of resources in propagules to guarantee population maintenance after biomass destruction (Grime & Pierce 2012).

Climate data

For each plot in each region, we assessed the average of the following bioclimatic variables: annual precipitation (MAP), precipitation seasonality (PS – coefficient of variation of monthly values), temperature seasonality (TS – standard deviation of monthly values multiplied by 100) and Potential Evapo-Transpiration (PET – the amount of water expected to be removed by the atmosphere through evapo-transpiration processes annually). These were obtained from the new WorldClim version 2.0 (Fick & Hijmans 2017), which is an updated high-resolution global geo-database (30 arc seconds or ~ 1km at equator) of monthly average data for the recent half-century (1970-2000). This is based on spatial interpolation using thin-plate splines of a high number of climate station observations, with covariates including elevation, distance to the coast and other satellite data. Nonetheless, the PET data were built by Trabucco & Zomer (2018) from a set of WorldClim variables. This is based on the equation proposed by the Food and Agriculture Organization of the United Nations (FAO) to estimate PET, which take into account the minimum, maximum and average temperature; solar radiation, wind speed and water vapor pressure, thus being mainly a function of temperature (Trabucco & Zomer 2018).

Data analyses

We first applied Nonmetric Multidimensional Scaling (NMDS) on taxonomic composition of tree assemblages to visually check cross-region floristic similarities, using function 'metaMDS' from R package 'vegan' (Oksanen et al. 2015). Then, functional traits were scaled-up to community-level by calculating the Community-Weighted Mean ('CWM' – i.e. species' trait values weighted by their abundances), which reflect the dominant trait-strategy in a community (Muscarella et al. 2017). Functional analyzes were performed using function 'dbFD' from R package 'FD' (Laliberté & Legendre 2010). Before proceeding with the statistical analysis, we log-transformed species leaf area and seed mass values, and scaled all species and community trait values. Then, we tested for individual correlation among species- and community-level traits using Pearson's correlation tests with Bonferroni correction for multiple tests, given that the response of one trait to environmental gradients may not be independent of others. To examine overall trait co-variation patterns at both species- and community-level, we applied principal component analyses (PCA) on trait matrices, using function 'prcomp' (Venables & Ripley 2002).

To evaluate biogeographical patterns in community functional composition, we first compared CWM traits and strategy mean values between regions by applying one-way ANOVA and Tukey post-hoc tests with functions 'aov' and 'TukeyHSD', respectively, in R 'stats' package (Chambers et al. 1992). Then, we used the C-, S-, R-scores of each species to produce CSR triangles for each region, highlighting variation in species relative abundance to visually check changes in the dominant strategies across regions, using software SigmaPlot 12.0. Finally, to assess changes in community functional composition in response to latitudinal and climatic variation, we constructed linear mixed-effects models (LMM) for each trait and C-, S-, R-strategies, with latitude and climatic variables as fixed-effects terms in separated models, and a random-effect term for 'region' in all models (making standard assumptions of normality, independence and equal variance). The region random-effect was included to account for the nestdness structure of our sampling design, and to allow us to measure among-region variation not explained by climatic variables. We tested the effects of latitude and climate separately because they are generally correlated (Table S2). When testing latitudinal effects, we compared linear and quadratic models, as the last would describe a pattern in response to the distance from equator, while the linear model would point to a south-north gradient. We only selected the quadratic model when it explained significantly more than the linear model and if the quadratic term were significant. After running a full model for each response variable (i.e. CWM trait-strategy) using the maximum likelihood method with R package LME4 (Bates et al. 2015), we performed a model selection procedure to select the best-fit models as those with lowest Akaike information Criterion values (ΔAICc < 2; Burnham & Anderson, 2002). Finally, we applied model averaging to make inferences on how individual climatic variables influence community-weighted mean trait-strategy. First, for each variable, we averaged coefficients and 95% confidence intervals across the best-fit models. Second, we considered variables to be significant only when the 95% confidence intervals did not include 0. Model selection and averaging were carried out using the ‘MuMin’ package in R. To assess the variance in traits and strategies among regions and the strength of trait-climate or -latitude relationships, we partitioned the R^2 of each model into the total variance between-regions (“conditional R^2”) and the component explained by climate or latitude (“marginal R^2”; Nakagawa & Schielzeth 2013). The difference among these measures thus represents the variance between-regions not explained by climate/latitude, while the within-region component is the remaining unexplained variance (i.e. 1 – conditional R^2). For this, we used the R package ‘piecewiseSEM’.

Results

Neotropical floras

The studied regions presented very distinctive floristic composition, with four major regions evident: Mexican forests, Amazonia, northern and southern Atlantic forest (Fig. 2). Within these major regions, the more disturbed regions are generally subgroups of those less disturbed, such as among the Los Tuxtlas regions (which are also relatively distinct from Lacandona), and between Miriri and João Pessoa, both in the same regional context but the latter in an urban and the former in a rural context. Although the small floristic variation among communities within UNA may result from the higher DBH cut-off (Table S1), the composition of this region completely overlapped to those of Atlantic forest regions above the São Francisco river, which has been considered an important geographical barrier driving strong floristic differences among these regions (Santos et al. 2007).

Trait variation and co-variation patterns of Neotropical tree species and assemblages

Individual traits presented large cross-species variation, but generally the range of species mean trait values were similar across regions (Fig. S1, Table S3). Some cross-region differences in the distribution of species trait values were however evident, such as a higher frequency of species with softer woods in the Mexican flora and of small-leaved species in the extreme South of the Neotropical forest distribution (Fig. S1). Furthermore, the largest seed in Amazonia is 2.38- and 8.43-fold heavier than the largest seeds in other regions from Southern- and Northern-hemisphere, respectively (Table S3).

In contrast to the high within-region and low cross-region variation in species trait values, community-weighted mean (CWM) trait values were more constrained within-regions but their distribution varied strongly across regions (Table S4). For instance, CWM seed mass in Amazonia was 21.55- and 13.18-fold higher than in the extremes south and north of the

Neotropical forest distribution, respectively (Table S4). Moreover, the maximum CWM values observed for wood density and LDMC in some regions at extreme-north latitudes were similar to, or even lower than the minimum values observed across Atlantic forest regions (Table S4).

Most trait pairwise correlations were statistically significant but in general they were weaker at the species- than at the community-level (Table S5). The main spectrum of functional specialization evident for both trees and communities reflects mainly variation in economic traits and regenerative strategies, from acquisitive (i.e. high SLA) strategies and small seeds, to more conservative strategies (i.e. high LDMC and wood density) and large seeds (Figs. S2 and S3, Table S6). Also, in both PCAs the second axis was mainly explained by variation in leaf area and maximum height, which co-varied positively (Table S6).

Neotropical tree ecological strategies across regions

Just as for individual traits, some cross-region differences in the CSR-functional space covered by species were evident, but the most striking changes observed were in the dominant strategies in each context (Fig. 3). Specifically, Neotropical tree species were in general widely spread between the extremes C- and S- of the global CSR triangle, but the overall dominant strategies within each region (i.e. the most abundant species at the regional scale) shifted from extreme S- to more C-selected species along a south to north gradient (Fig. 3). A similar trend was evident at the community-level: average CWM C- and R-selection increased, while S-selection declined from the extreme south to the north of the Neotropical forest distribution (Fig. 4). Although R-scores were in general much lower than C- and S-scores at both species and community-level, its CWM variation among regions was even higher, with a 3-fold difference between the average values observed in Amazonia or at the extreme south (~ 5%) and at the Los Tuxtlas region in the extreme north (~ 15%; Fig. 4).

Trait-latitude and -climate relationships across Neotropical tree assemblages

Traits related to high stress-tolerance (i.e. leaf dry matter content and wood density) and reproductive investment (i.e. seed mass) increased in prevalence at lower-latitudes, thus presenting a unimodal relation with latitude at the community-level. However, mean values for these traits were in general much lower in assemblages at the extreme-north than in those at the extreme-south of the Neotropical forest distribution (Fig. 5). On the other hand, traits related to competitive dominance (LA) and fast growth-rates (SLA), as well as CSR strategies, changed linearly as a function of latitude, thus following a south-north gradient. Specifically, community-weighted mean LA, SLA, C- and R-selection increased from south to north, while CWM S-selection decreased along this same gradient (Fig. 5). The responses of LA and C-selection to latitudinal variation were relatively weak compared to the response of other traits and strategy-dimension (Fig. 5). Only variation in CWM maximum height was not significantly related to latitude ($p > 0.05$). When significant, latitudinal variation explained between 20% and 56% of the variation in CWM trait-strategy values across regions (Fig. 5).

While temperature seasonality correlates strongly and positively with distance to equator, other climatic factors (MAP, PET, PS) tended to increase from south to north (Table S2). Climatic factors explained together between 17% and 79% of the variation in community-weighted mean trait-strategy values across regions, while the variation between regions not explained by climatic variation ranged from 25% to 87% (Tables 1 and S7). Increasing PET and especially TS led to a strong decrease in the relative abundance of species with dense tissues (i.e. high LDMC and WD) and large seeds (Fig. 6a-f). Tree species with low wood density and large leaves increased in prevalence with increasing mean annual precipitation (Fig.6g-h). Also, increasing seasonality of both temperature and precipitation reduced the dominance of species capable of reaching great heights (Fig. 6i-j). Finally, changes in the relative abundance of CSR strategies in response to climatic variation were relatively weak compared to its response to latitudinal gradients, with only a slight increase in C-selection and a relatively stronger decrease in S-selection with increasing PET (Fig. 6k-l). Although all climatic factors considered were retained in the best-fit models for CWM SLA and R-selection (Table S7), they did not have significant effects on these variables (Table 1). Such less responsive traits (SLA) and CSR-dimensions (particularly R-) presented however the strongest differences among regions (i.e. conditional R^2; Table 1), though not explained by climatic variation.

Discussion

Our results sugest that Neotropical forest floras consist of distinct taxonomy assemblages and exhibit a wide spectrum of trait variation. In general, regional species pools cover the same spectrum of trait variation, with some regions supporting particular deviations such as those relative to wood density, seed mass and SLA. Despite such an overlap relative to species-level trait distribution, regional floras exhibit distinc functional profiles at community-level (CWM). Variation in trait dominance across regions reflect differences in terms of resource-use (i.e. economic specrtrum) and regeneration strategies. Regional floras also exhibit distinct functional strategy (CSR) composition, with most species and community-level scores distributed close to the extremes C- and S- of the global CSR triangle. Finally, there is a consistent distribution of community-level traits and functional strategies associated to latitudinal and climatic gradients, such as temperature (i.e. potential evapo-transpiration [PET] and seasonality [TS]). It implies the occurrence of functionally structured tropical floras at the continental scale, which have critical implications for predictions on the impact of future climate change and human-induced disturbances on plant community composition and ecosystem functioning.

Numerous studies have previously analyzed the functional assembly of local communities from regional species pools (e.g. Kraft & Ackerly 2010), or variation in trait composition at large spatial scales from species occurrence data (see Moles et al. 2018). In contrast, little is known on how the dominant functional strategies change across tree communities in response to macro-environmental drivers or biogeographical gradients. Globally, Bruelheide et al. (2018) have shown that variation in plant community functional composition is weakly related to macroclimate, while here we found strong trait-climate relationships across neotropical rainforest regions (Fig. 6, Table 1). The inclusion of contrasting vegetation types in global-scale analysis may be biased by the relative frequency of different growth-forms, thus basically reflecting functional differences among them (Moles et al. 2007). For instance, global studies on both species- and community-level trait distribution suggest increasing average wood density (WD) with PET ($R^2 < 0.15$; Bruelheide et al. 2018, Moles et al. 2018). However, this should largely result from the increase in relative frequency of tree-dominated vegetation or the clade filtering of angiosperms (i.e. hard-wooded species) in more productive (low latitude) environments worldwide, as warmer and wetter sites should actually favor more acquisitive stem and leaf traits among rainforest trees (Wright et al. 2004, Zhang et al. 2013), as showed here (Fig. 6a,g). Furthermore, traits co-varying positively with WD across Neotropical trees (i.e. LDMC and seed mass) also decreased in prevalence with increasing PET and TS (Table 1), indicating increasing dominance of fast-growing tree species with soft tissues and small seeds in potentially more productive environments with higher temperature seasonality across tropical forests. Nevertheless, substantial within-region variation in community composition is also evident (Fig. 6). These findings reinforce the notion that tropical forest floras or tree species assemblages are functionally structured from landscape to regional scale, with climatic conditions playing a key role in trait filtering at broad biogeographic scales (Swenson et al. 2012).

In fact, excepting the increase in wood density with PET, our findings largely agree with studies on species-level global trait-climate relationships (Moles et al. 2018). For instance, seed mass is generally lower in plants growing in more seasonal sites (Moles et al. 2007, Swenson et al. 2012, Malhado et al. 2015), as larger seeds are less likely to have dormancy and to develop and survive under seasonal conditions for growth (Thompson et al. 1993, de Casas et al. 2017). Moreover, species under higher MAP tend to have larger leaves to maximize light capture (Wright et al. 2017), and plant maximum height is generally limited under more seasonal precipitation or temperature (Moles et al. 2009, 2014, Swenson et al. 2012), as we found here (Fig. 6, Table 1). Finally, specific leaf area (SLA) is not consistently related to large-scale environmental gradients, and precipitation have low or inconsistent effects on plant traits as it does not really predict water availability for plants (Moles et al. 2018). While variation in PET had a stronger effect on economic traits, temperature seasonality was more tightly related to seed mass. We thus suggest that the coordinated response of multiple traits to TS and PET (Fig. 6a-f) may partly result from the interspecific correlation among economic traits and seed mass (Table S5). Additionally, less seasonal forests tend to have more closed canopies, which may provide competitive advantages for species with either large seeds or more conservative traits in shaded conditions (Leishman & Westoby 1994, Kitajima & Poorter 2010). While we found here similar trends as observed in species-level analyses (Fig. 6), the patterns we uncovered, which take into account variation in species abundances in tree communities, have much higher predictive powers (Table 1). This suggests that while species spatial ranges may extend over relatively unsuitable climates, their abundances are more strongly constrained by climatic factors.

While individual traits often correlate strongly with specific environmental variables, species coexistence and response to multiple factors are better predicted by combination of multiple ecological dimensions (Kraft et al. 2015, Muscarella & Uriarte, 2016). In fact, here we found that dominance of CSR-strategies, which are proposed to have evolved in response to varying stress and disturbance levels (Grime & Pierce 2012), is poorly related to individual climatic factors (except for S-selection; Fig. 6l) but was strongly related to a south-north latitudinal gradient along the Neotropics (Fig. 5). Forests in the extreme south of the Neotropical forest distribution are dominated by highly stress-tolerant species, while the decrease in S-selection northwards is compensated by increases in both C- and R-selection. These patterns are in concordance with the predictions from the CSR theory (Grime & Pierce 2012), given that (1) both PET and MAP are strongly positively correlated with the south-north latitudinal gradient (Table S2), suggesting overall less productive sites southwards favoring stress-tolerance strategies; and (2) tropical forests in Central-northern America have suffered relatively more frequent natural disturbance events along their evolutionary history compared to those in South America, according to paleoecological evidences (Burnham & Graham 1999, Cole et al. 2014), which should favor more ruderal strategies. Finally, tree communities in Amazon presented the most extreme values of C-selection (Figs. 5), which may reflect its higher geological stability and less variable present-day and past climate (Colinvaux 1996, Stropp et al. 2009).

Although correlative, the evidences we found may provide important insights to explain trait patterns across tropical rainforests. Moreover, as they imply environmentally mediated fitness differences among species with contrasting functional strategies, and ecosystem functions are ultimately determined by the dominant traits in plant communities (Garnier et al. 2004, Poorter et al. 2017), our findings have critical implications for predictions on the impact of future climate change and human-induced disturbances on community composition and ecosystem functioning. For instance, as previously suggested from global species-level analyses (Moles et al. 2014), we found that temperature mean and seasonality are the main driver of trait dominance in Neotropical tree assemblages, and temperature is indeed the main factor expected to change in the near future (IPCC 2014). With the predicted increase in temperature mean and seasonality in the tropics, we can forecast increasing dominance of fast-growing tree species with more acquisitive strategies and smaller seeds across Neotropical rainforests. Ultimately, this should translate into a more dynamic and resilient vegetation, with lower stability of ecosystem functions and limited provisioning of important ecosystem services such as carbon storage (Poorter et al. 2017). However, we must call attention for the high within-region variation in community patterns, which could be clarified with the integration of local environmental drivers (e.g. soil attributes and disturbance) and phylogenetic analyses at multiple spatial scales. This would allow us to better elucidate the mechanisms responsible for the origin and maintainance of functional differences across rainforests, advancing our understanding of the relative importance of niche (habitat filtering and competition) and historical process (e.g. dispersal limitation) as drivers of functional composition at multiple spatial scales.

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Table 1. Results of the best-fitted models (ΔAICc < 2) analyzing the effects of climatic factors on the community-weighted mean of traits and CSR strategies across 10 Neotropical rainforest regions. For each variable retained in some best-fit model, we have indicated the mean coefficient (β), the unconditional standard error (*SE*), the 95% confidence intervals (95% CI), the *p*-value and relative variable importance (RVI). P-values of significant variables (according to 95% confidence intervals) are in bold. The ranges of marginal R² (variance explained by climatic factors) and conditional R² (the latter plus aditional among-regions variance not explained by climatic factors) values for the best-fitted models are also shown. For a complete description of the best-fitted models, see Table S6. Abbreviations: MAP, mean annual precipitation; PET, potential evapo-transpiration; PS, precipitation seasonality; TS, temperature seasonality; n.a. = not applicable (when only one model has been selected).

Model factors	**β/10−3**	**SE/10−3**	**95% CI**		**p-value**	**Models R²**
			Lower/10−3	**Upper/10−3**		**marginal/conditional**
Leaf area						0.17-0.19/0.23-0.25
MAP	0.17	0.04	0.09	0.26	**3.53E-05**	
PET	0.02	0.04	-0.03	0.16	0.56	
PS	0.01	0.02	-0.04	0.12	0.73	
Leaf dry matter content						0.69-0.70/0.79
PET	-23.85	6.3	-36.22	-11.49	**0.0001**	

PS	5.09	6.66	-7.64	17.83	0.43	
TS	-40.9	6.5	-53.95	-27.84	**< 2e-16**	
Specific leaf area						0.00-0.17/0.79-0.87
MAP	0.47	1.68	-1.94	10.23	0.18	
PET	1.55	3.36	-2.23	14.07	0.15	
PS	2.76	4.01	-2.4	13.59	0.17	
TS	-1.53	4.35	-20.44	6.71	0.32	
Wood density						0.53/0.68
MAP	-0.03	0.01	n.a.	n.a.	**0.02**	
PET	-0.03	0.01	n.a.	n.a.	**0.006**	
TS	-0.04	0.01	n.a.	n.a.	**0.009**	
Seed mass						0.79/0.80
MAP	0.19	0.07	n.a.	n.a.	**0.01**	
PET	-0.8	0.11	n.a.	n.a.	**4.35E-07**	
PS	0.4	0.09	n.a.	n.a.	**0.0003**	
TS	-0.9	0.06	n.a.	n.a.	**9.81E-07**	

Maximum height						0.27/0.41-0.42
MAP	0.04	0.19	-0.54	0.81	0.84	
PS	-0.84	0.37	-1.57	-0.11	**0.02**	
TS	-1.1	0.44	-1.97	-0.23	**0.01**	
C-score						0.16-0.32/0.45-0.56
MAP	0.42	0.78	-0.42	3.01	0.58	
PET	2.93	1.37	0.22	5.64	**0.03**	
PS	-0.53	1.06	-4.25	0.76	0.61	
TS	1.34	1.45	-0.26	4.67	0.35	
S-score						0.24-0.49/0.69-0.74
MAP	-0.52	1.01	-3.94	0.68	0.6	
PET	-5.27	1.69	-8.62	-1.93	**0.002**	
PS	0.55	1.23	-1.22	5.13	0.65	
TS	-2.34	2.2	-6.98	-0.13	0.28	
R-score						0.00-0.26/0.78-0.84
MAP	0.62	0.56	-0.48	1.74	0.26	
PET	1.03	0.71	-0.35	2.43	0.14	

PS	0.94	0.69	-0.41	2.3	0.17
TS	-0.59	1.13	-2.83	1.63	0.6

Figure legends

Figure 1. Location of the studied regions along the Neotropics, four in Mexico and six in Brazil.

Figure 2. Non-metric multidimensional scaling (NMDS) ordination showing tree taxonomic compositional (Chao–Jaccard dissimilarities) variation among each of the 233 communities studied in 10 Neotropical rainforest regions: four in Mexico (LTX- and Lacandona) and six in Brazil – one in Amazonia (Balbina) and five across the Atlantic forest. Stress = 0.10.

Figure 3. Species C-, S- and R-scores and their relative abundances in the regional pool of the 10 studied regions, measured using the globally calibrated CSR analysis tool 'StrateFy'. The triangles are organized from the extreme north to the south of the Neotropics: (a) LTX-LDL, (b) LTX-HDL, (c) LTX-IDL, (d) Lacandona, (e) Balbina, (f) Miriri, (g) João Pessoa, (h) Serra Grande, (i) UNA, (j) Serra Tabuleiro. See Table S1 for details on each region.

Figure 4. Differences in community-weighted mean C-, S-, R-selection between 10 Neotropical rainforest regions, from the extreme north (left) to the south (right) of the distribution of rainforests in the Neotropics. Plots from each region are pooled and represented as box plots illustrating the median (center line), quartile (box edges) and extreme values (bars). Different letters indicate significant differences.

Figure 5. Significant relationships from mixed effects models between community-weighted mean trait or C-, S-, R-strategy and latitude, for 233 tree communities distributed across 10 Neotropical rainforest regions. LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; WD, wood density; SM, seed mass.

Figure 6. Significant relationships from mixed effects models (see Table 2) between community-weighted mean (CWM) trait or C-, S-, R-strategy and climatic factors, for 233 tree communities distributed across 10 Neotropical rainforest regions. Abbreviations: LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; WD, wood density; SM, seed mass. MAP, mean

annual precipitation; PET, potential evapo-transpiration; PS, precipitation seasonality; TS, temperature seasonality; SD, standard deviation; CV, coefficient of variation.

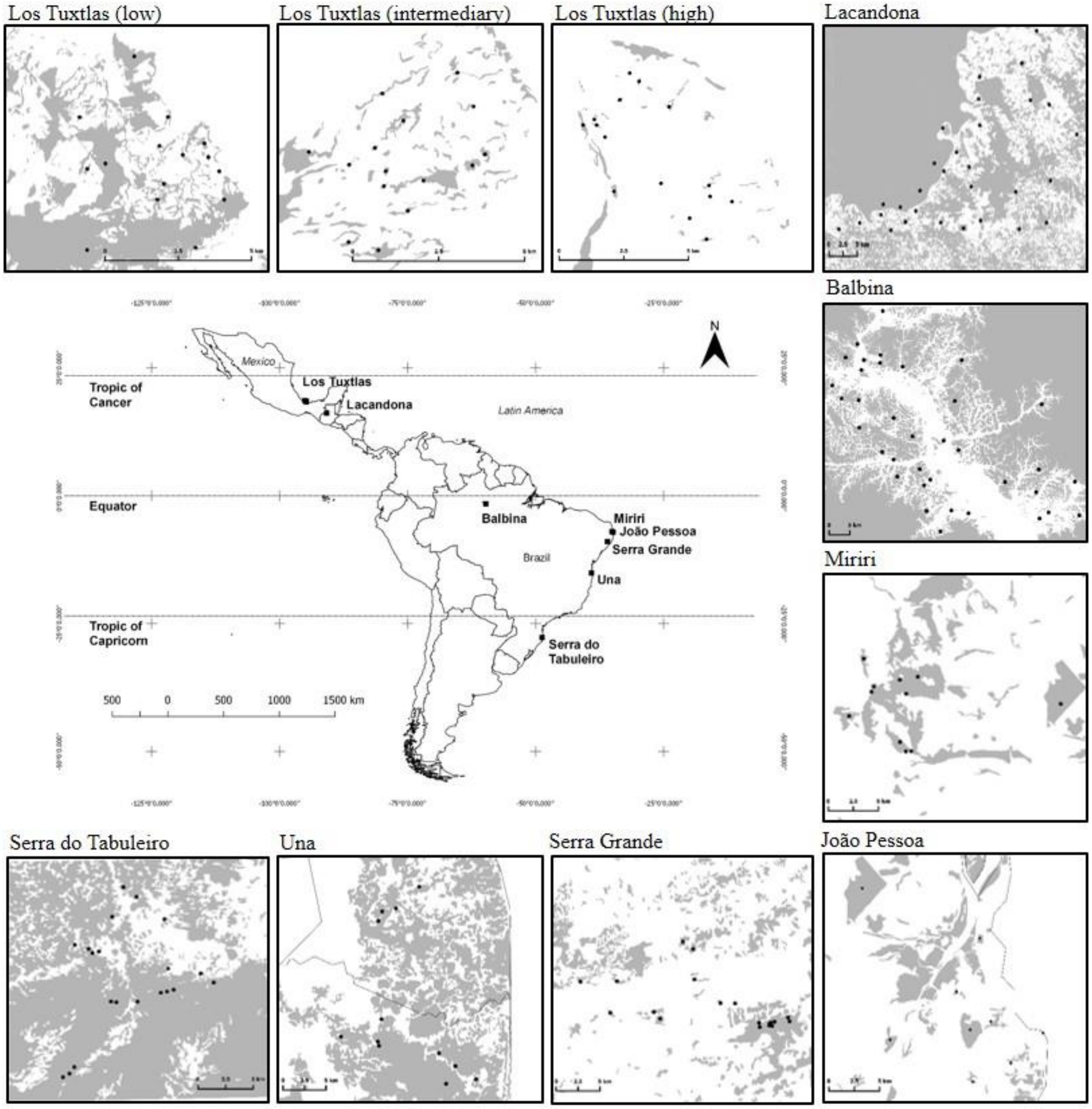
Los Tuxtlas (low)
Los Tuxtlas (intermediary)
Los Tuxtlas (high)
Lacandona
Balbina
Miriri
Serra do Tabuleiro
Una
Serra Grande
João Pessoa
N
Mexico
Los Tuxtlas
Lacandona
Latin America
Tropic of Cancer
Equator
Tropic of Capricorn
Balbina
Miriri
João Pessoa
Serra Grande
Brazil
Una
Serra do Tabuleiro
500
0
500
1000
1500 km

Figure 1.

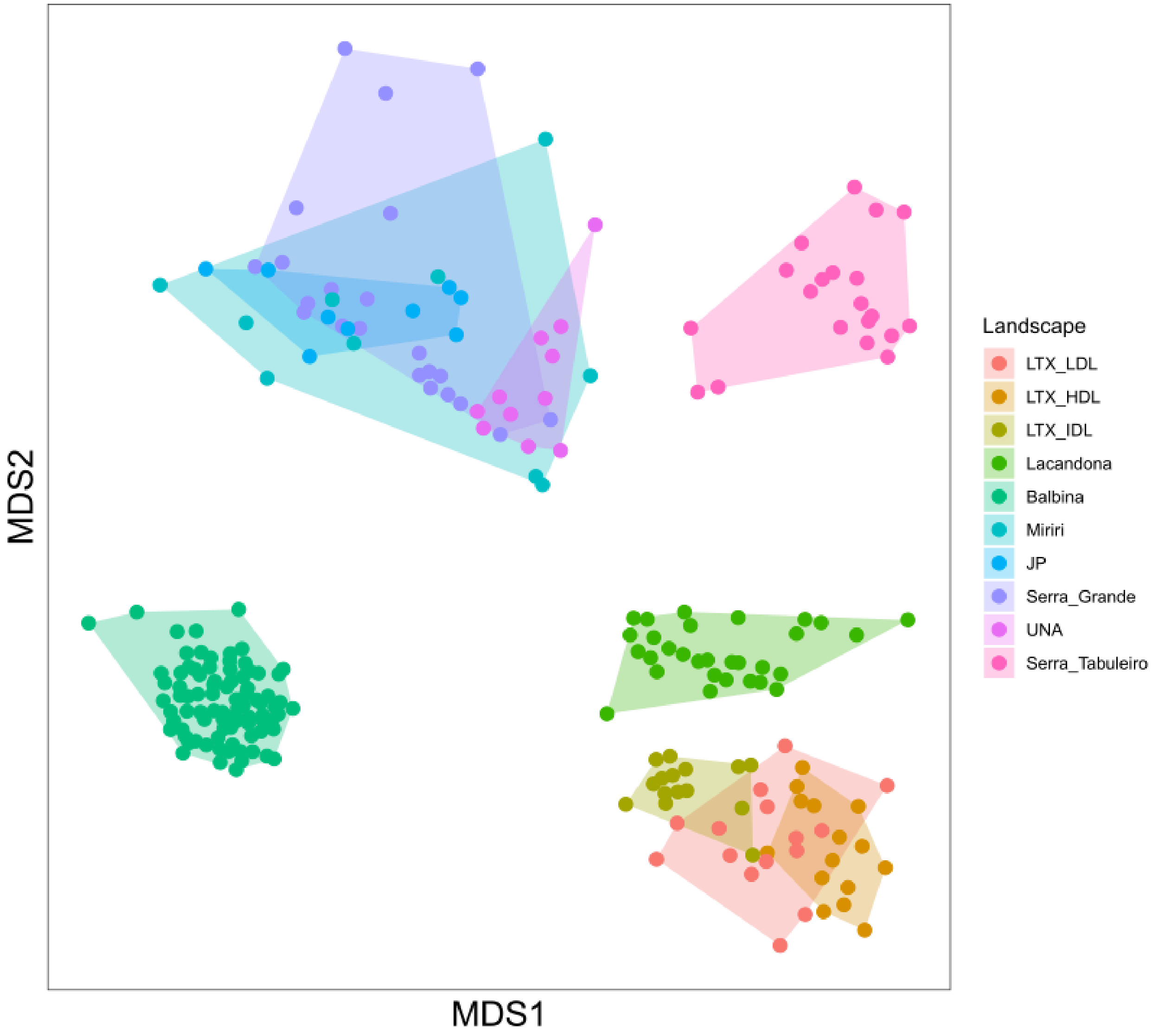
MDS1
MDS2
Landscape
LTX_LDL
LTX_HDL
LTX_IDL
Lacandona
Balbina
Miriri
JP
Serra_Grande
UNA
Serra_Tabuleiro

Figure 2.

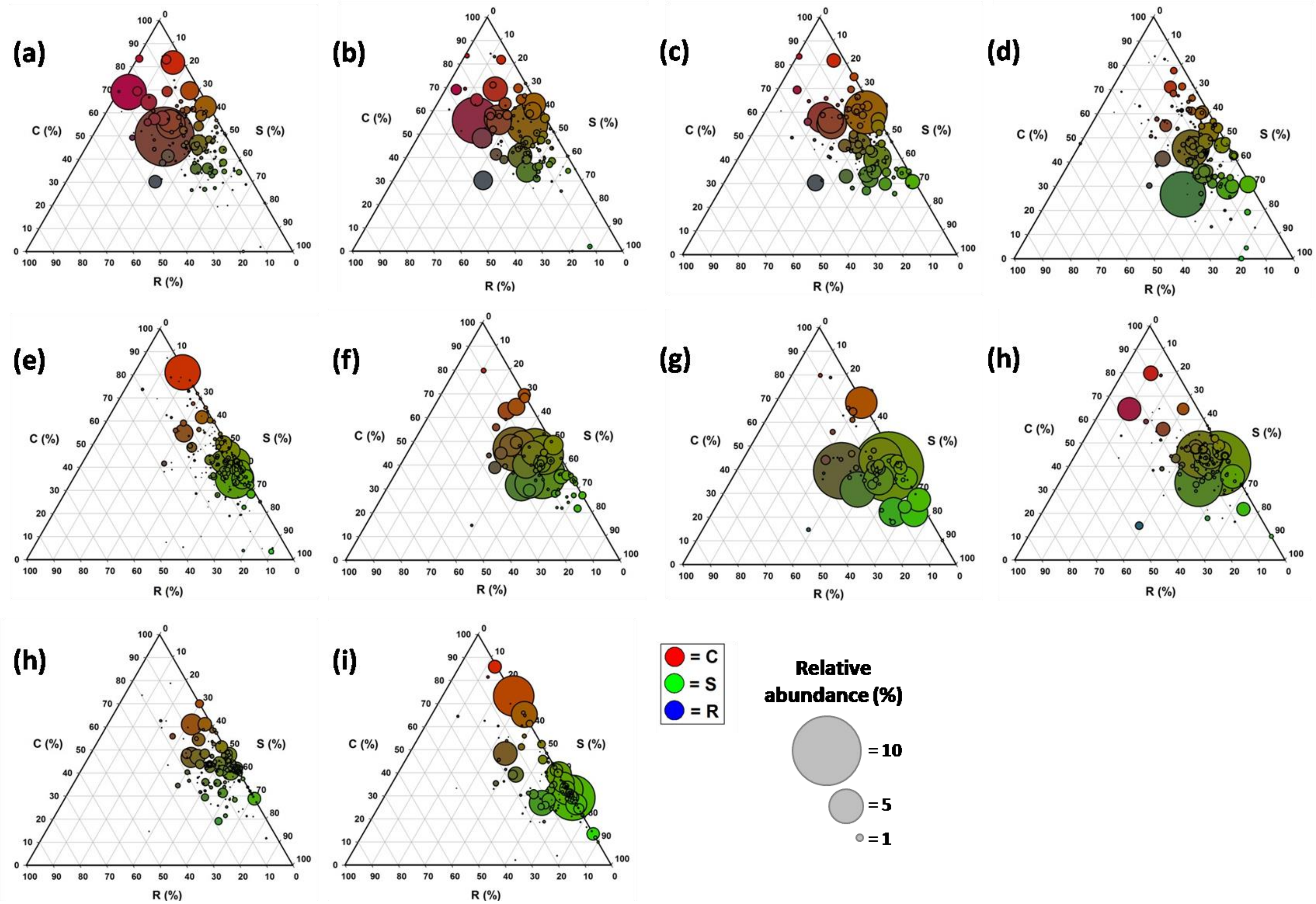
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(h)
(i)
C (%)
S (%)
R (%)
0
10
20
30
40
50
60
70
80
90
100
= C
= S
= R
Relative abundance (%)
= 10
= 5
= 1

Figure 3.

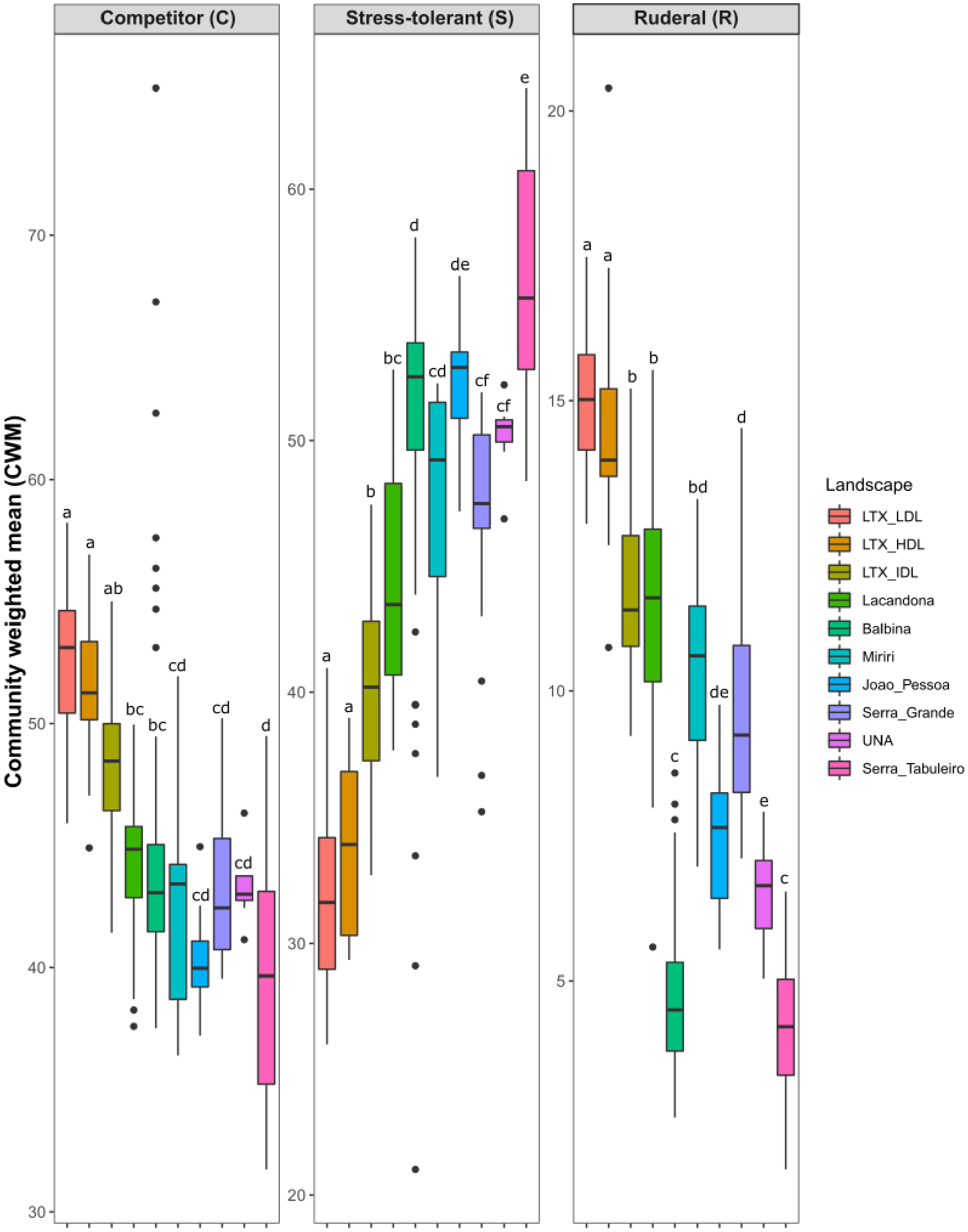
Competitor (C)
Stress-tolerant (S)
Ruderal (R)
Community weighted mean (CWM)
30
40
50
60
70
20
30
40
50
60
5
10
15
20
a
a
ab
bc
bc
cd
cd
cd
cd
d
a
a
b
bc
d
cd
de
cf
cf
e
a
a
b
b
c
bd
de
d
e
c
Landscape
LTX_LDL
LTX_HDL
LTX_IDL
Lacandona
Balbina
Miriri
Joao_Pessoa
Serra_Grande
UNA
Serra_Tabuleiro

Figure 4.

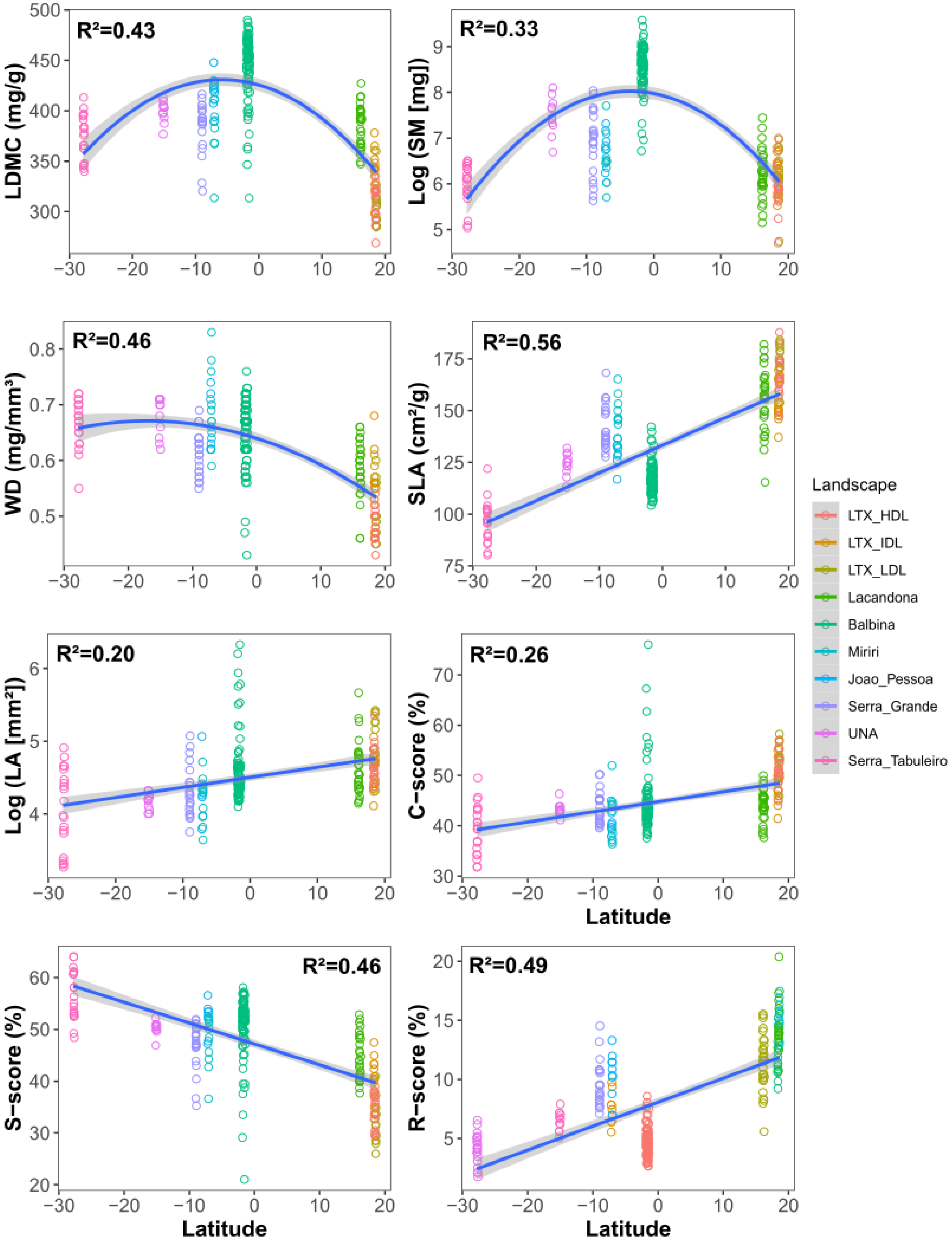
R²=0.43
LDMC (mg/g)
500
450
400
350
300
R²=0.33
Log (SM [mg])
9
8
7
6
5
R²=0.46
WD (mg/mm³)
0.8
0.7
0.6
0.5
R²=0.56
SLA (cm²/g)
175
150
125
100
75
R²=0.20
Log (LA [mm²])
6
5
4
R²=0.26
C−score (%)
70
60
50
40
30
R²=0.46
S−score (%)
60
50
40
30
20
R²=0.49
R−score (%)
20
15
10
5
−30
−20
−10
0
10
20
Latitude
Landscape
LTX_HDL
LTX_IDL
LTX_LDL
Lacandona
Balbina
Miriri
Joao_Pessoa
Serra_Grande
UNA
Serra_Tabuleiro

Figure 5.

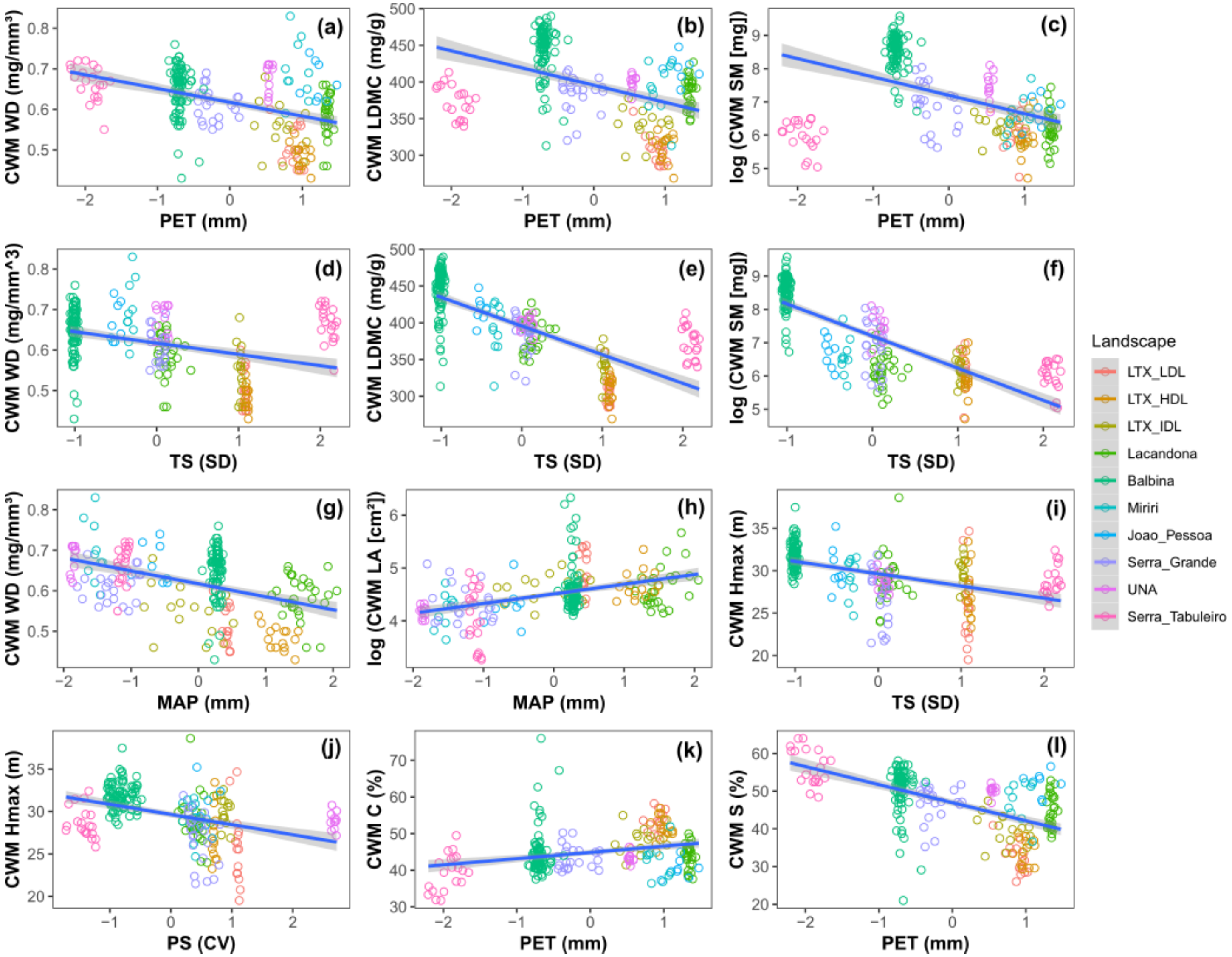
(a)
CWM WD (mg/mm³)
PET (mm)
(b)
CWM LDMC (mg/g)
PET (mm)
(c)
log (CWM SM [mg])
PET (mm)
(d)
CWM WD (mg/mm^3)
TS (SD)
(e)
CWM LDMC (mg/g)
TS (SD)
(f)
log (CWM SM [mg])
TS (SD)
(g)
CWM WD (mg/mm³)
MAP (mm)
(h)
log (CWM LA [cm²])
MAP (mm)
(i)
CWM Hmax (m)
TS (SD)
(j)
CWM Hmax (m)
PS (CV)
(k)
CWM C (%)
PET (mm)
(l)
CWM S (%)
PET (mm)
Landscape
LTX_LDL
LTX_HDL
LTX_IDL
Lacandona
Balbina
Miriri
Joao_Pessoa
Serra_Grande
UNA
Serra_Tabuleiro

Figure 6.

Table S1. Latitude, location, sampling effort and level of disturbance at the landscape-level (i.e. forest loss and fragmentation, matrix heterogeneity) in the Neotropical rainforest regions studied in Mexico and Brazil. Within Los Tuxtlas in Mexico, we studied three independent regions, as there have been demonstrated strong floristic and phylogenetic differences between them, as well as different deforestation levels (LDL = low deforestation level, 24% of remaining forest cover; IDL = intermediate deforestation level, 11%; HDL = high deforestation level, 4%) and land-use history (Arroyo-Rodríguez et al. 2013).

Regions	**Latitude (mean)**	**Location**	**Plot size (ha)**	**N sites**	**Landscape disturbance level**
Los Tuxtlas - LDL	18.6	Veracruz, Mexico	0.1	15	High
Los Tuxtlas - HDL	18.5	Veracruz, Mexico	0.1	15	Very high
Los Tuxtlas - IDL	18.37	Veracruz, Mexico	0.1	15	High
Lacandona	16.15	Chiapas, Mexico	0.1	30	Low
Balbina	-1.67	Amazonas, Brazil	0.25	87	Low
Miriri	-7.03	Paraíba, Brazil	0.03	10	High
João Pessoa	-7.12	Paraíba, Brazil	0.1	8	Very high
Serra Grande	-8.97	Alagoas, Brazil	0.1	22	High
UNA	-15.09	Bahia, Brazil	0.08	11	Intermediate

Serra do Tabuleiro	-27.72	Santa Catarina, Brazil	0.1	20	Intermediate

Table S2. Bivariate relationships (*r*-values) between relative and absolute (i.e. degrees from equator) latitude and climatic factors in 233 rainforest sites distributed across the Neotropics. Bold *r*-values represent significant correlations according to Bonferroni adjustment for multiple tests. PET, potential evapo-transpiration.

	Latitude	Degrees from equator	Annual precipitation	Precipitation seasonality	PET
Degrees from equator	0.04				
Annual precipitation	**0.76**	-0.07			
Precipitation seasonality	**0.4**	**0.31**	-0.12		
PET	**0.74**	**0.19**	**0.37**	**0.77**	
Temperature seasonality	-0.01	**0.97**	-0.15	**0.24**	0.08

Table S3. Range and average of species mean trait values in 10 Neotropical rainforest regions (organized from North to South). LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; WD, wood density; SM, seed mass.

Region	**LA (cm^2)**		**SLA (cm^2/g)**		**LDMC (mg/g)**		**WD (mg/mm^3)**		**SM (mg)**		**Hmax (m)**	
	Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*
Los Tuxtlas LDL	0.25 - 1,777	101.45	71.76 - 453.60	165.24	148.63 - 532.92	327.93	0.09 - 0.96	0.53	0.06 - 17,770	734.81	5 - 65	26
Los Tuxtlas HDL	0.25 - 1,777	111.54	74.25 - 394.90	157.49	168.39 - 532.92	329.79	0.11 - 0.83	0.51	0.05 - 17,770	912.50	4 - 60	26
Los Tuxtlas IDL	0.25 - 1,440	90.23	43.50 - 394.90	152.91	168.39 - 500.00	342.16	0.16 - 0.96	0.55	0.06 - 17,770	705.41	2 - 70	27
Lacandona	0.25 - 2,506	136.05	43.50 - 453.60	155.43	148.63 - 580.00	367.30	0.09 - 0.94	0.56	0.03 - 21,741	651.68	5 - 70	26
Balbina	0.05 - 1,118	91.22	51.57 - 417.86	123.50	179.90 - 592.40	427.60	0.28 - 1.01	0.66	0.24 - 183,230	3,775.68	3 - 70	31
Miriri	0.11 - 607	63.49	61.91 - 443.33	141.50	233.43 - 507.46	391.10	0.38 - 0.96	0.69	0.40 - 26,100	1,105.72	4 - 50	26
João Pessoa	2.52 - 967	82.21	60.98 - 443.33	142.90	233.43 - 540.00	394.32	0.28 - 0.96	0.65	0.72 - 26,100	1,475.69	8 - 50	27
Serra Grande	2.52 - 967	67.65	66.62 - 443.33	139.04	143.51 - 533.86	385.22	0.14 - 0.98	0.65	0.09 - 50,000	1,901.54	10 - 50	27
UNA	0.05 - 967	58.80	48.24 - 443.33	127.52	159.32 - 678.89	399.59	0.26 - 1.10	0.69	0.09 - 76,923	1,933.49	6 - 60	27
Serra Tabuleiro	0.06 - 1,475	50.01	31.91 - 274.90	108.38	183.00 - 584.00	381.81	0.35 - 1.00	0.65	0.02 - 25,000	645.91	4 - 40	25
Neotropics	0.06 - 2,506	86.04	31.91 - 453.60	132.52	148.63 - 678.89	387.34	0.09 - 1.10	0.63	0.02 - 183,230	1939.75	2 - 70	27

Table S4. Range and average of community-weighted mean (CWM) trait values of tree assemblages in 10 Neotropical rainforest regions (organized from North to South). LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; WD, wood density; SM, seed mass.

Region	**LA (cm^2)**		**SLA (cm^2/g)**		**LDMC (mg/g)**		**WD (mg/mm^3)**		**SM (mg)**		**Hmax (m)**	
	Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*
Los Tuxtlas LDL	75.17 - 226.85	144.59	153.89 - 183.96	173.36	284.97 - 359.97	306.72	0.45 - 0.60	0.51	114 - 1,067	517	20 - 35	26
Los Tuxtlas HDL	78.94 - 211.04	112.54	147.20 - 187.81	167.79	268.99 - 335.13	309.73	0.43 - 0.54	0.48	110 - 1,097	423	23- 33	27
Los Tuxtlas IDL	61.06 - 157.86	104.2	137.08 - 169.68	153.64	298.21 - 378.09	339.85	0.46 - 0.68	0.55	251 - 900	527	27 - 33	30
Lacandona	63.27 - 289.33	110.19	115.41 - 181.96	155.44	347.09 - 427.15	385.23	0.46 - 0.66	0.59	171 - 1,708	574	24 - 39	29
Balbina	60.44 - 561.82	113.91	104.21 - 142.16	117.30	313.36 - 489.77	444.85	0.43 - 0.76	0.65	829 - 14,460	5763	28 - 37	32
Miriri	38.26 - 111.75	70.07	128.96 - 165.26	145.99	313.52 - 428.68	390.44	0.59 - 0.83	0.70	299 - 2,227	831	25 - 32	29
João Pessoa	44.44 - 158.71	78.90	116.82 - 145.32	131.37	389.14 - 447.78	418.39	0.62 - 0.74	0.67	413 - 1,512	895	27 - 35	30
Serra Grande	42.66 - 160.13	79.39	127.54 - 168.26	141.79	320.41 - 416.31	384.69	0.55 - 0.69	0.61	278 - 3,098	1225	21 - 32	27
UNA	54.83 - 75.52	65.17	113.12 - 131.85	124.16	376.84 - 413.00	399.26	0.62 - 0.71	0.68	809 - 3,304	1912	27 - 31	29
Serra Tabuleiro	26.24 - 135.99	66.86	80.19 - 121.91	96.47	339.83 - 413.23	373.84	0.55 - 0.72	0.66	154 - 671	435	26 - 32	29
Neotropics	26.24 - 561.82	102.01	80.19 - 187.81	133.97	268.99 - 489.77	395.65	0.43 - 0.83	0.62	110 - 14,460	2630	20 - 39	30

Table S5. Bivariate relationships (*r*-values) between species mean trait values (n = 930) and between community-weighted mean trait values (n = 233) from the 10 studied regions spread across the Neotropics. LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; WD, wood density; Hmax, maximum height; SM, seed mass. Bold *r*-values represent significant correlations according to Bonferroni adjustment for multiple tests.

Trait	**Species-level**					**Community-level**				
	SLA	LDMC	WD	SM	Hmax	SLA	LDMC	WD	SM	Hmax
LA	0.00	**-0.25**	**-0.28**	-0.08	-0.02	**0.32**	**-0.34**	**-0.63**	-0.08	-0.08
SLA		**-0.5**	**-0.33**	**-0.24**	**-0.11**		**-0.68**	**-0.66**	**-0.52**	**-0.5**
LDMC			**0.5**	**0.47**	**0.25**			**0.75**	**0.78**	**0.62**
WD				**0.41**	**0.09**				**0.5**	**0.4**
SM					**0.27**					**0.56**

Table S6. Trait loadings of principal component analysis (PCA) on Neotropical tree species mean traits (n = 930) and community-weighted mean traits (n = 233), for rainforest sites distributed across the Neotropics.

Functional trait	**Species-level**		**Community-level**	
	PC1 (40.4%)	PC2 (18.00%)	PC1 (59.6%)	PC2 (19.55%)
Leaf area	0.22	**-0.75**	0.25	**-0.75**
Specific leaf area	**0.41**	0.19	**0.43**	-0.03
Leaf dry matter content	**-0.54**	0.01	**-0.49**	-0.11
Wood density	**-0.48**	0.28	**-0.45**	0.34
Seed mass	**-0.44**	-0.21	**-0.41**	-0.38
Maximum height	-0.25	**-0.54**	-0.37	**-0.41**

Table S7. Best-supported models (ΔAICc<2) analyzing the effects of climatic factors on the community-weighted mean (CWM) traits and CSR strategies across 10 Neotropical rainforest regions. Abbreviations: MAP, mean annual precipitation; PET, potential evapo-transpiration; PS, precipitation seasonality; TS, temperature seasonality.

CWM trait/strategy (response variable)	Models rank	Variables Selected	df	AICc	ΔAICc	Weight	R^2 marginal /conditional
Leaf area	1	MAP	4	242.8	0.00	0.24	0.17/0.24
	2	MAP+PET	5	243	0.17	0.23	0.19/0.25
	3	MAP+PS	5	244.1	1.26	0.13	0.18/0.23
Leaf dry matter content	1	PET+TS	5	2214.2	0.00	0.49	0.70/0.79
	2	PET+PS+TS	6	2215.7	1.51	0.23	0.69/0.79
Specific leaf area	1	Intercept	3	1774.0	0.00	0.15	0.00/0.84
	2	PS	4	1774.4	0.39	0.12	0.05/0.82
	3	PET	4	1774.7	0.68	0.11	0.09/0.79
	4	TS	4	1775.0	1.03	0.09	0.08/0.87
	5	MAP+PS	5	1775.3	1.29	0.08	0.14/0.79
	6	PET+PS	5	1775.4	1.44	0.07	0.17/0.80

	7	PS+TS	5	1775.7	1.71	0.06	0.08/0.85
	8	MAP	4	1776.0	2.00	0.05	0.001/0.83
Wood density	1	MAP+PET+TS	6	-692.4	0.00	0.49	0.53/0.68
Seed mass	1	MAP+PET+PS+TS	7	372.0	0.00	0.78	0.79/0.80
Maximum height	1	PS+TS	5	1074.7	0	0.3	0.27/0.41
	2	MAP+PS+TS	6	1076.6	1.96	0.11	0.27/0.42
C-score	1	PET+TS	5	1405.1	0.00	0.16	0.32/0.55
	2	MAP+PET+TS	6	1405.4	0.32	0.14	0.30/0.50
	3	PET+PS+TS	6	1405.5	0.42	0.13	0.29/0.56
	4	PET	4	1406.1	1.06	0.1	0.16/0.49
	5	MAP+PET	5	1406.1	1.07	0.09	0.19/0.45
	6	PET+PS	5	1406.4	1.28	0.09	0.16/0.53
S-score	1	PET+TS	5	1447.5	0.00	0.22	0.48/0.74
	2	MAP+PET+TS	6	1447.9	0.35	0.19	0.49/0.71
	3	PET+PS+TS	6	1448.3	0.77	0.15	0.44/0.73
	4	PET	4	1448.9	1.33	0.11	0.28/0.71

	5	PET+PS	5	1449.3	1.78	0.09	0.24/0.71
	6	MAP+PET	5	1449.5	1.92	0.08	0.32/0.69
R-score	1	PET	4	942.2	0.00	0.14	0.11/0.78
	2	Intercept	3	942.2	0.05	0.13	0.00/0.83
	3	MAP+PS	5	942.7	0.50	0.11	0.17/0.78
	4	PS	4	942.8	0.59	0.1	0.05/0.81
	5	PET+PS	5	943.3	1.17	0.08	0.17/0.80
	6	MAP	4	943.8	1.60	0.06	0.01/0.81
	7	MAP+PET	5	943.9	1.69	0.06	0.14/0.77
	8	MAP+PET+PS	6	944.0	1.79	0.06	0.26/0.78
	9	TS	4	944.1	1.89	0.05	0.02/0.84

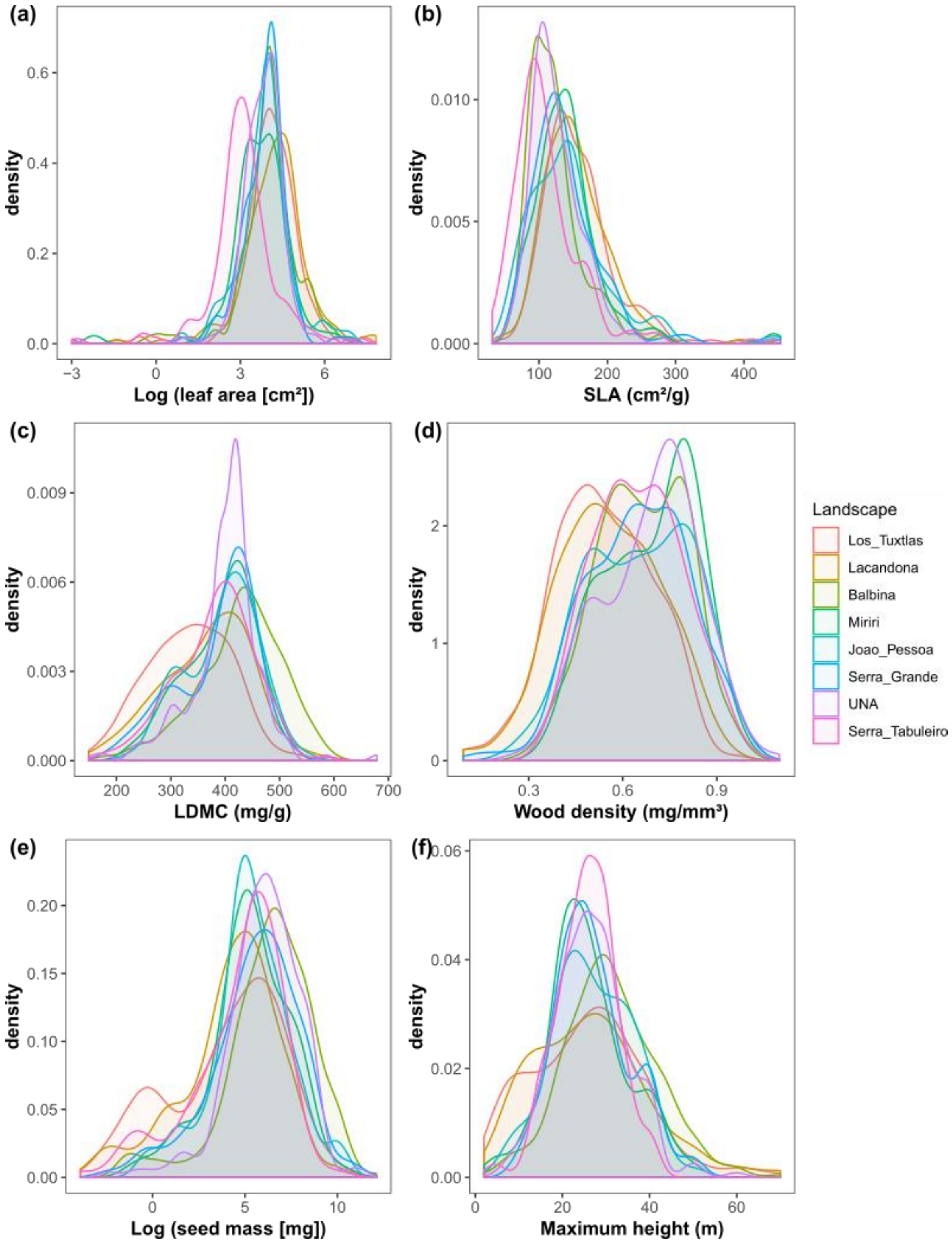

Figure S1. Probability density distribution of functional trait mean values of Neotropical tree species in 10 Neotropical rainforest regions.

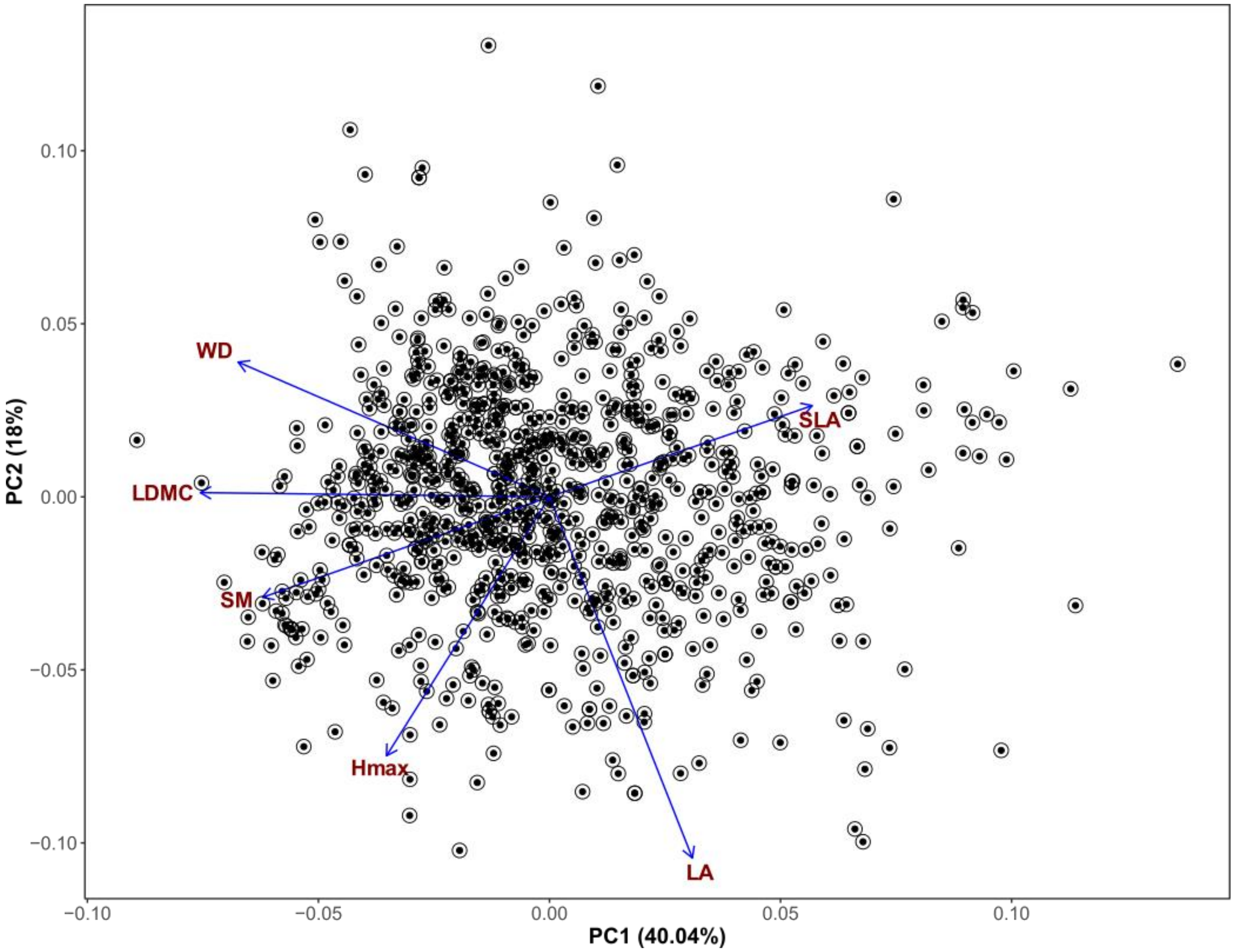

Figure S2. Ordination diagram of the two first axes of principal component analysis (PCA) of Neotropical tree species mean trait values (n = 930). LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; WD, wood density; SM, seed mass; Hmax, maximum height.

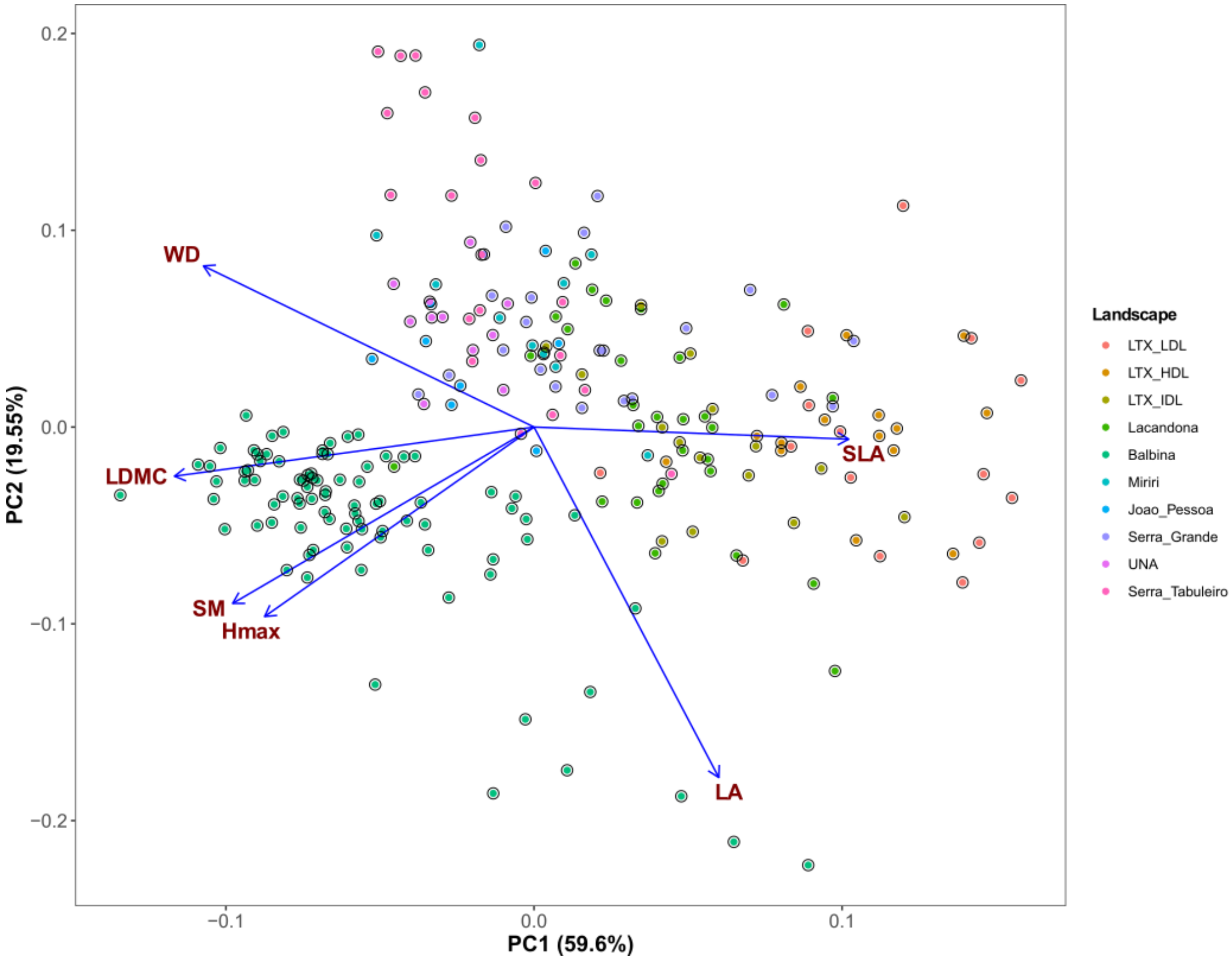

Figure S3. Ordination diagram of the two first axes of principal component analysis (PCA) of community-weighted mean trait values for 233 tree assemblages distributed across 10 Neotropical rainforest regions. LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; WD, wood density; SM, seed mass; Hmax, maximum height.

3.2 ARTIGO 2

Manuscrito a ser submetido ao periódico *Ecography*

Original research – *Ecography*

Context-dependent functional responses of Neotropical tree assemblages to forest loss

Bruno X. Pinho[1], Marcelo Tabarelli[1], Gabriel Mendes[1], Victor Arroyo-Rodriguez[2], Bráulio A. Santos[3], Valdecir Junior[3], Valério Pillar[4], Sandra Muller[4], Miguel Martínez[2], Madelon Lohbeck[5,6], Frans Bongers[5], Carlos A. Peres[7], Maíra Benchimol[8], Deborah Faria[8], Rodrigo Orihuela[9], Renato A.F. de Lima[10], [...] and Felipe P.L. Melo[1*]

[1]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Brazil

[2]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico

[3]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil

[4]Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[5]Forest Ecology and Forest Management group, Wageningen University, Wageningen, The Netherlands

[6]World Agroforestry Centre (ICRAF), Nairobi, Kenya

[7]School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, UK

[8]Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Ilhéus, Brazil

[9]Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[10]Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

*Corresponding author: fplmelo@gmail.com

Abstract

Habitat loss due to land-use intensification is a major threat for biodiversity and ecosystem functions in human-modified tropical landscapes. Yet, there is a major uncertainty on the traits underlying tree species sensitivity to forest loss, and thus on the mechanisms reorganizing tree assemblages in fragmented landscapes. Also, the consistency of forest loss effects on biodiversity patterns across regions is an open question. Here we used a large database (29,551 trees of 907 species) to test the effect of landscape-scale forest loss on tree community functional profile in 178 rainforest sites distributed across 10 Neotropical regions in contrasting biogeographic and land-use contexts. We considered resource-use and size-related species traits, as well as continuous variation in adaptive (CSR) strategies. We scaled traits/strategies to community-level by calculating the community weighted-mean (CWM) of each one and the multi-trait functional diversity (RaoQ). We evaluated the response of community functional properties to forest cover across different-sized landscapes (multi-scale approach), to determine the scale at which effects of forest loss manifest stronger (i.e. “scale of effect” – SE). Tree community functional profile changed comprehensively in response to forest loss, with ~ 12 to 80% of variation in trait diversity or dominance explained by forest cover. However, such effects vary widely in direction, magnitude and SE across traits and regions, and some traits are not responsive (i.e. SLA). Despite such a context-dependence, changes in trait dominance in general supports a sort of ‘retrogressive succession’ as trait values typical of early-successional species increment as forest loss proceeds, probably in response to the increment of edge-affected habitats. We refer to traits and strategies related to regeneration (seed mass) and survival (leaf dry matter content and wood density) under abiotic conditions typical of old-growth forests (i.e. deep shade and infertile soils). Forest loss thus operates as a key assembly force, filtering major tree life-history strategies in fragmented landscapes. Variation in trait sensitivity across regions is still an open question that may be related to disturbance regimes or biogeographic histories. Notwithstanding, regardless of regional differences, habitat loss tends to comprehensively drive Neotropical forests towards a functional composition that is typical of early-successional communities.

Key-words: community weighted-mean, edge-effects, forest fragmentation, functional diversity, functional traits, habitat amount, retrogressive succession, Neotropics.

Introduction

Tropical forests harbour most of the global biodiversity but are increasingly threatened by land-use intensification, which leads to an ever-growing conversion of old-growth forests into small and isolated forest patches within human-dominated landscapes (Laurance et al. 2014, Lewis et al. 2015). Thus, global biodiversity retention and ecosystem services provisioning largely rely on our ability to understand and predict the effects of land-use changes on biodiversity (Melo et al. 2013, Newbold et al. 2015). Yet, efforts in this sense have been mainly focused on taxonomic patterns, while the functional response of ecological communities remains poorly known (Hatfield et al. 2018, but see Santos et al. 2008, Magnago et al., 2014, Mendes et al. 2016). As plant functional traits have proven to drive species response to environmental changes and its effects on ecosystem functioning (Suding et al. 2008, Funk et al. 2016), filling this gap is critical to identifying mechanisms underlying vegetation changes in fragmented landscapes and propose management actions accordingly.

Besides the reduction of habitat area, forest loss usually implies increased habitat fragmentation and relative proportion of edge-affected habitats (Tscharntke et al. 2012, Fahrig 2013). The effects of such processes on tree community patterns have been extensively studied across tropical forests over the last decades (see Laurance et al. 2018). Collectively, they usually lead to reduced tree biomass and increased biotic homogenization due to the decline of large old-growth forest trees and the proliferation of disturbance-adapted, pioneer tree species with forest loss and fragmentation (Laurance et al. 2002, 2006, Santos et al. 2008, 2010, Tabarelli et al. 2012, Lôbo et al. 2011). This is commonly translated into a trajectory of ‘retrogressive succession’, where communities persist indefinitely in an early or mid-successional state (Tabarelli et al. 2008). On the other hand, evidences from specific biogeographic contexts suggest that forest patches in highly fragmented tropical landscapes can maintain the integrity of the original biota (Arroyo-Rodriguez *et al*. 2009, 2012, 2013, Santo-Silva et al. 2018) independently of forest remnant size (Hernández-Ruedas *et al*. 2014). Thus, biodiversity response to forest loss seems to not be consistent across tropical regions, but rather should depends on regional disturbance patterns and the composition of species-pools (Arroyo-Rodriguez et al. 2017, Spasojevic et al. 2018). The integration of multiple landscapes across contrasting biogeographic and land-use scenarios is thus needed to understand inconsistencies and identify generalities (Melo et al. 2013).

The functional dimension of biodiversity has been revealed in recent years as ubiquitous, continuous axes of specialization that show trade-offs in plant strategies from the co-variation of species functional (adaptive) traits (Diaz et al. 2016, Pierce et al. 2017). The scaling of species traits to community-level has proven to be a powerful approach to understand and predict the response of ecological communities to environmental changes and its consequences to ecosystem functioning (Westoby and Wright 2006). For instance, slow-growing plants typically dominate under abiotic limitation to growth by conserving resources in well-protected, dense tissues with long life-span, but are outcompeted in resource-rich environments by fast-growing plants with more acquisitive traits (Westoby et al. 2002, Reich 2014). Also, large seeds may provide competitive advantages under low resource (e.g. light) availability but smaller-seeded species present greater seed output and usually do not depend on large-bodied animals for dispersal, which may favour recruitment across less stressful conditions (Muller-Landau et al. 2010) or isolated forest patches (Santo-Silva et al. 2013).

In fact, vegetation changes in response to landscape-scale forest loss result mainly from abiotic changes (more illuminated, desiccated and hotter conditions) due to increased edge effects (Laurance et al. 2002, Magnago et al. 2015), and dispersal limitation due to increased inter-patch isolation distances (Haddad et al. 2015). Changes in tree species composition in response to such processes are likely to be mediated by functional traits, as landscape modification exposes species to different physical and ecological filters (Kraft et al. 2015). Indeed, the effects of habitat loss have proven to be non-random, particularly affecting some ecological groups such as shade-tolerant, biotically-dispersed, large-seeded tree species (Santos et al. 2008, Benchimol et al. 2017). However, such ‘functional guilds’ are arbitrarily defined and do not take into account within-group variation, as opposed to approaches based on continuous traits related to universal trade-offs in plant strategies (Westoby and Wright 2006, Diaz et al. 2016). More importantly, a comprehensive study assessing tree community functional changes across landscapes within contrasting biogeographic and land-use contexts is surprisingly still missing, despite its scientific and conservation relevance.

The habitat amount (i.e. forest cover) in local landscapes surrounding forest sites was recently recognized as a landscape variable that account for patch area and isolation effects of habitat loss (i.e. “the habitat amount hypothesis”, *sensu* Fahrig 2013). Also, the scale at which landscape structure affect biological patterns (i.e. “scale of effect”, SE) has been shown to vary according to the response variable and regional context. For instance, forests within more disturbed regions are expected to respond to landscape structure at smaller spatial scales due the disruption of dispersal movements between forest patches (Miguet et al. 2016). Moreover, it would be reasonable to expect regional variation in species pool trait diversity and composition to drive differential responses to landscape structure (Spasojevic et al. 2018), such as a higher degree of resilience in regions dominated by fast-growing strategies (Haddad et al. 2008). Nevertheless, this topic is still in its infancy and no cross-region comparison has been performed for plants to date (Jackson and Fahrig 2015, Miguet et al. 2016).

Here we assess how the functional diversity and composition of Neotropical rainforest tree assemblages change in response to forest loss at multiple spatial scales within contrasting biogeographic and land-use contexts. We considered a comprehensive set of economic- and size-traits related to basic trade-offs in plant strategies (Westoby et al. 2002, Diaz et al. 2016). Additionally, as constraints to species assembly may act more strongly on multivariate phenotypes (Muscarella and Uriarte 2016), we also analysed continuous variation in plant ecological strategies according to Grime’s competitor, stress tolerator, ruderal (CSR) theory (Grime and Pierce 2012, but see Pierce et al. 2017). Plant CSR strategies represent viable combinations of traits that have evolved in response to varying stress and disturbance levels. These should select for competition in relatively productive and stable conditions (C), stress-tolerance under abiotic limitation to growth (S), and high reproductive investment under frequent disturbance (R). Overall, we expected increasing prevalence of colonizing, fast-growing strategies such as small seeds and acquisitive traits with forest loss. Nevertheless, given the wide variation in biogeographic history, climatic conditions and disturbance regimes across Neotropical forests (Burnham and Graham 1999, Poorter et al. 2017), we expected trait-landscape relationships to vary in direction and magnitude across regions. Moreover, we expected (1) lower SE for resource-use traits compared to regenerative strategies (seed mass), given their constraints mainly by local conditions to growth and inter-patch connectivity to dispersal, respectively, and the orthogonal variation among economic- and size-traits (Diaz et al. 2016); (2) lower SE in more disturbed regions; and (3) weaker responses in regions dominated by few fast-growing species.

Material and Methods

Study landscapes and regions

We studied 178 local landscapes distributed across 10 Neotropical lowland rainforest subregions, four from Mexico (Lacandona and three in Los Tuxtlas) and six in Brazil (Balbina, Miriri, João Pessoa, Serra Grande, Una e Serra do Tabuleiro), which have distinct disturbance patterns and encompass the whole latitudinal distribution of Neotropical forests (Fig. 1, Table 1). Within Los Tuxtlas, we studied three independent subregions because they have different deforestation levels (LDL = low deforestation level, 24% of remaining forest cover; IDL = intermediate deforestation level, 11%; HDL = high deforestation level, 4%) and previous studies have shown strong floristic differences among them. Also, two subregions in northeastern Atlantic forest are within the same regional context, but are considered separately given their very distinctive disturbance patterns as one is located in the countryside (Miriri) and the other in an urban context (João Pessoa) (Fig. 1; Table 1). Therefore, we studied 10 subregions (hereafter, regions) distributed across seven regions. All plots were located in old-growth forests, including both continuous forests and fragments of varying size. Mean annual precipitation ranged from 1167 to 3351 mm and mean annual temperature from *c*. 17 to 27 ºC among regions.

Vegetation data

We used data on 29,551 adult trees (stems with diameter at breast height, DBH ≥ 10 cm; except for UNA where cut-off used was ≥ 15 cm) from 907 species. Tree inventories within each region have been described elsewhere (Santos et al., 2008, Arroyo-Rodríguez et al., 2009, 2012, Pardini et al. 2009; Hernández-Ruedas et al., 2014, Orihuela et al. 2015, Benchimol and Peres, 2015, Pinho et al. 2018) and sampling strategies are summarized in Table 1. Briefly, we used the Gentry's (1982) protocol in the Mexican regions (Lacandona and Los Tuxtlas) and in João Pessoa, by identifying and recording all trees in 10 50 × 2-m plots randomly located at each forest site (totalling 0.1 ha per site). In Miriri, we adapted the Gentry’s protocol by establishing three parallel plots of 50 x 2 m (0.03 ha) in each site. Similarly, in Una we established two parallel 2-m wide and 200-m long plots (0.08 ha). In the other regions, we established only one plot in the centre of each forest site, measuring 250 x 10 m (0.25 ha) for Balbina, and 10 x 100 m (0.1 ha) for Serra Grande and Serra do Tabuleiro. The slightly different sampling effort (i.e. plot size) among regions (Table 1) should not prevent cross-regions comparisons as here we focused on variation in the dominant functional traits and strategies in tree communities (Muscarella et al. 2017).

Functional traits and CSR strategies

We considered a comprehensive set of both economic- and size-related traits from different plant organs (leaves, stems and seeds) and the whole-plant, which are related to basic trade-offs in plant strategies (Westoby et al. 2002, Diaz et al. 2016). These were measured in the field (following Pérez-Harguindeguy et al. 2013) and compiled from global databases (e.g. ‘TRY’; Kattge et al. 2011). The species covered by our trait data represented at least 70% of the total tree abundance in each plot. For leaf traits, we considered leaflets as the sample unit for compound-leaved species. Economic-traits considered for both leaves (specific leaf area – SLA and leaf dry matter content – LDMC) and stems (wood density – WD) are related to a *trade-off* between rapid resource-acquisition and long life-span (Wright et al. 2004, Chave et al. 2009), also known as the “fast-slow continuum” (Reich 2014). The size-related traits (leaf size – LA, seed mass – SM, maximum height – Hmax) are related to competitive dominance (Grime and Pierce 2012) and to specific trade-offs. Larger leaves favor light capture and a slow heat exchange with the surrounding air, but also leads to a higher transpirational water loss. Large seeds generally produce seedlings with higher performance in stressful environments while smaller-seeded species have greater seed output and higher survival rate in the soil (see Moles et al. 2018). Finally, potentially taller trees tend to have greater access to light and belowground resources (Muller-Landau et al. 2006, Brum et al. 2019); but shorter trees are often more tolerant to abiotic stress (Grime and Pierce 2012).

Additionally, we calculated continuous C-, S- and R-scores (summing up to 100%) for each species, with the "*Stratefy*" spreadsheet developed by Pierce et al. (2017). This CSR classification system was built from the two globally-evident axes of species traits co-variation (i.e. economic- and size-axis), using LA, SLA and LDMC values to define the relative position of each species in a CSR functional space calibrated from more than 3,000 species worldwide (Pierce et al. 2017). Although based only on few morphological leaf traits, the method is assumed to capture variation in other organ-level (e.g. wood density) and whole-plant traits (e.g. maximum height), given the co-variation patterns among such traits (Pierce et al. 2017). Specifically, 'competitors' (C-selected) are expected to dominate under relatively stable and productive habitats by investing resources in continuous vegetative growth and resource pre-emption. Stress tolerators (S-selected) are favored in seasonal and resource-poor environments by growing slowly and producing dense, durable tissues. They have greater longevity at both organ- and plant-level, and can be small or gradually achieve a large size over their long life-span. Finally, ruderalists (R-selected) have evolved in a particular situation of frequent disturbances, thus having a very short life-span and investing most of resources in propagules to guarantee population maintenance (Grime and Pierce 2012).

Landscape-scale forest cover

As usually (Tscharntke et al. 2012, Fahrig 2013), patch-scale variables (i.e. patch size and edge distance) and landscape configurational variables (e.g. edge density) were in most cases strongly correlated (positively and negatively, respectively) with landscape composition (i.e.

forest cover). Then, we only considered the habitat amount in all analyses, as it has been pointed out as the most important landscape-scale predictor of ecological communities (Fahrig 2013). We assessed the effect of landscape composition on the functional structure of tree assemblages by relating each response variable (community weighted mean traits and functional diversity) to the percentage of forest cover in the landscape surrounding each sampling site within five concentric buffers (5, 10, 25, 50, 100 ha), except for Balbina where we considered different scales (31, 78, 314 ha). Forest cover was estimated based on maps elaborated from aerial photographs, satellites images, and field measurements after supervised classification with GIS SPRING and ArcGIS software.

Data analyses

First, we checked for spatial independence of our samples within each region by assessing whether differences between plots for each response variable were related to the geographic distances among them, using Mantel tests with the R package *vegan* (Oksanen et al. 2009). We did not find spatial autocorrelation in any of our datasets, which allowed us to include all sites as independent samples in the following analyses. Then, we used Nonmetric Multidimensional Scaling (NMDS) on taxonomic composition of tree assemblages to visually check for differences among regions. To assess whether tree taxonomic and functional diversity differed across regions, and if our sampling effort for each region was sufficient to run subsequent analyses, we used rarefaction techniques on both taxonomic and functional diversity for each region. For taxonomic diversity, we used multiplicative diversity decompositions of effective number of species (i.e. “Hill numbers”, Jost 2007), considering different sensitivity to the relative abundances (i.e. “q-orders”): q0 (species richness), q1 (exponential of Shannon’s entropy index, or the number of “typical species”) and q2 (inverse of Simpson concentration, or the number of “dominant species”) (Jost 2010, Chao, Chiu and

Hsieh 2012). For this, we used the R package iNEXT (Hsieh, Ma and Chao 2016). In turn, for the functional diversity we applied rarefaction on FD (i.e. functional richness, Walker et al. 2008) and RaoQ (i.e. functional divergence, Ricotta et al. 2012).

As the response of one trait to forest loss may not be independent of others (Carrié et al. 2016), we analysed species trait co-variation patterns for each region, as it may deviate from global patterns (Wright and Sutton-Grier 2012). For this, we first log-transformed species leaf area and seed mass, and scaled all species trait values. Then, we applied principal component analyses (PCA) on species trait matrices, using R function ‘prcomp’ (Venables and Ripley 2002). To scale species functional traits and CSR strategies to community-level, we calculated two complementary metrics: the Community-Weighted Mean trait-strategy (‘CWM’ – i.e. species’ trait values weighted by their abundances), which reflect the dominant strategies in a community (Muscarella et al. 2017); and the multi-trait RaoQ quadratic entropy index from de Bello et al. (2010), which is corrected based on equivalent numbers as proposed by Jost (2007), and indicate the functional divergence of dominant species (Ricotta and Moretti 2011). CWM analyses were performed using function ‘dbFD’ from R package ‘FD’ (Laliberté and Legendre 2010).

To determine the scale at which forest loss most strongly affect each of the functional properties of tree assemblages (i.e. scale of effect), we fitted linear models for each response variable (CWM traits and multi-trait RaoQ) with forest cover as predictor for each spatial scale considered, and selected the scale with the highest coefficient of determination, i.e. R^2 (Jackson and Fahrig 2015). For automatizing this task, we used the R function ‘Multifit’ for multi-scale analysis in landscape ecology (Huais 2018). Finally, for each region, we applied linear regression models for each response variable with forest cover in the scale of effect as predictor. All statistical analyses were performed in software R (R Core Team, 2016).

Results

Cross-region patterns

Although rarefied species richness (q = 0) did not achieve an asymptote in some regions, our sampling effort was sufficient to capture the typical (q = 1) and dominant (q = 2) species in all regions (Fig. S1). The study regions largely differed in their floristic composition, with four main groups evident: Mexican forests, Amazon forest, northeast and southeast Atlantic forest (Fig. S2). Cross-region variation in functional diversity was not consistently related to their disturbance regime. For instance, regions such as Balbina and Los Tuxtlas IDL, which represent one of the best and worst disturbance scenarios, respectively (Table 1), presented the highest values for functional divergence (RaoQ) at the regional scale (Fig. S3). Similarly, while three regions from northeast Atlantic forest with high landscape disturbance level presented consistently lower values for functional richness (FD), the highest FD values occurred in both well-conserved (UNA) and very disturbed (Los Tuxtlas) regions (Fig. S3).

Neotropical forest floras exhibit a wide spectrum of trait variation, but species-level trait distribution largely overlap across regions (Fig. S4). However, the dominant functional traits differed markedly across regions (Fig. S5). Specifically, the Mexican forests were dominated by species with more acquisitive traits (i.e. higher specific leaf area, lower wood density and leaf dry matter content) compared to regions southwards, while the Amazon region presented consistently higher values for community weighted mean seed mass and LDMC (Fig. S5). Cross-region differences in dominant functional strategies were not consistently related to landscape disturbance level across biogeographic scenarios. However, within a similar biogeographic context, increasing landscape disturbance level may increase relative frequency and dominance of fast-growing, highly competitive species (i.e. C-selected), while declining the relative proportion and abundance of more ‘stress-tolerant’ (S-selected) species (Fig. S6).

Trait co-variation patterns varied across regions, while also presenting some similarities (Table S1). The first PCA axis explained from 31 to 40% of the variance in species trait values in each region, while the second and third axes explained similar proportions (14 – 21%; Table S1). Leaf dry matter content presented the highest loadings on the first PCA axis in all regions, followed by wood density and seed mass which in all but one and two regions, respectively, co-varied strongly and positively with LDMC (Table S1). Yet, other traits did not present consistent patterns. Size-related traits at the organ-level (leaf area) and whole-plant (maximum height) co-varied either positively or negatively in a common axis, or varied orthogonally in separated axes (Table S1). Also, SLA may either covary negatively with conservative traits along the first axis, or vary orthogonally in relation to other traits in a separate axis (Table S1).

Trait-landscape relationships

Excepting SLA, all traits were significantly related to landscape-scale forest cover in at least one region; and excepting the Serra do Tabuleiro region in the extreme South (Fig. 1), at least one trait was significantly related to forest cover in each of the other nine regions (Fig. 2, Table S2). Among these, the well-conserved region in Amazonia (Balbina; Fig. 1, Table 1) presented a much larger variety of traits-strategies significantly related to forest cover (8/9), while other regions presented only one to three significant relations (Fig. 2). When significant, landscape-scale forest cover explained from ~ 12 to 80% of variation in community-weighted mean traits (CWM) or functional diversity (RaoQ) across landscapes. Functional diversity and the relative abundance of traits related to competitive dominance (i.e. LA and Hmax) varied in response to forest cover in very contrasting directions and magnitudes. On the other hand, some resource-use traits (i.e. LDMC and WD) and regenerative strategies (i.e. SM) presented stronger and directionally more consistent responses to forest cover across regions (Fig. 2, Table S2). Specifically, increasing landscape-scale forest cover tended to increase dominance of species with more conservative traits and large seeds (Fig. 2). For instance, variation in community-weighted mean LDMC was significantly positively related to forest cover in all but three regions (Fig. 2). Increasing forest cover also had relatively consistent effects in CSR strategies, tending to increase the dominance of S-selected species and decrease the relative extent of C-selection across regions. However, the responses of CSR strategies were in general weaker compared to individual traits, and only significant for C- and S-selection in two regions (Fig. 2, Table S2).

Finally, the scale of effects varied widely both within and among traits and regions (Fig. 2, Table S2). While in most cases (7/10) community-weighted mean seed mass responded more strongly to landscape structure at small spatial scales (5 – 25ha), the SE for resource-use traits and especially C- and S-strategies were mostly at larger scales (> 50 ha; Fig. 2, Table 2). Cross-region differences in SE (Table S2) was apparently not related to disturbance regime (Table 1) nor to the functional composition (Fig. S5) and diversity (Fig. S3) of species-pools.

Discussion

Our results suggest that Neotropical forest floras or tree species assemblages (i.e. regional floras) are both taxonomically and functionally distinct, considering either functional diversity or trait dominance. Moreover, tree assemblage functional profile apparently changes in response to landscape-scale forest loss, but such response varies widely relative to direction, magnitude and scale of effect across traits and regions. However, a set of few co-varying traits typical of old-growth forest species tend to consistently decrease in prevalence with forest loss. We refer to traits related to survival (wood density, leaf dry matter content) and regeneration (seed mass) under low resource (e.g. light) availability, as well as to the stability of important ecosystem functions (e.g. carbon storage). Furthermore, there is a general tendency of turnover from stress-tolerant (S-) to more competitive (C-selected) strategies with forest loss. Regardless of regional differences in biogeographic history, disturbance regime and species pool composition, habitat loss tends to comprehensively drive Neotropical forests towards a functional composition that is typical of early-successional communities.

Our findings reinforce the notion that tropical tree floras are taxonomically and functionally relatively distinct at regional scale, what has been recognized to emerge due to a combination of biogeographic and ecological forces such as climate and altitude (Gentry 1982, Burnham and Graham 1999, Blonder et al. 2018). In addition to a regional organization, our findings reinforce the notion that conversion of old-growth forest into human-modified landscapes reorganise tree assemblages from local to landscape spatial scales (see Arroyo-Rodriguez et al. 2017). In this context, one of the consistent patterns refers to decline of old-growth forest trees and the proliferation of few “disturbance-adapted”, short-lived tree species in fragmented landscapes (the ‘winners’ *sensu* Tabarelli et al. 2012). This replacement results on the establishment of impoverished tree assemblages particularly across edge-affected habitats (Tabarelli et al. 2008, Metzger et al. 2014). Although tropical forests do differ in terms of the intensity they experiment this phenomenon, such a winner-loser replacement (Tabarelli et al. 2012) has been documented extensively (Laurance et a. 2006, Tabarelli et al. 2008, Pütz et al. 2011, Solar et al. 2015, Newbold et al. 2018). However, there is a major uncertainty on the traits underlying tree species sensitivity to forest loss, and therefore, on the mechanisms governing compositional changes or reorganizing tree assemblages in fragmented landscapes (Arroyo-Rodriguez et al. 2017). The available evidence suggests a decline of specific (categorical) functional groups in fragmented landscapes, such as shade-tolerant, large-seeded and mast-fruiting tree species (Santos et al. 2008, Benchimol et al. 2017, Tabarelli et al. 2010, Rocha-Santos et al. 2017). Our findings help to disentangle tree-assemblage reorganization in human-modified landscapes by documenting consistent and gradual declines in a set of continuous, co-varying traits as forest cover is reduced at the landscape-scale. We refer to traits and strategies that have been recognized to be connected with regeneration and survival under abiotic conditions typical of old-growth forests, i.e. deep shade and infertile soils (Leishman and Westoby 1994, Hodgson et al. 2010, Kitajima and Poorter 2010, Muller-Landau 2010, Reich 2014). Forest loss thus operates as a key assembly force, filtering major tree life-history strategies in fragmented landscapes.

Compositional changes or tree assemblage reorganization in human-modified landscapes are mainly driven by species replacements (Collins et al. 2017) as habitat loss modify colonization and local extinction dynamics due to area, isolation and edge effects (MacArthur and Wilson 1967, Laurance et al. 2006, Fahrig 2013, Haddad et al. 2015). We cannot properly distinguish among such effects, as here we have only analysed the overall effect of forest loss. However, our results suggest that the ecological bottleneck for tree species persistence in fragmented landscapes relies mainly on recruitment and survival ability under the abiotic conditions imposed by edge-effects. For instance, forest loss typically increases edge-related environmental changes, among which the most evident is an increase in light radiance due to either abrupt boundaries or increased gap-dynamic owing to elevated mortality of large canopy-trees (Saunders et al. 1991, Laurance et al. 2000). Furthermore, soil nutrient availability is expected to be lower in old-growth forests compared to early-successional systems (i.e. edge-affected habitats), given the retention of nutrients in larger amounts of living biomass and the slower nutrient cycling due to dominance of longer-lived trees (Bazzaz 1996, Nascimento and Laurance 2004, Pinho et al. 2018). Accordingly, those traits with more consistent (negative) responses to forest loss across regions (LDMC and WD; Fig. 2) are leaf and stem economic traits that have been identified as part of an integrated plant economic spectrum (i.e. the fast-slow continuum, *sensu* Reich, 2014), which underlie the growth-survival trade-off in plants (Poorter et al., 2008; Wright et al., 2010) and thus mediate species responses to gradients of resource availability (Greenwood et al., 2017). Tree species with conservative traits (i.e. dense tissues, such as high LDMC and WD) generally grow slowly, but have higher survival rates and dominate when resources are scarce, given their low metabolic resource demand and reduced resource loss through long-lived tissues (Kitajima and Poorter 2010, Grime and Pierce 2012). However, they are usually replaced by species with more acquisitive traits that grow faster with increasing resource availability, particularly light and nutrients in tropical rainforests (Lohbeck et al. 2013, Jager et al. 2015, Pinho et al. 2018; see Reich 2014). In addition, community-level seed mass also presented a relatively consistent decrease with forest loss across regions (Fig. 2) and larger seeds are in fact known to promote higher seedling performance under conditions of low soil fertility and deep shade in closed-canopy forests (Leishman and Westoby 1994, Muller-Landau 2010).

At the same time, large seeds typically have lower colonization rates (Muller-Landau 2010), and their dispersal is likely to be hampered with forest loss due to both defaunation and increasing isolation among forest patches (Costa et al., 2012; Dirzo et al., 2014). However, contrarily to our expectation, community-level seed mass was more responsive to variation in forest cover at very small spatial scales (mostly < 10 ha; Fig. 2), suggesting edge proximity as a key driver, either due to abiotic conditions or the influx of disturbance-adapted species from nearby matrix (Laurance et al. 2006). In turn, resource-use traits (i.e. LDMC and WD) tended to be more affected by variation in landscape structure at larger scales (mostly > 50 ha; Fig. 2). In fact, metapopulation dynamics and extinction threshold in fragmented landscapes depend on the interaction between local and regional processes (Zartman and Shaw 2006). For instance, while edge-effects can lead to the local extinction of some species (Laurance et al. 2002, 2006), metapopulation theory suggest that colonization-extinction equilibrium (i.e. regional processes) is more important than local population dynamics in determining the persistence of metapopulations (Levins 1969, Thrallet al. 2000, Zartman and

Shaw 2006). The amount of habitat (i.e. forest cover) at larger scales may determine the overall proportion of edge-affected habitats and thus the regional abundance of disturbance-sensitive species, which in turn influence immigration rates and thus the probability of local extinction (i.e. the “rescue effect” hypothesis; Brown and Kodric-Brown 1977).

Finally, we shall mention that despite such a relatively consistent response across few co-varying traits, our findings suggest that tree community functional response to forest loss is highly context-dependent as evident for other biological groups (e.g. Neotropical vertebrates; Vetter et al. 2011), with the occurrence of some non-responsive traits (i.e. SLA). Although the importance of assessing ecological patterns at the landscape-scale has been highlighted (Fahrig 2013, Arroyo-Rodriguez et al. 2017), many factors determining community functional patterns operate at the local-scale (e.g. habitat structure), which may or may not correlate with landscape structure as thus explain our findings. For instance, gap-dynamics in tropical rainforests is very unpredictable and may determine variation in microclimate conditions and resource availability (Yamamoto 1992). Moreover, drift and stochastic processes may play a key role in driving community patterns (Orrock and Watling 2010). Finally, inconsistent responses may result from many concurrent processes determining community functional structure and varying across regions, such as disturbance patterns (e.g. matrix quality; Driscoll et al. 2013), climatic factors and broad regional process related to specific biogeographical history of each region (Violle et al., 2014).

In synthesis, tropical tree floras are naturally organized at regional scale in response to biogeographic or ecological forces such as altitude and climate. However, human encroachment of old-growth forests is reorganizing tree assemblages at local and landscape scale. In fact, forest loss is consistently associated with the reorganization of tree assemblages at landscape scale, although some plant traits are not sensitive and others respond in contrasting directions across regions. Specificities determining variation in trait sensitivity across regional contexts is still an open question that may be related to disturbance regimes or biogeographic histories. Despite such a context-dependence, changes in trait dominance in general supports a sort of 'retrogressive succession' as trait values typical of early-successional species increment as forest loss proceeds, probably in response to the increment of edge-affected habitats. As land-use changes procced (Lewis et al. 2015) such a "disassembly" (Collins et al. 2017) is likely to gain magnitude and alter patterns of ecosystem functioning. Traits responsive to landscape modification (i.e. leaf dry matter content, wood density) are clearly related to carbon storage and 'slow' nutrient dynamics (Garnier et al. 2004, Pütz et al. 2014, Reich 2014). Thereby functionally distorted assemblages are unlikely to support the provisioning of ecological services that have been considered essential for sustainability from local to global scale (e.g. productivity, carbon storage; Malhi 2012). To move forward in elucidating the mechanisms governing compositional trajectories in fragmented landscapes, future studies should consider long-term demographic drivers of community functional composition dynamics (Muscarella et al. 2017), also exploring the role of other landscape features (e.g. matrix quality). This would ultimately help us to avert biodiversity collapse and move towards biodiversity-friendly landscapes (Melo et al. 2013).

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Table 1. Description of the study rainforest regions, with the location (state, country), latitude and mean annual precipitation (MAP) averaged across plots, relative total forest cover, approximate time since forest fragmentation, defaunation level, matrix heterogeneity and sampling strategy and effort (i.e. plot size and number of sampled sites) The regions are listed from the northern extreme to the southern end of the Neotropical rainforest distribution.

Regions[a]	**Latitude (mean)**	**Location**	**MAP (mm)**	**Forest cover (%)**	**Time since fragmentation (years)**	**Defaunation level**	**Matrix heterogeneity**	**Plot size (ha)**	**N sites**	**Refs**[b]
Los Tuxtlas (LDL)	18.6	Veracruz, Mexico	2448	~ 24	~ 60	Intermediate	Low	0.1	15	1,2
Los Tuxtlas (HDL)	18.5	Veracruz, Mexico	2880	~ 4	~ 60	Very high	Low	0.1	15	1,2
Los Tuxtlas (IDL)	18.37	Veracruz, Mexico	2130	~ 11	~ 60	High	Low	0.1	15	1,2
Lacandona	16.15	Chiapas, Mexico	3053	~ 40	~ 40	Low	High	0.1	29	3,4
Balbina	-1.67	Amazonas, Brazil	2366	~ 62	~ 30	Low	Low	0.25	33	5
Miriri	-7.03	Paraíba, Brazil	1370	~ 24	~ 200	Very high	Low	0.03	10	6
João Pessoa	-7.12	Paraíba, Brazil	1864	~ 15	~ 200	Very high	Intermediate	0.1	8	7
Serra Grande	-8.97	Alagoas, Brazil	1523	~ 9	~ 200	Very high	Low	0.1	22	8
UNA	-15.09	Bahia, Brazil	1192	~ 58	~ 50	Intermediate	High	0.08	11	9

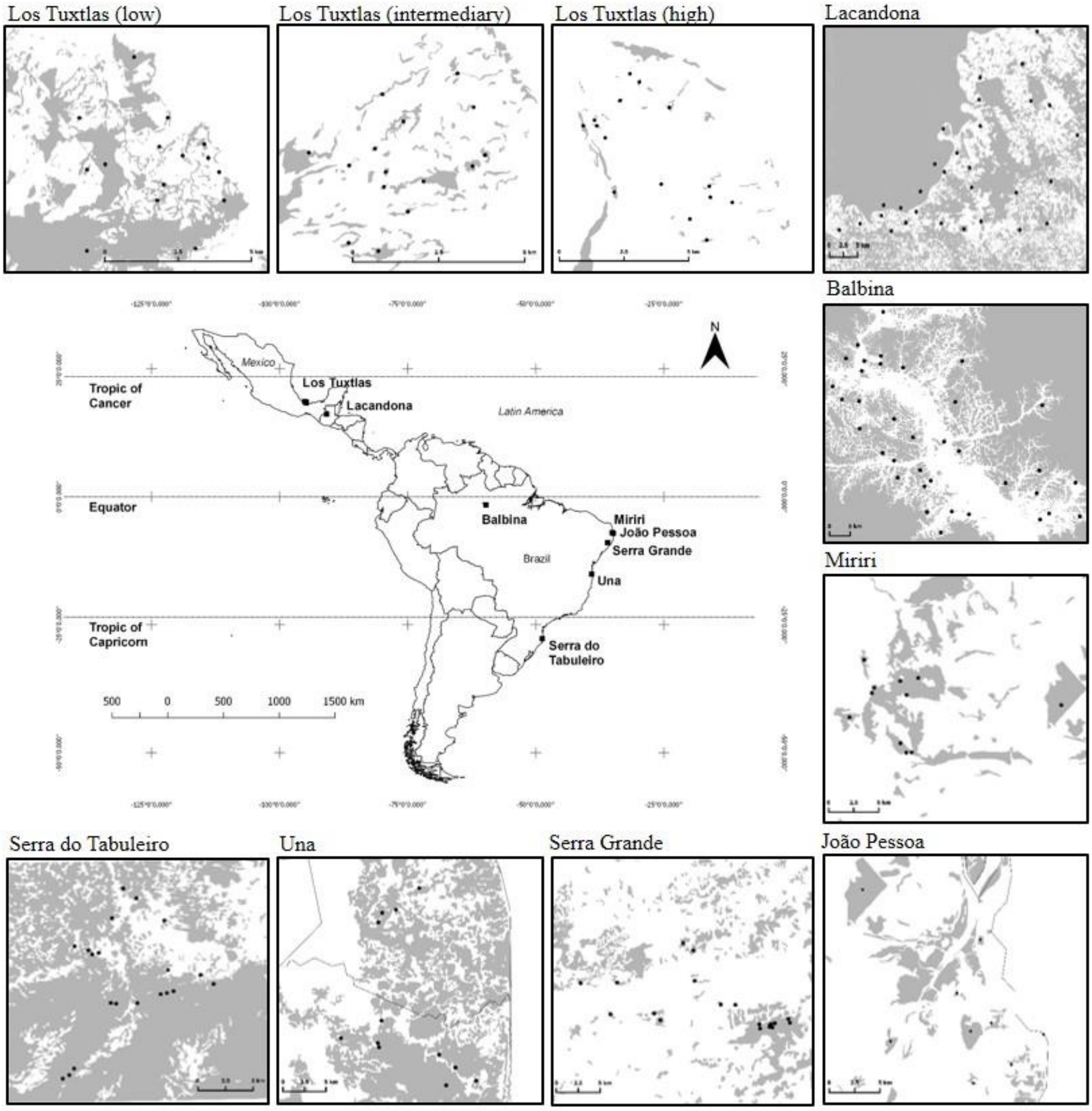
Serra do Tabuleiro	-27.72	Santa Catarina, Brazil	1600	~ 71	~ 100	low	Intermediate	0.1	20	10

[a] In Los Tuxtlas, we studied three regions with low (LDL), intermediate (IDL) and high (HDL) deforestation levels. [b] References: 1. Arroyo-Rodríguez et al. (2009); 2. Arroyo-Rodríguez et al. (2012); 3. Garmendia et al. (2013); 4. Hernández-Ruedas et al. (2014); 5. Benchimol and Peres (2015); 6. Pinho et al. (2018); 7. Junior (2017); 8. Santos et al. (2008); 9. Pardini et al. (2009); 10. Orihuela et al. (2015).

Figure legends

Figure 1. Location of the studied regions along the Neotropics (four in Mexico and six in Brazil) and the detailed distribution of forest cover (grey) in each one (See Table 1 for more details on each region).

Figure 2. Summary of results from linear regression models with community functional properties (community weighted mean trait – CWM and multi-trait functional diversity – RaoQ) as response variables and forest cover in the scale of effect as predictor. Coefficients (i.e. the strength of the relationship) of each model are denoted by solid dots, and model standard errors by bars. The scale of effect is shown for each parameter and region analysed. Significant relations ($p < 0.05$) are indicated by asterisks. See Table S2 for details on each model.


Los Tuxtlas (low)
Los Tuxtlas (intermediary)
Los Tuxtlas (high)
Lacandona
Balbina
Miriri
Serra do Tabuleiro
Una
Serra Grande
João Pessoa
N
Mexico
Los Tuxtlas
Lacandona
Latin America
Tropic of Cancer
Equator
Balbina
Miriri
João Pessoa
Serra Grande
Brazil
Una
Tropic of Capricorn
Serra do Tabuleiro
500
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500
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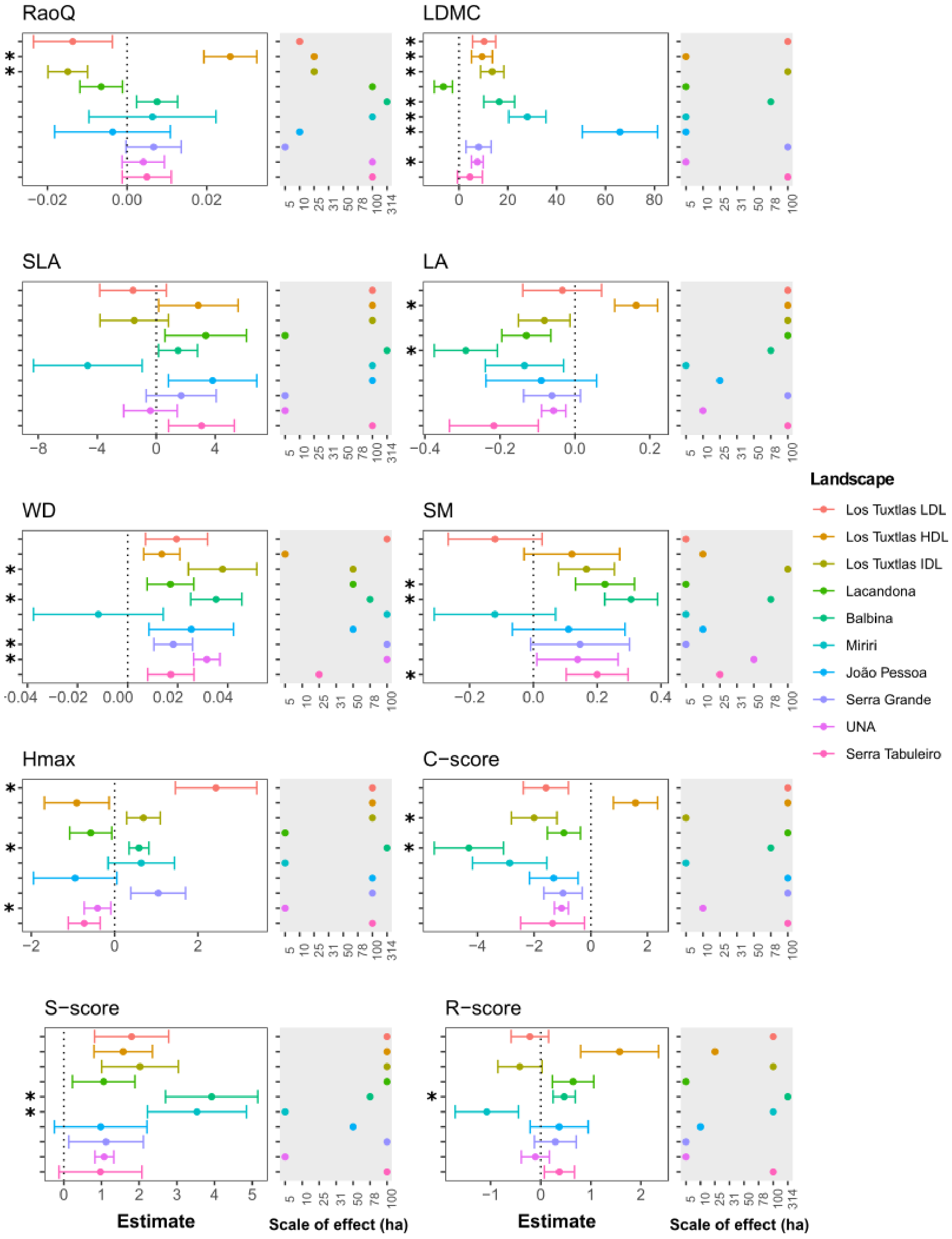
1500 km

Figure 1.


RaoQ
−0.02
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LDMC
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WD
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0.00
0.02
0.04
SM
−0.2
0.0
0.2
0.4
Hmax
−2
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C−score
−4
−2
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2
S−score
0
1
2
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R−score
−1
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10
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31
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78
100
314
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Estimate
Scale of effect (ha)
Landscape
Los Tuxtlas LDL
Los Tuxtlas HDL
Los Tuxtlas IDL
Lacandona
Balbina
Miriri
João Pessoa
Serra Grande
UNA
Serra Tabuleiro

Figure 2.

Table S1. Principal component analyses of species functional traits in 10 Neotropical regions.

Regions/Traits	**PCA loadings**		
	PC1	PC2	PC3
Los Tuxtlas LDL *(120 sp.)*			
Leaf area	0.22	**-0.72**	0.41
Specific leaf area	**0.42**	0.25	0.18
Leaf dry matter content	**-0.56**	0.03	-0.14
Wood density	**-0.49**	0.29	0.33
Seed mass	-0.40	-0.25	**0.56**
Maximum height	-0.23	-0.51	**-0.59**
Proportion of variance explained	0.39	0.19	0.15
Los Tuxtlas HDL			
Leaf area	0.26	**-0.68**	0.08
Specific leaf area	0.37	0.30	**0.67**
Leaf dry matter content	**-0.55**	0.11	-0.23
Wood density	**-0.47**	0.30	0.27
Seed mass	-0.39	-0.28	**0.64**
Maximum height	-0.32	**-0.50**	0.051
Proportion of variance explained	0.39	0.19	0.15
Los Tuxtlas IDL			
Leaf area	0.18	0.42	**0.43**
Specific leaf area	0.38	**-0.53**	0.23
Leaf dry matter content	**-0.56**	0.09	-0.09
Wood density	**-0.54**	-0.25	-0.003
Seed mass	-0.43	-0.02	**0.48**

Maximum height	-0.17	0.45	**0.64**
Proportion of variance explained	0.37	0.19	0.18
Lacandona			
Leaf area	0.28	**-0.67**	0.15
Specific leaf area	0.38	**0.64**	0.021
Leaf dry matter content	**-0.55**	-0.21	-0.08
Wood density	**-0.53**	0.11	-0.31
Seed mass	**-0.34**	0.26	0.09
Maximum height	-0.25	0.09	**0.93**
Proportion of variance explained	0.37	0.20	0.15
Balbina			
Leaf area	0.18	**-0.77**	0.18
Specific leaf area	0.32	**0.61**	0.32
Leaf dry matter content	**-0.52**	-0.02	-0.20
Wood density	**-0.49**	0.16	-0.36
Seed mass	**-0.48**	-0.02	0.33
Maximum height	-0.34	0.01	**0.76**
Proportion of variance explained	0.38	0.20	0.17
Miriri			
Leaf area	0.28	**-0.60**	0.20
Specific leaf area	**0.53**	0.34	0.003
Leaf dry matter content	**-0.55**	-0.03	0.17
Wood density	-0.36	-0.03	**-0.78**
Seed mass	-0.44	0.14	**0.56**
Maximum height	0.02	**0.71**	0.03

Proportion of variance explained	0.31	0.21	0.16
João Pessoa			
Leaf area	0.25	**0.66**	-0.55
Specific leaf area	**0.49**	-0.23	0.45
Leaf dry matter content	**-0.58**	0.01	-0.07
Wood density	**-0.37**	-0.06	0.19
Seed mass	**-0.45**	-0.06	-0.09
Maximum height	0.13	**-0.71**	-0.67
Proportion of variance explained	0.39	0.18	0.14
Serra Grande			
Leaf area	0.19	0.63	**-0.68**
Specific leaf area	**0.49**	-0.07	0.42
Leaf dry matter content	**-0.53**	-0.04	-0.002
Wood density	**-0.46**	0.01	0.07
Seed mass	**-0.47**	0.15	0.05
Maximum height	-0.03	**0.76**	0.59
Proportion of variance explained	0.40	0.19	0.15
UNA			
Leaf area	0.19	0.49	**-0.71**
Specific leaf area	**0.49**	-0.07	0.29
Leaf dry matter content	**-0.57**	-0.01	0.03
Wood density	**-0.43**	-0.39	-0.02
Seed mass	**-0.45**	0.44	-0.08
Maximum height	-0.05	0.63	**0.63**
Proportion of variance explained	0.35	0.19	0.17

Serra do Tabuleiro			
Leaf area	-0.40	0.21	**-0.52**
Specific leaf area	-0.31	0.20	**0.77**
Leaf dry matter content	**0.59**	-0.31	0.03
Wood density	**0.46**	0.31	-0.22
Seed mass	**0.42**	0.41	0.27
Maximum height	-0.02	**-0.74**	0.10
Proportion of variance explained	0.31	0.19	0.18

Table S2. Results from linear regression models applied to tree community functional attributes (community-weighted mean – CWM and functional diversity - RaoQ) with forest cover measured at the scale of effect (SoE) as predictor, in forest patches across 10 Neotropical regions. The estimates (β) and standard errors (SE) are shown. Significant relations are indicated in bold. **p* ≤ .05, ***p* ≤ .01, ****p* ≤ .001.

Landscape	**N sites**	**Assemblage attributes**	**Forest cover**			
		(FD and CWM)	**SoE (ha)**	**β**	**SE**	**R^2 (%)**
Los Tuxtlas LDL	15	RaoQ	10	-0.01	0.01	12.68
		Leaf area	100	-0.03	0.11	0.78
		Leaf dry matter content	100	10.30	4.70	**27.02***
		Specific leaf area	100	-1.57	2.26	3.59
		Wood density	100	0.02	0.01	16.04
		Seed mass	5	-0.12	0.15	4.89
		Maximum height	100	2.43	0.98	**32.31***
		C-score	100	-1.58	0.80	23.32
		S-score	100	1.80	0.99	20.4
		R-score	100	-0.22	0.38	2.53
Los Tuxtlas HDL	15	RaoQ	25	0.03	0.01	**54.05****
		Leaf area	100	0.16	0.06	**38.68***
		Leaf dry matter content	5	9.43	4.27	**27.29***
		Specific leaf area	100	2.85	2.69	7.92
		Wood density	5	0.01	0.01	21.46
		Seed mass	10	0.12	0.15	4.74
		Maximum height	100	-0.91	0.78	9.5
		C-score	100	1.58	0.78	24.00

		S-score	100	1.58	0.78	13.79
		R-score	25	1.58	0.78	3.68
Los Tuxtlas IDL	15	RaoQ	25	-0.01	0.00	**40.56***
		Leaf area	100	-0.08	0.07	9.75
		Leaf dry matter content	100	13.62	4.80	**38.19***
		Specific leaf area	100	-1.49	2.32	3.06
		Wood density	50	0.04	0.01	**37.30***
		Seed mass	100	0.17	0.09	21.63
		Maximum height	100	0.69	0.40	18.39
		C-score	5	-2.00	0.80	**32.15***
		S-score	100	2.02	1.02	23.37
		R-score	100	-0.42	0.44	6.43
Lacandona	29	RaoQ	100	-0.01	0.01	5.09
		Leaf area	100	-0.13	0.07	12.71
		Leaf dry matter content	5	-6.40	3.74	9.78
		Specific leaf area	5	3.35	2.76	5.18
		Wood density	50	0.02	0.01	11.14
		Seed mass	5	0.22	0.09	**17.77***
		Maximum height	5	-0.57	0.50	4.57
		C-score	100	-0.95	0.58	8.87
		S-score	100	1.06	0.83	5.73
		R-score	5	0.65	0.41	8.39
Balbina	33	RaoQ	314	0.01	0.01	6.58
		Leaf area	78	-0.29	0.08	**27.86****
		Leaf dry matter content	78	16.47	6.31	**17.99***

		Specific leaf area	314	1.47	1.33	3.83
		Wood density	78	0.04	0.01	**27.88****
		Seed mass	78	0.31	0.08	**30.65*****
		Maximum height	314	0.53	0.24	13.43
		C-score	78	-4.30	1.22	**28.49****
		S-score	78	3.92	1.22	**24.93****
		R-score	314	0.47	0.22	**12.81***
Miriri	10	RaoQ	100	0.01	0.02	1.98
		Leaf area	5	-0.13	0.10	17.23
		Leaf dry matter content	5	27.98	7.60	**62.91****
		Specific leaf area	100	-4.65	3.68	16.61
		Wood density	100	-0.01	0.03	2.48
		Seed mass	5	-0.12	0.19	4.8
		Maximum height	5	0.64	0.79	7.5
		C-score	5	-2.86	1.31	37.35
		S-score	5	3.53	1.31	**47.48***
		R-score	100	-1.08	0.63	26.57
João Pessoa	8	RaoQ	10	0.00	0.01	1.02
		Leaf area	25	-0.09	0.15	5.8
		Leaf dry matter content	5	65.90	15.40	**78.56****
		Specific leaf area	100	3.82	2.99	21.41
		Wood density	50	0.03	0.02	27.42
		Seed mass	10	0.11	0.18	6.1
		Maximum height	100	-0.95	1.00	12.97
		C-score	100	-1.31	0.86	27.93

		S-score	50	0.98	1.23	9.6
		R-score	10	0.37	0.58	6.28
Serra Grande	22	RaoQ	5	0.01	0.01	4.42
		Leaf area	100	-0.06	0.08	3.13
		Leaf dry matter content	100	8.05	5.20	10.7
		Specific leaf area	5	1.69	2.38	2.46
		Wood density	100	0.02	0.01	**22.07***
		Seed mass	5	0.15	0.16	4.25
		Maximum height	100	1.05	0.66	11.24
		C-score	100	-0.98	0.68	9.42
		S-score	100	1.12	0.99	6.05
		R-score	5	0.29	0.42	2.38
UNA	11	RaoQ	100	0.00	0.01	6.26
		Leaf area	10	-0.06	0.03	25.26
		Leaf dry matter content	5	7.52	2.39	**52.43***
		Specific leaf area	5	-0.40	1.81	0.53
		Wood density	100	0.03	0.01	**80.10*****
		Seed mass	50	0.14	0.13	11.59
		Maximum height	5	-0.41	0.32	15.56
		C-score	10	-1.03	0.25	**66.10****
		S-score	5	1.08	0.25	**67.01****
		R-score	5	-0.11	0.28	1.58
Serra Tabuleiro	20	RaoQ	100	0.00	0.01	3.53
		Leaf area	100	-0.22	0.12	15.52
		Leaf dry matter content	100	4.48	5.08	4.15

Specific leaf area	100	3.07	2.23	9.53
Wood density	25	0.02	0.01	16.25
Seed mass	25	0.20	0.10	19.13
Maximum height	100	-0.73	0.38	16.74
C-score	100	-1.34	1.13	7.33
S-score	100	0.97	1.10	4.19
R-score	100	0.37	0.30	7.8

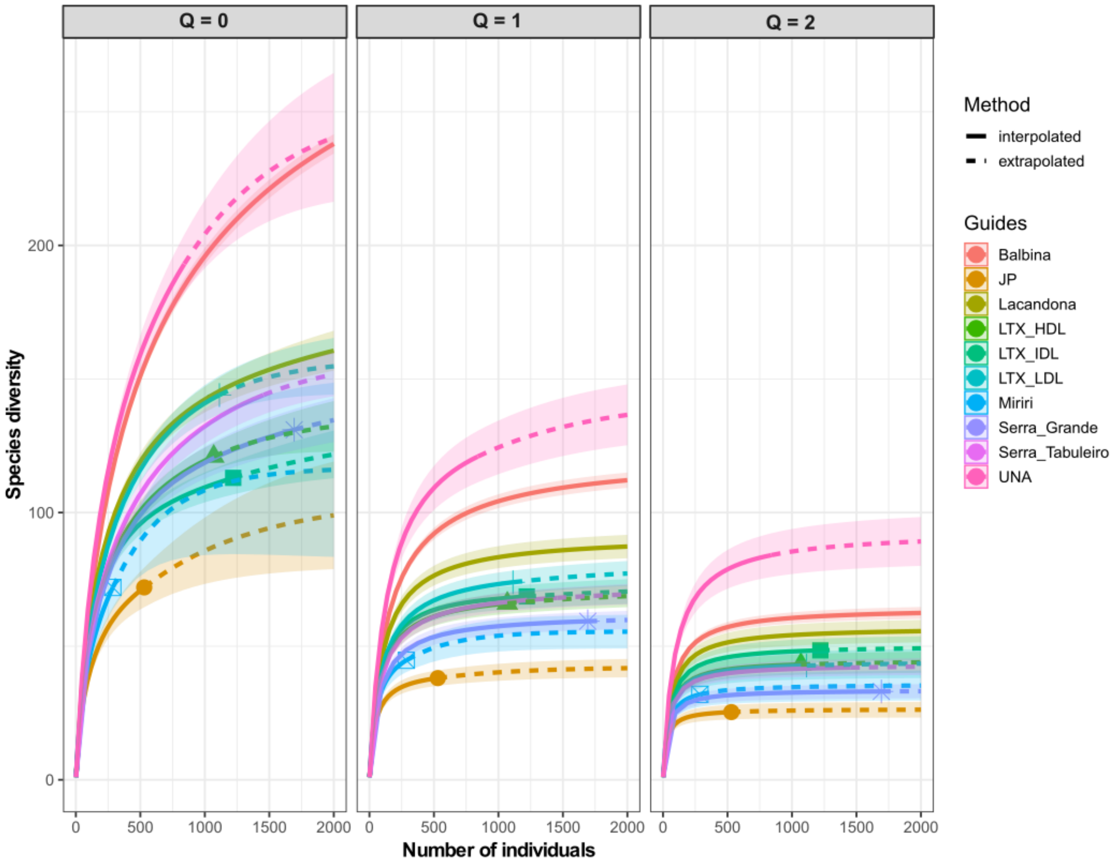

Figure S1. Comparison of sample-size-based rarefaction (solid lines) and extrapolation (dashed curves), up to the base sample size of 2000 individuals, of tree species diversity for Hill numbers of order q = 0 (left panel), q = 1 (middle panel), and q = 2 (right panel), in forest patches across 10 Neotropical rainforest regions (see details on each region in Table 1). Reference samples in each treatment are denoted by solid dots. The 95% confidence intervals (shaded regions) were obtained by a bootstrap method based on 200 replications.

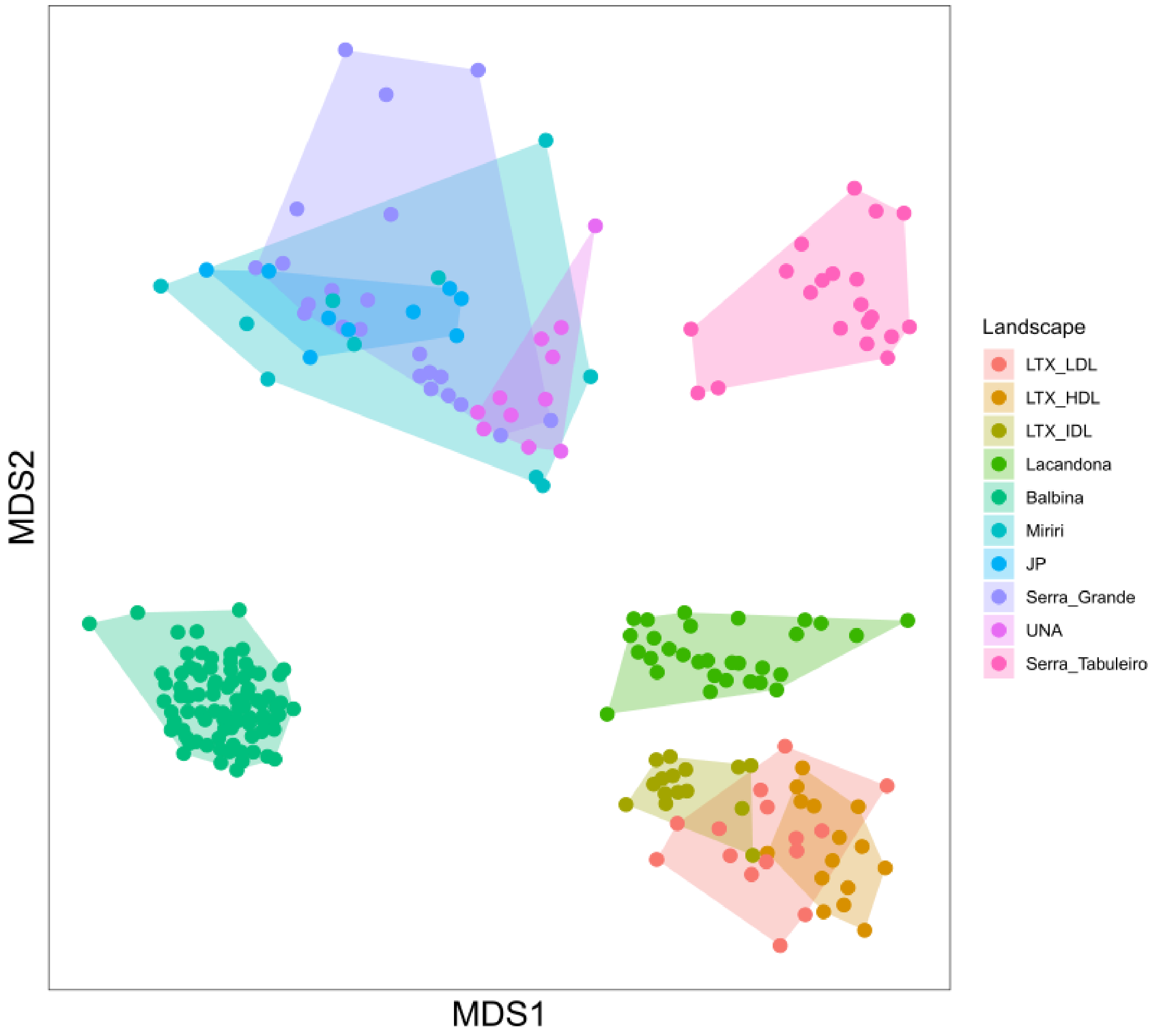

Figure S2. Non-metric multidimensional scaling (NMDS) ordination showing tree taxonomic compositional (Chao–Jaccard dissimilarities) variation among each of the 233 communities studied in 10 Neotropical rainforest regions: four in Mexico (LTX- and Lacandona) and six in Brazil – one in Amazonia (Balbina) and five across the Atlantic forest. Stress = 0.10.

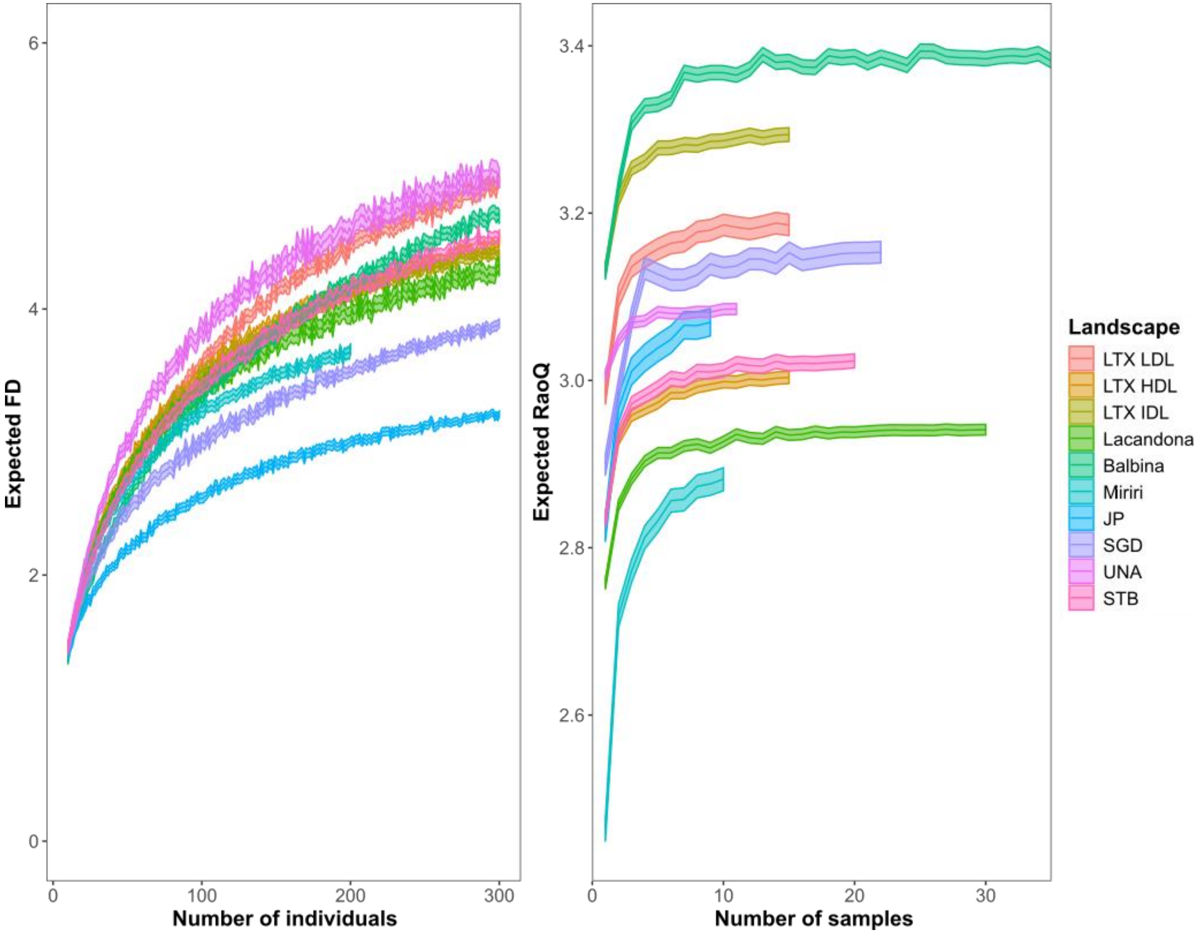

Figure S3. Rarefaction of functional diversity measured by Rao’s entropy Q (RaoQ, see Ricotta et al. 2012) and Petchey and Gaston’s functional diversity (FD, see Walker et al. 2008), in forest patches across 10 fragmented Neotropical regions (See table 1 for details on each region).

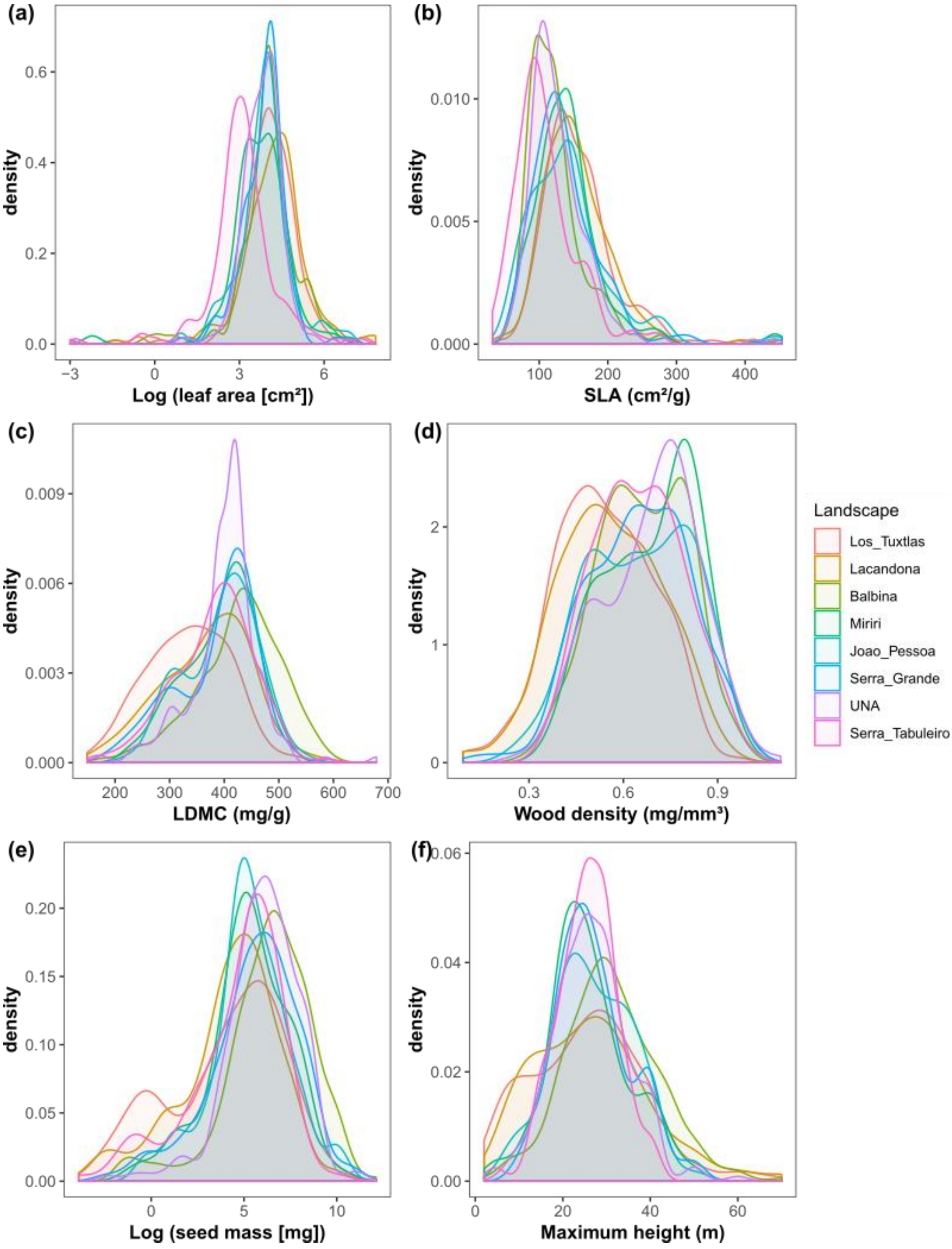

Figure S4. Probability density distribution of functional trait mean values of Neotropical tree species in 10 Neotropical rainforest regions.

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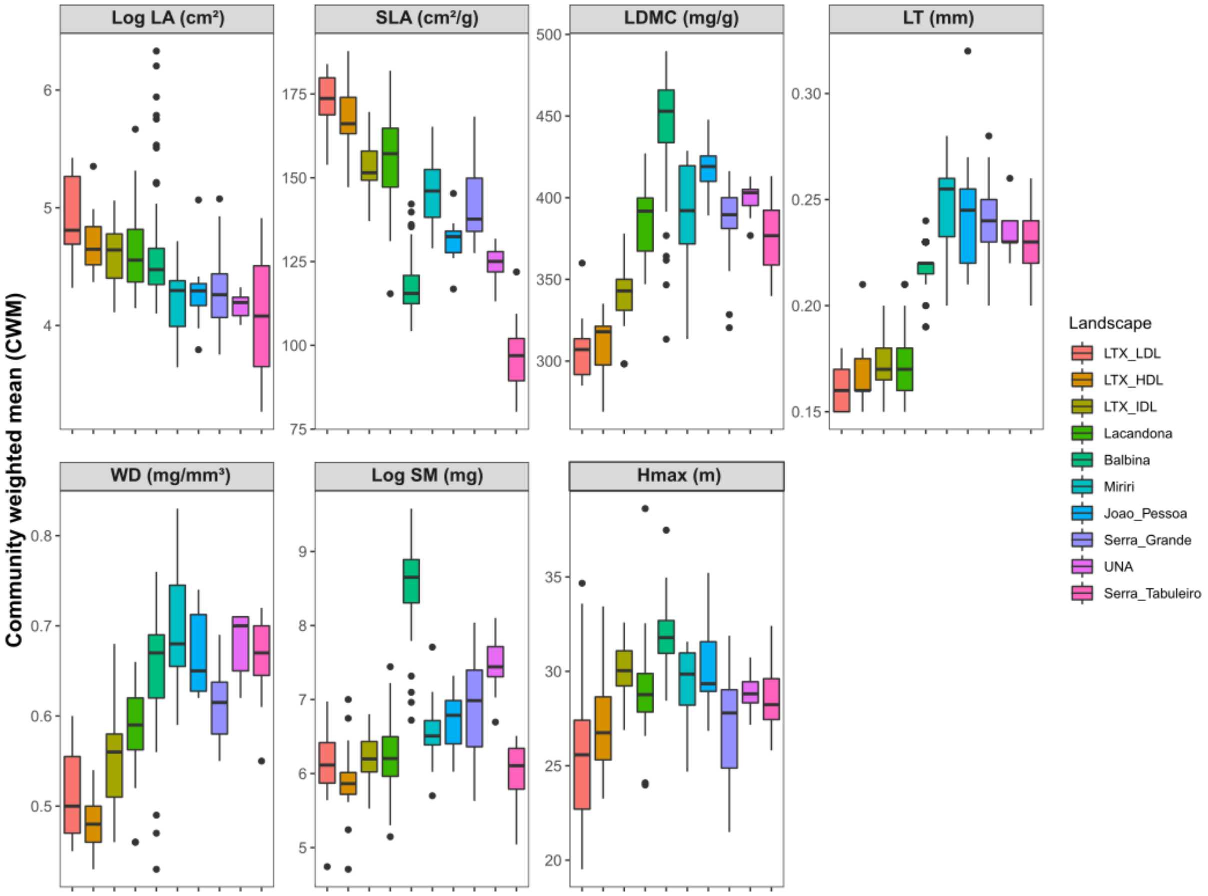

Figure S5. Community-weighted mean traits in tree assemblages across10 fragmented Neotropical rainforest regions, from the extreme north (left) to the south (right) of the latitudinal distribution of Neotropics forests. Plots from each region are pooled and represented as box plots illustrating the median (center line), quartile (box edges) and extreme values (bars).

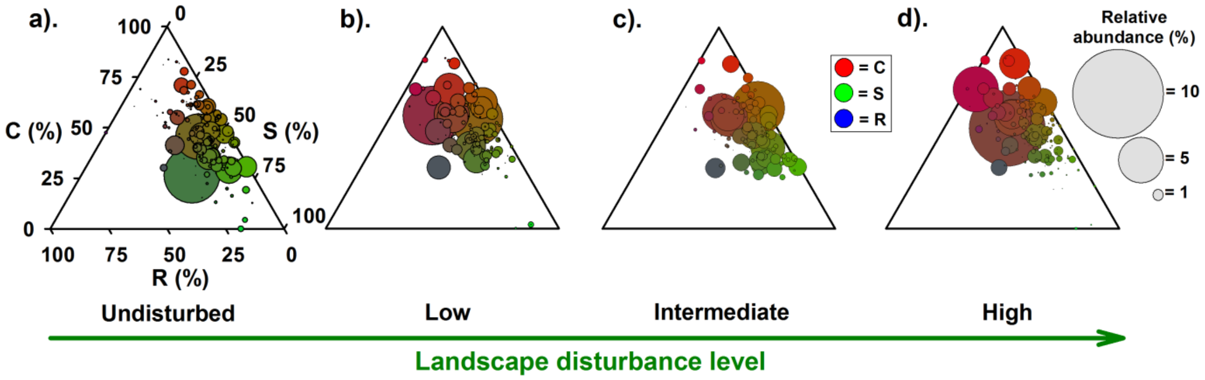

Figure S6. Species C-, S- and R-scores and their relative abundances in the regional pool of the four Mexican rainforest regions studied. Species CSR scores were measured using the globally calibrated analysis tool ‘StrateFy’. From left to right: Lacandona, Los Tuxtlas LDL, Los Tuxtlas IDL and Los Tuxtlas HDL (See Table 1 for details on each region).

3.3 ARTIGO 3

Manuscrito sob revisão no periódico *Basic and Applied Ecology*

Research paper – *Basic and Applied Ecology*

Plant species assembly is mediated by rainfall and soil conditions in a seasonally dry tropical forest

Bruno X. Pinho[1], Marcelo Tabarelli[1], Bettina M. J. Engelbrecht[2,3], Júlia Sfair[4] and Felipe P.L. Melo[1]*

[1]Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. MoraesRego s/n, 50670-901, Recife, Pernambuco, Brazil
[2]Department of Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstrasse 31, 95447 Bayreuth, Germany
[3]Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama
[4]Deparment of Botany, Faculty of Sciences, University of South Bohemia, Branišovská 1760, 370 05 ČeskeBudějovice, Czech Republic

*Corresponding author: felipe.plmelo@ufpe.br

Abstract

Understanding how species assembly is influenced by the interplay of climate, local environmental conditions and human-caused disturbances remains a central question in ecology and conservation. Here, we assess how plant species abundance is determined by combinations of functional traits (ecological strategies) and interacting gradients of rainfall, soil conditions (fertility and field capacity) and chronic anthropogenic disturbance in a Caatinga dry tropical forest, Brazil. We tested for trait-environment relationships using multivariate methods (RLQ) accounting for groups of species sharing similar responses to gradients and similar expression of multiple traits (i.e. response groups). Overall, species' abundances changed predictably in response to rainfall and soil fertility, and were mediated by functional traits, i.e. species with particular trait combinations tended to respond similarly to multifactorial conditions. Briefly, three ecological strategies emerged: species with low wood density and soft (i.e. lower dry matter content), thick leaves converged into a trait syndrome characterizing a drought-avoidance strategy through water storage. They were particularly abundant under extremely low precipitation and relatively high soil field capacity. Under conditions of increasing rainfall and decreasing soil field capacity, species with high wood density were favored, consistent with a drought-tolerance strategy. However, these species fell into two groups relative to leaf-investment: more conservative leaves (low SLA) through relatively fertile soils vs. thinner and softer (i.e. high SLA) leaves over unfertile soils. In seasonally dry tropical forests, low SLA on relatively fertile soils may represent a water conservation strategy. Unexpectedly, no ecological strategy emerged in response to disturbance. The patterns we uncovered help to understand the interplay between precipitation, soil fertility and anthropogenic disturbance in plant species filtering in seasonally dry tropical forests. Moreover, our results underline that impacts of future climate

change will depend on how rainfall patterns covary with finer-scale environmental factors such as soil fertility and field capacity.

Key-words: annual precipitation, Caatinga, environmental gradients, anthropogenic disturbance, functional traits, soil fertility, soil field capacity, species distribution.

Introduction

The understanding of how and why plant traits vary among species and how they respond to environmental conditions has been a major challenge in community ecology (Schimper, 1903; Grime & Pierce 2012). A better understanding of trait-environment relationships may enhance our ability to predict vegetation responses to both natural and human-generated environmental gradients (McGill, Enquist, Weiher, & Westoby, 2006). Functional traits mediate species responses to environmental conditions, and thus are considered a meaningful approach to address species distribution patterns along resource and disturbance gradients (Westoby & Wright, 2006). However, co-occurring species may also present substantial trait variation, sometimes even greater than among-site variation along environmental gradients (de Bello et al., 2009; Wright et al., 2004). Understanding trait-environment relationships is particularly challenging because multiple environmental drivers act simultaneously on community assembly (Bagousse-Pinguet et al., 2017; Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017) and species responses may depend on multiple ecological dimensions represented by co-varying traits (Laughlin & Messier, 2015; Muscarella & Uriarte, 2016).

Two functional dimensions are globally ubiquitous in plants (Díaz et al., 2016; Pierce et al., 2017). The first is related to the size of whole plants (i.e. maximum height) and their organs (e.g. leaf area), while the other reflects variation in resource-use and is related to the leaf (e.g. specific leaf area) and stem (e.g. wood density) economic spectra (Chave et al., 2009; Wright et al., 2004). The economic spectra suggest trade-offs where plants vary from acquisitive species that are able to exploit resources and grow rapidly, to conservative species which grow slowly and invest in durable tissues (see Reich, 2014). Additionally, larger seeds allow for higher seedling performance under low resource availability, while small seeds allow for greater seed output which favors recruitment across less stressful sites (i.e. the tolerance-fecundity trade-off, *sensu* Muller-Landau 2010). The exploration of relationships between combinations of co-varying traits, i.e. ecological strategies, and environmental gradients can help to elucidate both assembly mechanisms and responses to environmental changes, either natural or human-induced (Dwyer & Laughlin 2017; Muscarella & Uriarte, 2016). Specifically, recognizing groups of species that share similar traits and respond similarly to environmental gradients (i.e. “response groups", Lavorel & Garnier, 2002) will help to identify mechanisms underlying plant-environment relationships and will also allow to improve guidelines for environmental management.

Seasonally dry tropical forests are naturally exposed to low levels of precipitation and a long and severe dry season annually, with clear impacts on plant species distribution and species assembly/community organization (Grossiord et al. 2017, Rito et al. 2017). These ecological forces are expected to gain importance as climate change models have predicted more severity of drought events (Pachauri et al., 2014). Additionally, many dry forests support low-income rural populations which exert significant and continuous pressures on biodiversity (Ribeiro, Arroyo-Rodriguez, Santos, Tabarelli, & Leal, 2015; Rito et al., 2017; Ribeiro et al. 2019). Chronic anthropogenic disturbances (*sensu* Singh, 1998) occurs through grazing and the continuous extraction of firewood and non-timber forest products, which can for example disrupt nutrient cycling and reduce soil fertility (Villela, Nascimento, Aragão & Gama, 2006). Seasonal drought acts as a strong environmental filter for plants in seasonally dry forests and gives rise to adaptive traits related to avoiding drought stress (i.e. maintaining a high water status under conditions of low water availability through maximizing water uptake and storage and minimizing water loss), or tolerating of drought stress (i.e. maintaining tissue function despite of a low water status) (Bartlett, Detto, & Pacala, 2019; Borchert, 1994; O’Brien et al., 2017; Ramírez-Valiente & Cavender-Bares, 2017). Plant community functional composition also respond strongly to gradients of soil fertility that can be of both natural and human-induced origin, as well as to disturbance (Condit et al., 2013; Pinho et al., 2018; Sfair, Bello, Franca, Baldauf, & Tabarelli, 2018). Nutrient rich soils generally favor plants with acquisitive traits (Jager, Richardson, Bellingham, Clearwater & Laughlin, 2015; Pinho et al. 2018), and increasing disturbance generally favors fast-growing, colonizer strategies exhibiting for example small seeds and soft leaves and trunks (i.e. “ruderal” strategy; Grime & Pierce, 2012).

However, when water is scarce, as in seasonally dry tropical forests, plants must deal with a complex interplay of stressors that involve multiple trade-offs, which may give rise to distinct trait combinations (Bartlett et al., 2019; Wright, Reich & Westoby, 2001). Variation of stem and leaf economic traits may additionally be decoupled (Baraloto et al., 2010), and give rise to distinct functional strategies to deal with varying combinations of water/nutrient availability and disturbances. In fact, contrasting functional strategies may coexist in dry forests (Bagousse-Pinguet et al., 2017). For example, increasingly intense droughts as well as reduced soil fertility both generally favor shorter stature (Bagousse-Pinguet et al., 2017) and conservative resource-use traits, which leads to slow growth (see Reich 2014) but benefit plants under low resource availability by low metabolic resource demand and minimizing resource loss through dense, durable tissues (Grime & Pierce 2012). On the other hand, the production of cheap leaves with soft tissues, which is linked to an acquisitive strategy, may also favor plants in seasonally dry forests by allowing them to abscise leaves and avoid transpirational water loss during the dry season (i.e. dry season deciduousness), but also to take advantage of high water availability in the short wet season for carbon assimilation for growth and reproduction (Borchert 1994, Ramírez-Valiente & Cavender-Bares, 2017). To complicate matters more, disturbance can vary along natural environmental gradients, and these may operate simultaneously and impose contrasting or synergistic effects on plant assemblages (Peltzer, Kurokawa & Wardle, 2016; Rito et al., 2017; Sfair et al., 2018). However, to date our knowledge on the complex interactions between various natural environmental gradients and disturbance, and their effects on filtering of various traits is unfortunately still too limited to make specific predictions on trait combinations.

Here we aimed to identify trait-environment relationships that help to explain plant community composition across natural gradients in combination with human-caused disturbances in the Caatinga seasonally dry tropical forest biome in Brazil (Silva, Leal & Tabarelli, 2017). We explored how functional strategies of woody plants change in response to natural gradients of rainfall and soil conditions, as well as to different types of chronic anthropogenic disturbances. Specifically, we (1) determined the functional traits that are most responsive to environmental conditions (resources and disturbance); and (2) identified groups of species with similar trait combinations that respond similarly to environmental gradients (response groups). For this, we considered leaf, wood, seed and whole-plant traits related to both size and resource-use spectra. We expected that traits would covary in various different ways along multiple, interacting environmental gradients, and thus give rise to several distinct trait combinations that allow to cope with specific environmental constraints, rather than the general pattern that reduced resource availability (water and nutrients) leads to dominance of more conservative traits, while increasing disturbance favors colonizing, fast-growing strategies (Greenwood et al. 2017; Grime & Pierce 2012).

Methods

Study site

The study was carried out in the Catimbau National Park, located in Pernambuco state, Brazil (Fig. 1). This is one of the few protected areas of Caatinga, with an area of *c*. 60,000 ha. The vegetation is dominated by shrubs and trees, mostly deciduous. The climate is semi-arid (Koeppen's classification Bsh), with a mean annual temperature of 23ºC and a high variation of annual rainfall across the landscape (from 480 to 1100 mm/year). Approximately 70% of the Catimbau National Park has sandy soils. Despite being a protected area, approximately 300 families live inside the park due to poor implementation of land regulations. Such low-income populations depend on extensive goat farming, slash-and-burn agriculture and extraction of forest products, which exert significant pressures on biodiversity (Melo, 2017; Rito et al., 2017).

Floristic and trait data

We established 20, 20m × 50m vegetation plots, at least 2-km but mostly considerably further apart from each other (Fig. 1), along orthogonal gradients of precipitation (500-1000 mm) and chronic anthropogenic disturbance (see below for further detail on gradients). All plots were established on flat terrain to control for potential effects of slope. In each plot, all woody plants with diameter at soil level ≥ 3 cm and height ≥ 1 m were recorded and identified to species. For further detail on the floristic inventory, see Rito et al. (2017).

Among the recorded individuals in each plot, 10 to 20% were randomly sampled for trait measurements (following Paine, Baraloto, & Díaz, 2015). For all species with ≥ 5 sampled individuals, we calculated species mean trait values across all individuals for further analyses (5-95 individuals measured per species and trait, see Table S1 for details). We thus included trait data for 46 species from 18 botanical families (Table S1), which accounted for 35% of the total number of species recorded in all plots. The 46 species comprised *c*. 80% of the individual plants in each plot, which allowed meaningful calculations of community functional composition (Pérez-Harguindeguy et al. 2013). In this study we did not include intraspecific variability of traits across sites, because a previous study had shown that it is weak along the environmental gradients considered (Sfair et al., 2018). For further details on the trait sampling, see Sfair et al. (2018).

We assessed seven resource-use and size-related traits that are expected to reflect the basic trade-offs in leaves, wood, seeds and whole-plant among tree species (Díaz et al., 2016): 1. leaf area (LA); 2. specific leaf area (SLA); 3. leaf dry matter content (LDMC); 4. leaf thickness (Lth); 5. stem specific density (SSD); 6. seed size (SS); and 7. maximum height (Hmax). The maximum plant height (Hmax) of each species was defined according to Poorter, Bongers, & Bongers (2006), using data from the community inventory (Rito et al., 2017). Seed size was assessed as the seed length, which is positively related to seed mass ($R^2 = 0.76$) in the flora of the Catimbau National Park (unpublished data). Seed lengths were gathered from the literature and herbaria specimens (e.g. UFPE, Reflora database), since most species did not produce fruit during the study period. All other traits were measured following Pérez-Harguindeguy et al. (2013).

Environmental gradients

We considered the effects of multiple environmental and disturbance gradients in the studied landscape. As environmental variables, we included mean annual precipitation (MAP), soil fertility (SF) and soil field capacity. The mean annual precipitation in each plot was obtained from the updated WorldClim global climate data repository of monthly average data over all available years (1970-2000) with 1-km spatial resolution (Fig. 1), using the ‘maptools’ package for R (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Mean annual precipitation ranged considerably from 510 to 940 mm among plots (see Fig. 1). We collected in each plot 10 soil samples (0 - 30 cm deep) and measured physiochemical properties following the procedures recommended by the Brazilian Ministry of Agriculture (Claessen, 1997). Soil fertility (SF) was assessed as a "soil evaluation factor" (*sensu* Lu, Moran, & Mausel, 2002) according to the following formula:

$$SF = [Ca + Mg + K - \log(1+Al)] * OM + 5$$

where Ca, Mg, K, Al are the concentrations of the respective exchangeable ions (cmolc dm^{-3}), and is OM = organic matter (g kg^{-1}). Ca, Mg, and K are plant nutrients, whereas Al is toxic to plant growth and correlates negatively with soil pH. OM is related to various soil fertility factors, e.g. nutrient availability, soil structure, air infiltration and water infiltration and retention (Lu et al., 2002). Soil field capacity, i.e. the percentage of water the soil can hold at saturation, which varies mainly with soil texture and clay content, was measured as the soil water content (%) at 0.33 atm. Each soil attribute considered varied widely across plots, and the ranges, means and standard deviations are provided in Table S2.

Disturbance gradients

Human-caused disturbance in the study region is related to how people use natural resources rather than to deforestation, due to the poor conditions for profitable agriculture (Melo, 2017). In our study we used a subset from many variables, that were shown to represent the main axes of chronic disturbance in the area (Arnan et al., 2018): We considered a wood extraction index (WEI) and a grazing pressure index (GPI) (Arnan et al., 2018). The WEI is based on the basal area of all cut stems and the ratio between aboveground biomass of living plants to woody debris in the plot, where a higher ratio indicate that wood debris are more extracted for firewood. The GPI considers goat trail length and the frequency of goat and cattle dung. For further details, see Appendix S1 and Arnan et al. (2018).

Data analysis

We first examined pairwise correlations between traits (Table S3), and pairwise correlations between the environmental and disturbance variables (Table S4). Correlations were weak overall (all $r < 0.7$), and all traits and environmental and disturbance variables were maintained in further analyses.

We applied the Hellinger transformation on the species abundance matrix to reduce discrepancies on rarity of species (Legendre & Gallagher, 2001), and standardized trait values to zero mean and unit standard deviation, using *decostand* function from the *vegan* R package. To test for trait-environment relationships we performed an RLQ analysis, which allows to assess the covariation between the environmental and disturbance gradients (matrix R) and species trait values (matrix Q), which were linked to a species abundance table (matrix L) in a three-way ordination (Kleyer et al., 2012). The RLQ analysis explores the joint structure of the three tables by looking for a combination of traits and environmental variables of maximal covariance, weighted by the species abundances (Dolédec et al., 1996). The first RLQ axis summarizes the dominant trait-environment covariation, and each successive axis defines the remaining covariation. As environmental variables are commonly correlated and simultaneously affect community structure, RLQ is useful for reducing multidimensionality, allowing the exploration of the combined effect of such variables on species assembly. Moreover, by investigating species' relative positions along RLQ axes and their grouping in this multidimensional space, RLQ allows trait syndromes occupying different positions along multiple environmental gradients to be identified (see Gámez-Virués et al., 2015). We used the *ade* package in R for the RLQ analysis (Dolédec, Chessel, Braak, & Champely, 1996). To test the significance of the relations between traits and environmental/disturbance gradients, we first tested the links between site scores on the RLQ axes and the predictor variables, then we tested the links between species scores on the RLQ axes and their trait values (Gámez-

Virués et al., 2015), using Pearson correlations with Bonferroni adjustments for multiple comparisons, which reduces the risk of type I errors.

Finally, to identify groups of species with similar responses to the gradients considered (i.e. response groups) and with similar expressions of multiple traits underlying their response (i.e. ecological strategies), we identified clusters within RLQ component-space, based on Euclidean distances between species on the first two RLQ axes and clustered by Ward's hierarchical clustering (Everitt et al., 2001). The optimal number of clusters was verified by applying an automated *Calinski-Harabasz* stopping criterion that chose the most parsimonious number of clusters (Caliński & Harabasz, 1974), as recommended by Kleyer et al. (2012). In a comparison of multiple clustering methods with contrasting artificial datasets this was identified as the best procedure to predict the true cluster structure (Milligan & Cooper 1985). In short, it uses a ratio of between-cluster-means and within-cluster sums of squares for determining the number of clusters. All the analyses were performed in R 3.5.0 (R Core Team 2017).

Results

The first two axes of the RLQ analysis captured 91% of the joint covariance of species' abundances (L-table), trait values (Q-table) and environmental gradients (R-table). The first axis (55% of the covariance) describes mostly the precipitation gradient and changes in species' wood density, leaf thickness and LDMC (Table 1). The second axis (36% of the covariance) summarizes the orthogonal gradient of soil fertility and leaf traits related to resource use, i.e. SLA, LDMC and leaf thickness (Table 1). Changes of species traits were not related to any of the disturbance gradients (Table1).

The position of species in multivariate space separated into three groups based on a cluster analysis, according to their similarity in trait expressions and responses to environmental conditions (i.e. response groups) (Fig. 2a). Low precipitation and high soil field capacity (Fig 2a — axis 1, right side) favored species with a trait syndrome (S2) of mid to low wood density (Fig. 2b) and low LDMC (Fig. 2d). Conversely, increasing precipitation and decreasing soil field capacity favored species with denser wood and thinner but denser (high LDMC) leaves (Fig. 3; Table 1). Under relatively high precipitation two trait combinations (S1 and S3) occurred and the dominance depended on soil fertility (Fig 2a — axis 2): species on less fertile soils were characterized by mid to high wood density and acquisitive leaves (S1, i.e. high SLA, low LDMC and leaf thickness; Fig 2c-e); on the other hand, species abundant on more fertile soils were characterized by conservative leaf traits (S3, low SLA and thin leaves with high dry matter content; Fig 2c-e). The remaining traits were not responsive to environmental gradients and varied randomly and were unrelated to species' abundances (Fig. 3).

Discussion

Species assembly in seasonally dry tropical forests depends on the interaction among multiple traits and environmental variables. Specifically, we found that different environmental gradients may concomitantly affect several uncorrelated traits. Thus, although individual traits correlate with specific environmental variables, species with particular combinations of traits tend to respond similarly to environmental conditions when considering multiple factors (Muscarella & Uriarte, 2016). Specifically, our results suggest one main strategy of drought-avoidance through water storage, which is particularly favored under extremely low levels of precipitation but relatively high soil field capacity. This strategy is characterized by low wood density, which is correlated with high wood water content in species in our system (negative relation wood density-water content $R^2 = 0.70$; n = 23 species; Jung & Engelbrecht, unpublished data) as well as other tropical dry forests (Borchert, 1994); and by high leaf thickness and low LDMC, which indicates high leaf water contents. On the other hand, as rainfall increases and soil field capacity decreases, two strategies emerged. Both are characterized by high stem density, which is correlated with high resistance to hydraulic failures (Hacke, Sperry, Pockman, Davis, & McCulloh, 2001; Santiago et al. 2018) and thus allows for maintenance of water transport under low water status (i.e. drought-tolerance). The two strategies separate along the gradient of soil fertility, with species with high SLA prevailing under low nutrients, and those with low SLA prevailing in more fertile soils (see Fig. 4 for a summary). The functional characteristics distinguishing these strategies seem to be related to variation in leaf longevity and water-use efficiency expressed as a trade-off between LDMC and SLA. The patterns we have uncovered thus shed light on the poorly understood interplay between precipitation and soil fertility in plant species filtering in dry forests (Bagousse-Pinguet et al., 2017), highlighting the importance of including multiple environmental filters as drivers of species assembly. Surprisingly, human-caused disturbances did not affect the prevalence of species functional strategies in tree communities, suggesting that chronic sources of disturbance have a negligible effect on trait-environment relationships.

Overall, the reported changes in prevalence of species functional traits in response to soil conditions and precipitation support previous studies that have indicated variation in water availability and soil-fertility as key assembly forces in seasonally dry tropical forests (Bagousse-Pinguet et al., 2017; Grossiord et al., 2017; Rito et al., 2017). Species' abundances changed in response to environmental variation, mediated by their functional traits (Table1, Fig. 3), highlighting the role of niche partitioning along gradients of resource availability in driving species distributions and community assembly processes (Engelbrecht et al., 2007; Tilman, 1982). Nevertheless, species with conservative traits are thought to dominate under low resource (water and nutrients) availability, while species with more acquisitive traits tend to prevail with increasing resource availability across biomes (Chave et al., 2009; Greenwood et al., 2017; Grime & Pierce 2012; Hodgson et al., 2011; Jager et al., 2015; Muscarella &

Uriarte, 2016; Pinho et al., 2018; Wright et al., 2004). Conversely, our results suggest that at small spatial scales the opposite may be true for trees inhabiting seasonally dry tropical forests (Borchert, 1994; Ramírez-Valiente & Cavender-Bares, 2017).

The patterns we observed were not consistent with those observed across ecosystems (Bartlett et al., 2019; Greenwood et al., 2017). However, they can be interpreted in the specific case of seasonally dry habitats. For instance, while high wood density may prevent hydraulic failure under low soil moisture (Hacke et al. 2001), low wood density can allow plants to store water and thus maintain physiological activity during the dry season (i.e. reduced risk of damaging water potentials), what is particularly important under severe drought conditions (Borchert, 1994; Gleason et al., 2013; Ramírez-Valiente & Cavender-Bares, 2017). Also, the prevalence of more conservative traits (i.e. thicker and denser leaves, resulting in lower specific leaf area; Hodgson et al., 2011) in less fertile soils may be a result of selection for increased water-use efficiency under high soil fertility, as leaf nitrogen (i.e. photosynthetic enzymes) per area can increase when SLA decreases, thus favouring a larger drawdown of internal CO_2, which allows for reduced water loss at a given photosynthetic rate (i.e. higher efficiency at low stomatal conductance; Wright et al., 2001; Maire et al., 2015). This has been previously suggested to be particularly likely under high soil fertility in arid ecosystems that would demand higher water-use efficiency (Bagousse-Pinguet et al., 2017). Overall, the patterns we found demonstrate that different trait syndromes tend to dominate under contrasting environmental conditions at the landscape-scale, and thus may coexist in seasonally dry ecosystems (Borchert, 1994; Bagousse-Pinguet et al., 2017).

Finally, our findings do not support the notion that human chronic disturbances operate as species assembly force by affecting plant trait distributions. Previous studies in Caatinga dry forest documented the impact of particular sources of chronic disturbances such as grazing pressure or wood extraction on both the taxonomic and phylogenetic diversity of tree assemblage (Ribeiro et al., 2016; Rito et al., 2017). However, community-level functional composition can respond independently of its taxonomic or phylogenetic dimension (Cavender-Bares et al. 2009, Purschke et al., 2013). In fact, a recent study in Caatinga documented reduced functional diversity due to the prevalence of more acquisitive strategies as chronic disturbances increase (Ribeiro et al. 2019). However, the authors have not considered other potential drivers as we did. Furthermore, the much wider variation exhibited by precipitation across our focal plots (~ 500 to 1000 mm) may represent a stronger force selecting for trait syndromes, turning disturbance a force of marginal importance. In fact, while other studies have considered the isolated effects of different drivers, here we assessed the concomitant effects of multiple - and interacting - environmental and disturbance variables, which may reduce the significance of a specific factor when it has a secondary effect. For instance, wood extraction had a relatively high correlation coefficient with the second RLQ axis ($r = 0.60$), but this was not significant after correction for multiple comparisons, given the much stronger effect of soil fertility captured by this axis (Table 1).

Our findings highlight the usefulness of multi-trait approaches considering the joint effects of multiple gradients for predicting the responses of seasonally dry tropical forests to environmental changes, as species assembly depends on the interaction among multiple traits and environmental variables. For instance, the predicted impacts of global climate change in dry forests will depend on how rainfall patterns covary with other environmental factors across space, particularly soil fertility and the ability of soils to retain water. More importantly, as plant responses to changing conditions are mediated by functional traits, negative effects are expected to be non-randomly distributed across species. Improving our understanding of the mechanistic factors governing species assembly in tropical dry forests will require the integration of populational demographic parameters, intraspecific trait variation, spatial distributions and historical factors. Such an approach would ultimately promote a better understanding of the multiple mechanisms (physiological, ecological and evolutionary) underlying trait-environment relationships.

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Table 1. Correlation coefficients for the relationships between environmental variables and plant functional traits with the first two RLQ axes. Bold *r*-values represent significant correlations according to Bonferroni adjustment for multiple tests. *p < 0.05, **p < 0.01.

		RLQ axis 1	**RLQ axis 2**
Environmental variables	Precipitation	**-0.86****	0.26
	Soil field capacity	**0.66***	0.26
	Soil fertility	-0.20	**0.72****
	Wood extraction intensity	-0.48	-0.60
	Grazing pressure intensity	-0.36	-0.29
Functional traits	Wood density	**-0.89****	-0.05
	Leaf thickness	**0.54****	**0.63***
	Leaf dry matter content	**-0.54****	**0.67****
	Specific leaf area	-0.14**	**-0.88****
	Leaf area	0.21	0.33
	Seed size	0.45	0.23
	Maximum height	-0.13	0.09

Figure legends

Figure 1. Location of (a) the Caatinga domain (dark polygon) and the study site in Brazil (star), and (b) outline of the Catimbau National Park with the sampling plots along the precipitation gradient.

Figure 2. Trait syndromes detected from cluster analysis along the first two RLQ axes (a) and boxplots illustrating functional trait values for each trait syndrome (b-h). The boxplots show the median among species traits (bold line), 25-75% quartiles (boxes), and < 1.5 times the interquartile range (whiskers). Filled circles show extreme outliers. Colors refer to the respective trait syndrome. Precipitation and soil fertility account for most of the variance on RLQ axis 1 and 2, respectively. See Table 1 for correlations of species traits and environmental variables with the RLQ axes.

Figure 3. Correlations between species traits values and their scores on the first and second RLQ axes, representing variation in rainfall and soil fertility, respectively (see Table 1). 95% ellipses are shown for statistically significant Pearson's correlations after Bonferroni adjustment for multiple tests. Circles represent each plant species and colors refer to their respective trait syndromes (i.e. species groups based on co-varying traits and similar responses to environmental variables, see Fig. 2).

Figure 4. Schematic representation of the 'trait syndromes' in the form of a triangle where one combination of trait values representing tree species with soft-wood and soft leaves (S2) increase in prevalence under low precipitation while two syndromes of hard-wooded species, one with conservative (S3) and other with acquisitive leaves (S1), are favored under high precipitation varying according to soil fertility.

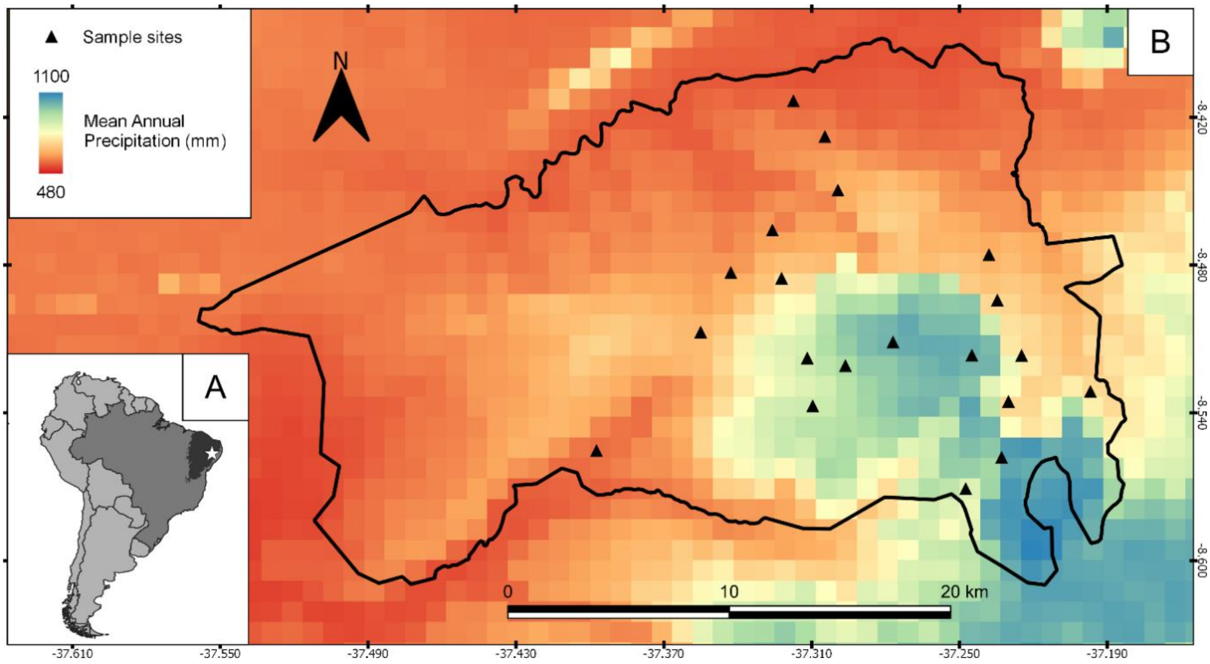
Sample sites
1100
Mean Annual
Precipitation (mm)
480
N
B
A
0
10
20 km
-8.420
-8.480
-8.540
-8.600
-37.610
-37.550
-37.490
-37.430
-37.370
-37.310
-37.250
-37.190

Figure 1.

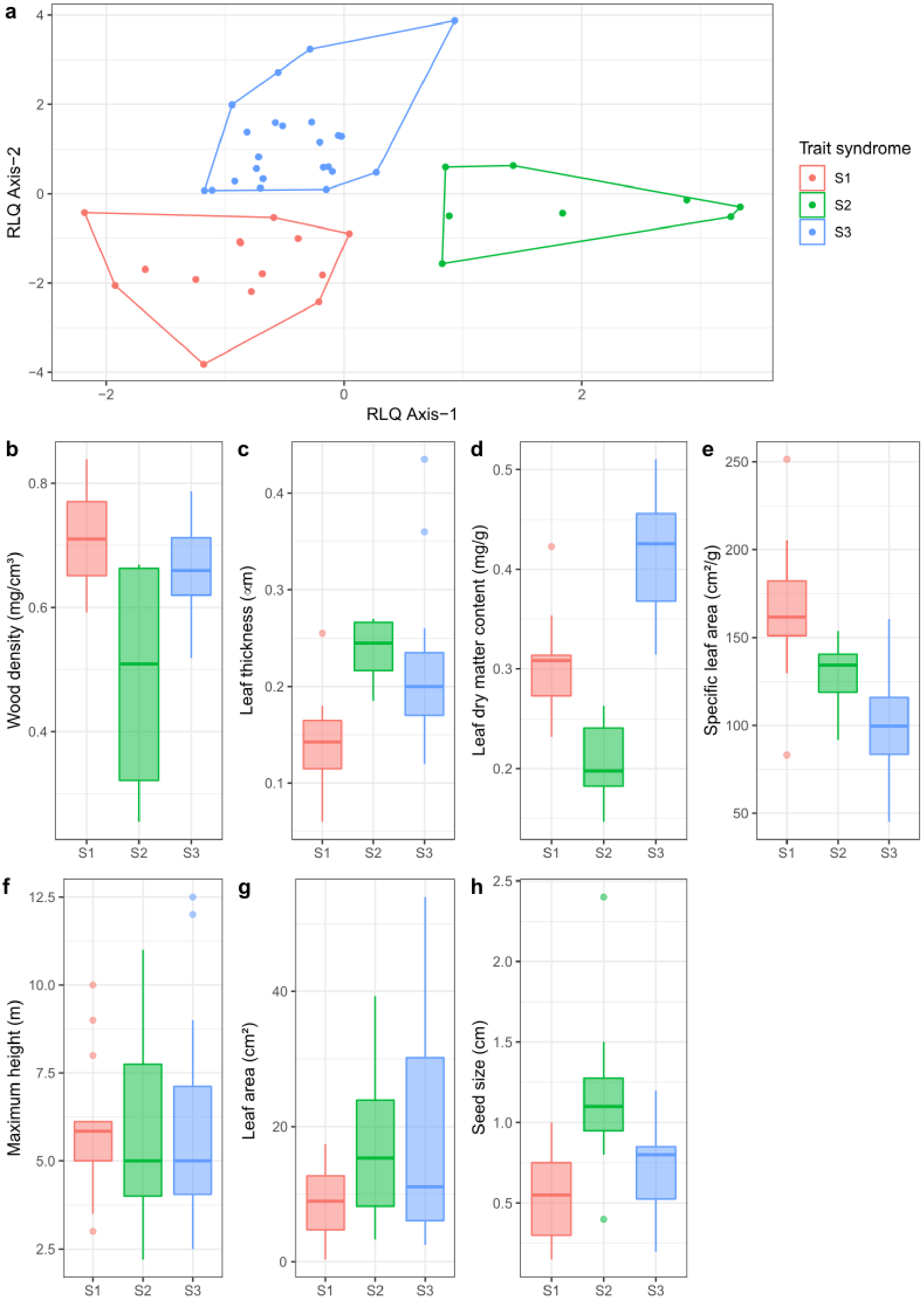
a
RLQ Axis−2
RLQ Axis−1
4
2
0
−2
−4
−2
0
2
Trait syndrome
S1
S2
S3
b
Wood density (mg/cm³)
0.8
0.6
0.4
c
Leaf thickness (∝m)
0.4
0.3
0.2
0.1
d
Leaf dry matter content (mg/g)
0.5
0.4
0.3
0.2
e
Specific leaf area (cm²/g)
250
200
150
100
50
f
Maximum height (m)
12.5
10.0
7.5
5.0
2.5
g
Leaf area (cm²)
40
20
0
h
Seed size (cm)
2.5
2.0
1.5
1.0
0.5
S1
S2
S3

Figure 2.

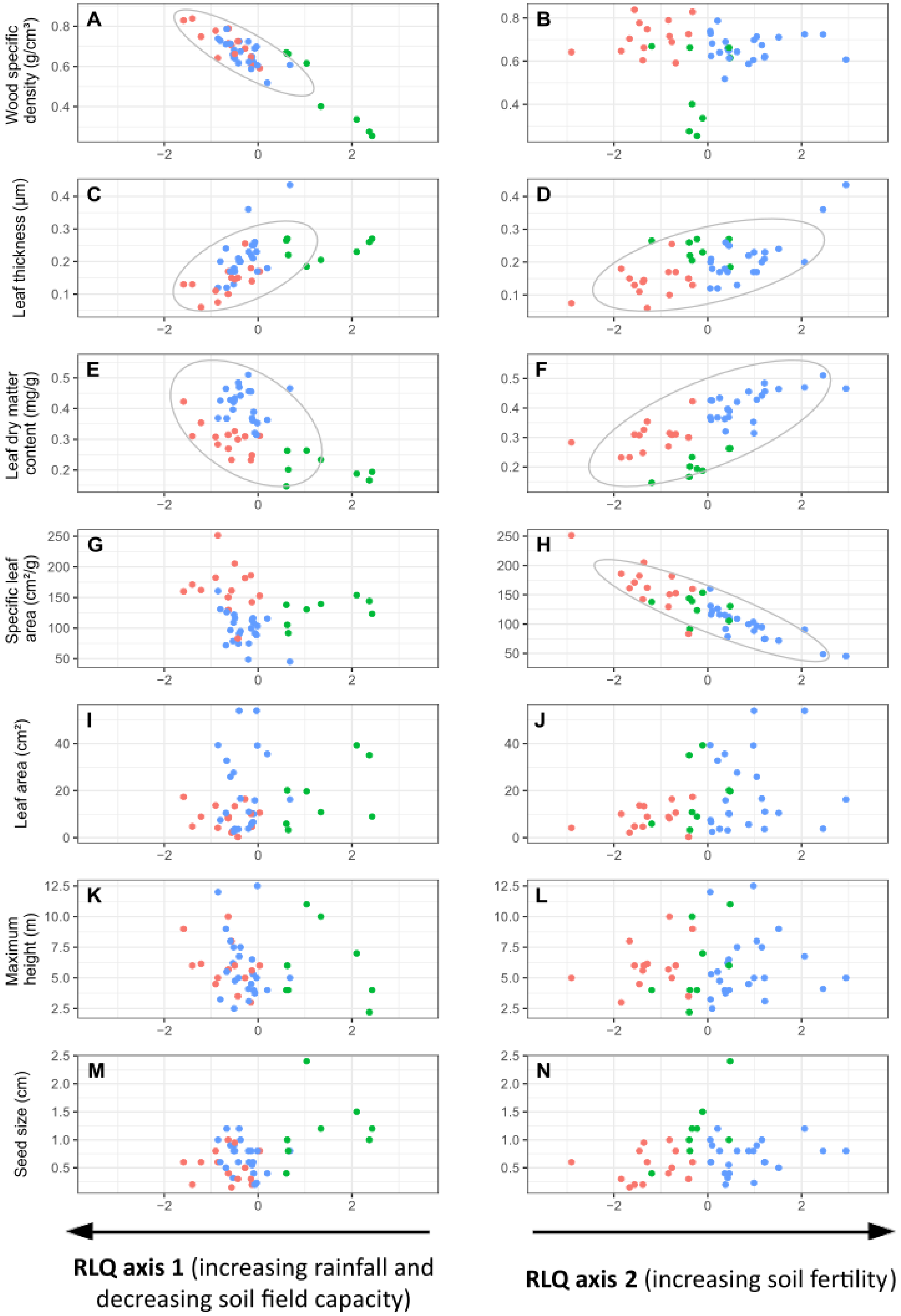
A
B
C
D
E
F
G
H
I
J
K
L
M
N
Wood specific density (g/cm³)
Leaf thickness (µm)
Leaf dry matter content (mg/g)
Specific leaf area (cm²/g)
Leaf area (cm²)
Maximum height (m)
Seed size (cm)
0.8
0.6
0.4
0.1
0.2
0.3
0.4
0.5
50
100
150
200
250
0
20
40
2.5
5.0
7.5
10.0
12.5
0.5
1.0
1.5
2.0
2.5
−2
0
2
RLQ axis 1 (increasing rainfall and decreasing soil field capacity)
RLQ axis 2 (increasing soil fertility)

Figure 3.

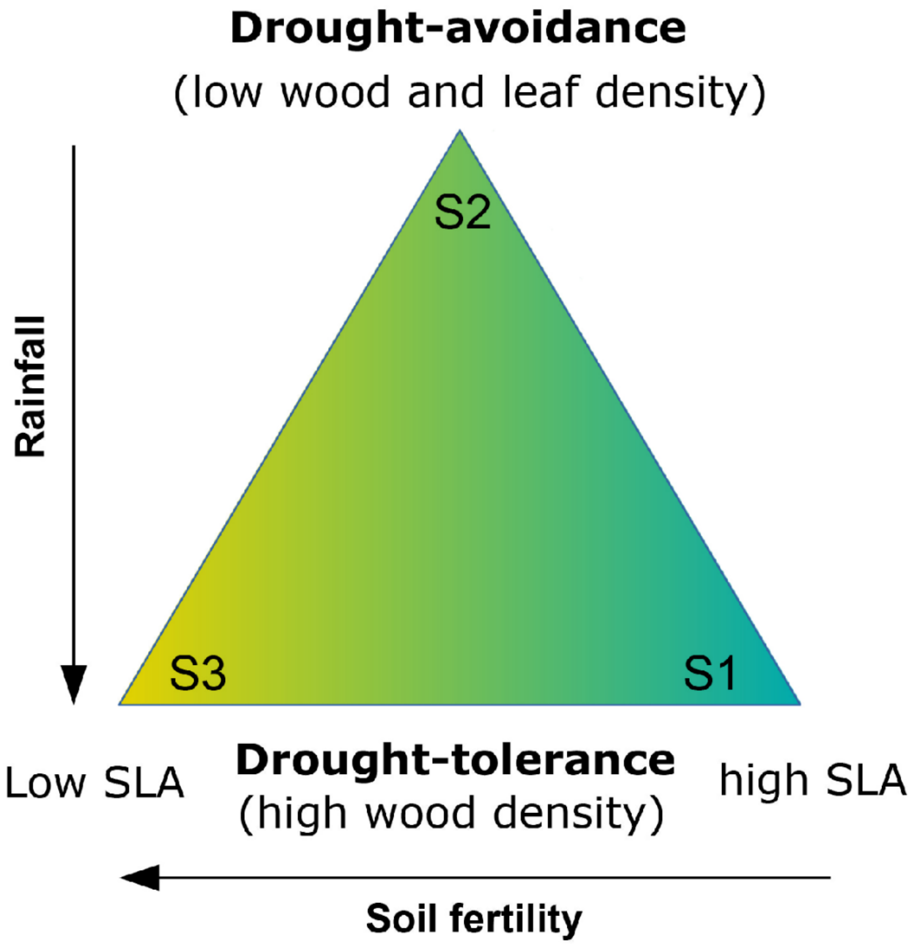
Drought-avoidance
(low wood and leaf density)
S2
Rainfall
S3
S1
Low SLA
Drought-tolerance
(high wood density)
high SLA
Soil fertility

Figure 4.

Table S1. Trait syndromes and mean trait values of woody plant species (n = 46) from Catimbau National Park, a seasonally dry tropical forest landscape in Pernambuco state, northeast Brazil. The number of individuals (N ind.) sampled for trait measurement is shown for each species. WD = wood specific density; LT = leaf thickness; LDMC = leaf dry matter content; SLA = specific leaf area; Hmax = maximum height; LA = leaf area; SS = seed size.

	Family	**N ind.**	**Traitsyndrome**	**WD (g/cm³)**	**LT (mm)**	**LDMC (g/g)**	**SLA (cm²/g)**	**Hmax (m)**	**LA (cm²)**	**SS (cm)**
Acalypha brasiliensis	Euphorbiaceae	5	S1	0.84	0.13	0.31	171.07	6.00	4.78	0.20
Annonaleptopetala	Annonaceae	23	S1	0.59	0.17	0.31	152.69	6.00	10.66	0.80
Balfourodendronmolle	Rutaceae	6	S2	0.62	0.19	0.26	130.51	11.00	19.74	2.40
Bauhiniaacuruana	Fabaceae	12	S1	0.69	0.26	0.31	181.79	5.00	16.45	0.50
Byrsonimagardneriana	Malpighiaceae	13	S3	0.61	0.25	0.39	108.04	4.00	10.09	0.40
Chloroleuconfoliolosum	Fabaceae	11	S1	0.75	0.06	0.35	162.07	6.15	8.96	0.60
Cnidoscoluspubescens	Euphorbiaceae	31	S2	0.34	0.23	0.19	153.66	7.00	39.28	1.50
Commiphoraleptophloeos	Burseraceae	18	S2	0.40	0.21	0.23	139.27	10.00	10.89	1.20
Crotongrewioides	Euphorbiaceae	5	S3	0.66	0.17	0.40	78.48	6.20	3.13	0.32
Crotonheliotropiifolius	Euphorbiaceae	6	S2	0.67	0.27	0.15	137.90	4.00	5.89	0.40
Crotonnepetifolius	Euphorbiaceae	19	S1	0.79	0.17	0.27	129.54	5.70	8.91	0.40

Crotonsonderianus	Euphorbiaceae	5	S3	0.62	0.21	0.36	116.22	5.30	6.60	0.60
Croton tricolor	Euphorbiaceae	41	S1	0.60	0.14	0.25	142.30	5.60	4.68	0.20
Cynophalla flexuosa	Capparaceae	8	S3	0.61	0.44	0.47	45.06	5.00	16.28	0.80
Erythroxylumrevolutum	Erythroxylaceae	19	S3	0.65	0.25	0.37	112.58	6.50	10.35	0.55
Erythroxylumsuberosum	Erythroxylaceae	5	S3	0.59	0.22	0.46	99.63	4.50	5.57	0.80
Guapiragraciliflora	Nyctaginaceae	22	S2	0.66	0.27	0.26	105.30	6.00	20.18	1.00
Jatrophamollissima	Euphorbiaceae	12	S2	0.28	0.26	0.17	144.09	2.20	35.09	1.00
Jatrophamutabilis	Euphorbiaceae	80	S2	0.25	0.27	0.19	123.36	4.00	9.00	1.20
Lantanacamara	Verbenaceae	5	S2	0.66	0.22	0.20	91.68	4.00	3.27	0.80
Libidibiaferrea	Fabaceae	5	S3	0.64	0.13	0.42	109.07	7.50	27.67	0.80
Lippia grata	Verbenaceae	23	S1	0.70	0.15	0.23	161.13	8.00	2.11	0.15
Maytenusrigida	Celastraceae	6	S3	0.72	0.36	0.51	48.65	4.10	3.82	0.80
Melochia tomentosa	Malvaceae	5	S1	0.65	0.18	0.23	185.98	3.00	10.13	0.30
Mimosa lewisii	Fabaceae	10	S1	0.64	0.08	0.28	251.43	5.00	4.18	0.60
Peltogyne pauciflora	Fabaceae	32	S3	0.67	0.20	0.44	94.87	7.50	16.65	1.00
Piptadeniastipulacea	Fabaceae	30	S1	0.72	0.10	0.31	150.51	10.00	8.14	1.00
Pityrocarpamoniliformis	Fabaceae	90	S3	0.61	0.17	0.35	103.45	12.50	39.18	0.80

Poincianellamicrophylla	Fabaceae	95	S3	0.71	0.17	0.43	96.46	8.00	25.88	0.90
Poincianellapyramidalis	Fabaceae	5	S3	0.72	0.20	0.47	90.41	6.75	53.96	1.20
Psidiumbrownianum	Myrtaceae	9	S3	0.71	0.24	0.46	71.75	9.00	10.54	0.50
Psidiumoligospermum	Myrtaceae	10	S3	0.62	0.23	0.46	74.88	3.10	11.09	0.60
Ruprechtia laxiflora	Polygonaceae	5	S3	0.64	0.17	0.43	116.19	4.75	3.71	0.80
Senegaliabahiensis	Fabaceae	27	S1	0.83	0.13	0.42	159.88	9.00	17.40	0.60
Senegaliapolyphylla	Fabaceae	7	S3	0.74	0.12	0.37	160.49	12.00	39.34	1.00
Senegaliapiauhiensis	Fabaceae	5	S3	0.79	0.12	0.37	126.19	5.50	32.74	1.20
Senna rizzinii	Fabaceae	6	S3	0.73	0.20	0.43	130.86	3.25	7.47	0.60
Senna trachypus	Fabaceae	5	S1	0.78	0.11	0.31	182.30	4.50	13.72	0.80
Sideroxylonobtusifolium	Sapotaceae	5	S3	0.62	0.21	0.48	74.55	5.00	3.62	0.60
Strychnosrubiginosa	Loganiaceae	5	S3	0.68	0.18	0.43	122.13	2.50	2.48	0.90
Trischidiummolle	Fabaceae	13	S3	0.52	0.18	0.36	115.49	4.00	35.60	0.40
Turneracearensis	Passifloraceae	5	S1	0.73	0.15	0.30	83.08	3.50	0.32	0.30
Waltheriabrachypetala	Malvaceae	7	S3	0.69	0.26	0.32	91.54	3.75	15.90	0.20
Zanthoxylumstelligerum	Rutaceae	7	S3	0.70	0.23	0.31	88.34	5.00	53.96	0.23
Ziziphusjoazeiro	Rhamnaceae	6	S1	0.66	0.15	0.33	205.24	6.00	13.41	0.95

Table S2. Variation, mean and standard deviation of soil variables measured in 20 plots in the Catimbau National Park, a seasonally dry tropical forest in Pernambuco state, northeast Brazil.

Soil attributes	Variation	Mean	SD
Field capacity (% 0.33 atm)	2.12 - 13.3	5.49	3.37
pH	4.2 - 6.2	5.11	0.66
Organic matter (g kg-1)	4.48 - 47.41	15.22	12.13
Ca (cmolc/dm3)	0.35 - 2.3	1.06	0.6
Mg (cmolc/dm3)	0.35 - 0.9	0.57	0.15
K (cmolc/dm3)	0.04 - 0.26	0.08	0.05
Al (cmolc/dm3)	0.05 - 0.65	0.24	0.26

Table S3. Bivariate relationships (*r*-values) between mean trait values of species (n = 46) from Catimbau, a dry forest landscapes in Pernambuco state, northeast Brazil. LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; LT, leaf thickness; SD, stem density; Hmax, maximum height; SS, seed size (length). Bold *r*-values represent significant correlations according to Bonferroni adjustment for multiple tests. *p < 0.05, **p < 0.01.

	Wood density	Leaf thickness	Leaf dry matter content	Specific leaf area	Maximum height	Leaf area
Leaf thickness	-0.372					
Leaf dry matter content	0.360	0.118				
Specific leaf area	0.054	**-0.608****	**-0.512****			
Maximum height	0.054	-0.262	0.076	0.053		
Leaf area	-0.256	0.092	0.057	-0.125	0.371	
Seed size	**-0.433***	0.126	0.018	-0.067	0.441	**0.516***

Table S4. Bivariate relationships (*r*-values) between the environmental and disturbance variables considered from 20 sampling plots in Catimbau, a dry forest landscapes in Pernambuco state, northeast Brazil. Variables were not significantly correlated.

	Wood extraction index	Precipitation	Soil fertility
Grazing pressure index	0.05	0.14	0.12
Wood extraction index		0.19	-0.11
Precipitation			0.36

Appendix S1. Details on the calculation of disturbance metrics.

In each of the studied plots, we took measures of chronic anthropogenic disturbance related to livestock (goats and cattle) usage and wood extraction. There were three variables related to livestock usage: (A) Goat trail length. Goats use well-defined trails to move within the Caatinga, and the total length of these trails within each plot was measured using an odometer. (B) Goat dung. We recorded numbers of goat dung pellets within four 5 x 5 m quadrats (total of 100 m^2) within each plot. (C) Cattle dung. We recorded the number of cattle dung pats within each entire plot. We used two variables related to wood extraction: (A) 'Live wood extraction'. Local people cut stems for use in fence and house construction, for craft, and sometimes fuel-wood. Within each plot, we measured the diameter of all cut stems, to obtain a measure of total basal area of removal (Urquiza-Haas et al. 2007). (B) 'Fire-wood collection'. We assumed an inverse relationship between the amount of wood litter as a proportion of total above-ground biomass and level of fire-wood collection. Within four 4 m^2 subplots within each plot, we measured the two diameters and length of each dead log or stem lying on the ground (minimum size of 0.5 cm diameter or 10 cm long). Dead biomass of wood litter was first computed following the equation of the volume of a conical frustum. We then used a mean value of the wood density (g cm^{-3}) of the tree species present in the area (mean wood density, p=0.634 g cm^3), to transform the volume values to biomass values. We collected most species in the field, and measured their wood density following the protocols of Perez-Harguindeguy et al. (2013). For the other species, we obtained wood density from http://datadryad.org/handle/10255/dryad.235. Total above-ground biomass per plot was estimated through field measures and further application of an allometric equation for Caatinga vegetation ($\text{Biomass}_{kg} = 0.173\ \text{DAS}_{cm}^{2.295}$; which is based on diameter at soil height (DAS) (Amorim et al. 2005; Rito et al. 2017). Finally, since low values of fire-wood biomass indicated high levels of disturbance, we computed the inverse such that the higher the value, the higher the disturbance intensity.

3.4 ARTIGO 4

Manuscrito a ser submetido ao periódico *Biological Reviews*

Review paper – *Biological Reviews*

Tropical mega-trees: critical role and collapse of a key global resource

Bruno X. Pinho[1], Marcelo Tabarelli[1], Inara R. Leal[1] and Carlos A. Peres[2*]

[1]Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego s/n, 50670-901, Recife, Pernambuco, Brazil

[2]School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich NR47TJ, UK

*Corresponding author: carlos.a.peres@gmail.com

ABSTRACT

Tropical rainforests play a central role in global-scale biodiversity retention and ecosystem services provisioning. Very large trees (i.e. 'mega-trees') represent a limited fraction of the overall tree abundance, but account for most of the tropical forest biomass, and thereby are likely associated with a large portion of the benefits provided by tropical forests. However, previous reviews of the ecology and conservation of this group have provided little emphasis on tropical forest environments. Here we review all available information on the ecology of tropical forests to define the ecological role of mega-tree species in supporting biodiversity and providing ecosystem goods and services essential for human well-being. We also examine the contemporary threats to mega-trees as tropical landscapes become increasingly exposed to extreme events (i.e. land-use and climate changes), and identify knowledge gaps and potential approaches to prevent the collapse of this key global resource. While some processes remain poorly investigated, our review reveals through a simple but useful framework a myriad of taxa/ecological groups and ecosystem services supported directly or indirectly by tropical

mega-tree species. Some supports are exclusively provided by mega-trees, such as microhabitats associated with immense trunks and highly illuminated crowns with complex three-dimensional structures. For instance, they provide irreplaceable sites for nesting and shelter of many vertebrate and invertebrate taxa, including birds (e.g. large raptors), bats, primates, amphibians and stingless bees. Moreover, some mega-tree species provide large amount of essential resources for whole communities of pollinators and frugivores during critical times of low resource availability (i.e. "keystone resources"). Indirectly, mega-trees support biodiversity by amplifying the resource spectra associated with non-redundant niche space, including thermal buffering and extended vertical microclimatic gradients. Furthermore, mega-trees make the largest contribution to forest productivity, and markedly determine variation in aboveground biomass at local, regional and continental scale, as tree biomass increases exponentially with stem diameter. Mega-trees have also supported the tropical timber market historically and provide a number of non-timber forest products essential for human populations. However, protecting this resource is challenging, as in addition to its natural rarity mega-trees are historically exposed to several threatening processes that is rapidly gaining magnitude globally. Logging of old-growth forests is typically followed by their conversion into human-modified landscapes, which implies habitat reduction and the expansion of edge-affected, unsuitable habitats for most mega-tree species as they experience lower recruitment and greater mortality due to strong winds, fires, and more desiccated and illuminated conditions. Finally, climate changes (i.e. severe droughts) adds new threats to the already declining mega-tree populations as they are more vulnerable to hydraulic failures. Thereby, the future of mega-tree flora depends on our ability of protecting large blocks of old-growth forest and their vulnerability to severe droughts. Both local and global demands could be tacked by establishment of productive forest landscapes combining forestry and provision of global relevant services (i.e. services market). However,

initiatives in this sense must be scaled up rapidly as agribusiness moves to the last pieces of old-growth forest globally and human-modified landscapes continues to be degraded.

Key-words: big trees, biodiversity, carbon market, droughts, ecosystem functioning, edge-effects, habitat loss, logging, tropical forests, timber, non-timber forest products.

CONTENTS

I. INTRODUCTION

Although tropical forest cover has recently experienced a gradual expansion in some regions (Hansen *et al.*, 2013), human populations worldwide continue to relentlessly convert old-growth tropical forests into human-modified landscapes (Lewis, Edwards, & Galbraith, 2015). China mega infrastructure projects are expected to provide access to the last remote tracts of Asian and African forests, while rapid agribusiness expansion has now intruded into the core of Amazonian forests (Laurance, Sayer, & Cassman, 2014; Laurance *et al.*, 2017). Human encroachment implies habitat loss and fragmentation (Fischer & Lindenmayer, 2007), but also the overexploitation of forest resources such as high-value timber, firewood, bushmeat and a myriad of other non-timber forest products (Peres, 2001; Tabarelli, Silva, & Gascon, 2004). Collectively, these sources of disturbance can shift remaining tracts of primary forest into alternative successional trajectories such as forest secondarization (Tabarelli, Lopes, & Peres, 2008; Berenguer *et al.*, 2018) or those dominated by tree species benefiting from climate change, including CO_2 fertilization and frequent droughts (Bartlett, Detto, & Pacala, 2019; Esquivel-Muelbert *et al.*, 2019).

This is particularly relevant if we consider the role of tropical forests in global-scale biodiversity retention, provision of ecosystem services and human well-being. Although tropical forests cover less than 10% of all land masses, they sustain over half of Earth's biological diversity (Groombridge & Jenkins, 2002). To give an idea of its extraordinary diversity, there are at least 40,000 tree species across tropical forests, compared to only 124 across the whole of Europe (Slik *et al.*, 2015). Furthermore, tropical forests play a prominent role at local, regional and global scales in the provisioning of livelihood goods (e.g. timber, fiber, fuelwood) and ecosystem services (e.g. climate regulation, carbon sequestration and storage) essential for human well-being. Tropical forest account for nearly 34% of the global terrestrial gross primary productivity, and one third of the total metabolic activity of the global land surface (Beer *et al.*, 2010; Malhi, 2012). Accordingly, tropical forests store ~25% of the entire terrestrial carbon pool in all ecosystems, controlling global biogeochemical (e.g. carbon and nutrient cycles) and biogeophysical processes (e.g. evapotranspiration) with direct impacts on climate regulation (Bonan, 2008; Houghton, Byers, & Nassikas, 2015).

It has been speculated that a large portion of the direct or indirect benefits provided by tropical forests are disproportionately related to very large trees. Although these mega-trees represent a small fraction of the overall tree abundance, they account for most of the tropical forest biomass, thereby contributing the lion share of the effects on biogeochemical cycles and ecosystem processes such as carbon storage and nutrient dynamics (Clark & Clark, 1996; Slik *et al.*, 2013; Sist *et al.*, 2014; Lutz *et al.*, 2018). Moreover, by over-towering the prevailing canopy height and interacting with the hotter, drier and more open conditions of the emergent canopy, mega-trees can add complexity to the vertical structure of vegetation, potentially providing unique microhabitats for several animal and plant species, such as cavity-nesting birds (Cockle, Martin, & Wiebe, 2011) and epiphytic plants (Woods, Cardelús, & Dewalt, 2015). However, the degree to which tropical biodiversity depends directly or indirectly on mega-trees is yet to be properly quantified as we have so far paid little attention to the biodiversity role of these very large trees.

Despite such a disproportionately important role, mega-trees are exposed to an increasing myriad of threats operating from local (e.g. selective logging; Sist *et al.*, 2014) to regional (e.g. forest fragmentation, Laurance *et al.*, 2000; Santos *et al.*, 2008; severe droughts and wildfires, Barlow *et al*., 2003; Nepstad *et al*. 2007) and global scales (e.g. climate change; Bennett *et al.*, 2015), with unanticipated impacts on biodiversity persistence, provision of ecological services, and human well-being. Recent reviews of the ecology and conservation of big trees have been published (Lindenmayer & Laurance, 2016, 2017), but these have provided little emphasis on the conservation status and ecological role of mega-trees in tropical forest environments.

Here we provide a more comprehensive perspective on the relative importance of tropical mega-tree species relative to support for biodiversity persistence and ecosystem functioning, economic/cultural value and threats experienced by this key global by reviewing available literature. Although information gaps prevent here a detailed picture the paper poses a framework emphasizing most of the potential connections between mega tress, dependent biodiversity and services as tropical forests move through predictable trajectories of degradation and become increasingly exposed to climate changes. Further, we integrate all findings across these issues to argue in favor of "productive forest landscapes" as a strategy to protect mega-tree species and highlight its connections with the sustainable development goals and other global targets. We hope to move research and conservation planning forward through this contribution.

II. TROPICAL MEGA-TREES: DEFINITION AND KEY FEATURES

As noted by Lindenmayer & Laurance (2017), defining mega-trees is not an easy task as maximum plant size varies in response to environmental factors within and among ecosystems (Poorter *et al.*, 2008a; Marks, Muller-Landau, & Tilman, 2016). For instance, canopy trees in Amazonia and tropical Australia are typically lower-stature at any given diameter compared with their counterparts in southern Asian and African forests (Banin *et al.*, 2012). In other words, it is difficult to define a minimum stature threshold for a plant to be considered a 'mega-tree'.

However, there is a wide consensus in the literature on what mega-trees are expected to represent physically, functionally and ecologically. Briefly, mega-tree species are those whose reproductive adults attain exceptional stature, with low-angled branches supporting crowns over the forest canopy. Although this is not perfect allometry, tree stem diameter and height are related in tropical forest trees (King, 1996; Banin *et al.*, 2012) and therefore in most cases trees exhibiting the largest diameters also support the largest emergent crowns (Clark & Clark, 1996). Such light demanding species at the reproductive stage include both fast- and slow-growing species, and in general can achieve exceptionally prolonged longevity and thus very large individuals. We are referring to individuals that often live for hundreds to over a thousand years (Chambers *et al.*, 1998; Laurance *et al.*, 2004).

In general, mega-trees tend to be better competitors for resources as they have greater access to light and belowground resources, given their higher crown exposure (Muller-Landau *et al.*, 2006) and deeper root systems compared to canopy or understorey tree species (Brum *et al.*, 2019). Accordingly, there is evidence suggesting that both growth and survival rates increase with size among tropical trees, probably as a result of greater access to light, greater total leaf area and intrinsically longer lifespan (Poorter *et al.*, 2008b; Thomas, Kellner, & Clark, 2013; Stephenson *et al.*, 2014).

Both tree stem diameter and height are related to specific ecological functions and ecosystem services mega-trees can provide. For instance, tree diameter is typically the main predictor of stem-specific carbon storage (Chave *et al.*, 2005), while tree height can distinguish emergent trees in providing irreplaceable functions for biodiversity (e.g. adequate microhabitats for several epiphytic plants and associated fauna in the upper canopy; Woods *et al.*, 2015). Moreover, plant height is a key component of the life history strategy of a species under different plant ecological schemes (e.g. Westoby *et al.*, 2002; Grime & Pierce, 2012), and is strongly correlated with lifespan, time to maturity and seed mass (Moles *et al.*, 2009; Díaz *et al.*, 2016). Crown width and length in tropical trees, which increase light interception and amplify niche space by promoting habitat heterogeneity, also scales closely to tree height and stem diameter (King, 1996; Muller-Landau *et al.*, 2006; Poorter *et al.*, 2008a). Large senescent tropical trees often exhibit extensive buttressing and numerous large cavities as a result of wood decay (Cockle, Martin, & Robledo, 2012), thereby providing critical microhabitats for particular components of tropical biodiversity (Cockle *et al.*, 2011a; Scheffers *et al.*, 2014; Hoek, Gaona, & Martin, 2017).

However, great stature also imposes costs (see Falster & Westoby, 2003), such as higher investment in supporting stem and root structures in relation to photosynthetic foliage, thereby reducing reproductive output (Kawecki, 1993); increased risk of hydraulic failures (i.e. lower resistance to cavitation) under extreme drought conditions (Brum *et al.*, 2019); and breakage due to strong winds (Laurance *et al.*, 2000). The higher variation in evaporative demand in the upper canopy of tropical rainforest also impose some challenges for mega-trees in regulating their water status, what may be partly compensated by their better capacity of storing water in large stems (Herwitz, 1985; Goldstein *et al*. 1998). Many of these features partly explain why mega-trees are highly sensitive to local human disturbances, such as creation of forest edges, and climate change as described below.

As a key attribute, we herein define mega-trees as those whose adults achieve stems ≥70 cm DBH (*sensu* Clark & Clark, 1996) because they share a common set of life history traits and functional role in tree assemblages. Another approach to define mega-trees would be to identify all trees above a certain percentile of height or diameter of all reproductively mature individuals (e.g. 5% of all trees >10 cm DBH). This could provide valuable information on what could be defined as a ‘mega-tree’ across tropical forest regions under contrasting conditions.

III. TROPICAL FLORAS AND DIVERSITY OF MEGA-TREES

Before we turn to how biodiversity benefits directly and indirectly from mega-trees, we consider the contribution of these tree species per se for the diversity of tropical floras.

Tropical forests are estimated to contain over 180,000 vascular plant species (Corlett & Primack, 2011), and 40,000-53,000 tree species: 19,000-25,000 in each of the Neotropical and Indo-Pacific regions but only 4,500-6,000 tree species in continental Africa (Slik *et al.*, 2015). A similar pattern occurs at local spatial scales: an average of 150-180 species per hectare in the Neotropical and Indo-Pacific regions, but only fewer than 100 in the Afrotropics (Corlett & Primack, 2011). Although estimating the contribution of mega-tree species for the overall diversity of tropical tree floras remains highly uncertain, some biogeographic and ecological patterns have already emerged.

African rainforests support tree assemblages with higher relative abundance and biomass of mega-trees, but present a less diverse large tree flora compared to Neotropical and Indo-Pacific forests (Slik et al., 2013; Lutz et al., 2018). Neotropical forests host large tree species particularly in Fabaceae, Sapotaceae, Chrysobalanaceae, Lecythidaceae and Bombacaceae, while dipterocarps account for most mega-tree species across Southeast Asian forests, including over 500 very large canopy tree species (Ghazoul, 2016), and in Afrotropical forests mega-trees are primarily represented by Fabaceae. However, a comprehensive assessments of mega-tree species richness and composition across tropical forests have not been performed to date.

Regardless of the biogeographic region and spatial scale, both the richness and the abundance of mega-tree species are not randomly distributed along environmental gradients. It has long been recognized that mega-trees are much more abundant and diverse in continental areas, lowland forests (< 1500 masl), flat terrains consisting of deep soils, and hurricane-free regions (Corlett & Primack, 2011). A decline along altitudinal gradients, marked by a decline of the forest emergent layer and a proliferation of the understorey flora consisting of small trees and shrubs, is particularly conspicuous (Whitmore, 1998; Balzotti *et al.*, 2017; Gonmadje *et al.*, 2017).We should mention lowland dipterocarp forests of Borneo, Sumatra and Peninsular Malaysia as supporting the highest richness of large-girthed tree species (Ghazoul, 2016).

IV. KEY ECOLOGICAL ROLES OF TROPICAL MEGA-TREES

(1) **Supporting biodiversity**

Biodiversity supported or dependent on mega-tree species encompasses a myriad of taxa through several processes, some of which remain poorly known. However, we can provide a preliminary overview by organizing all information into a framework considering direct and indirect support, driving processes and beneficiary taxa or functional groups (Table 1). Most physical supports are exclusively provided by mega-trees, including microhabitats associated with immense trunks and highly illuminated crowns with complex three-dimensional structures (Fig. 1). Mega-trees also amplify the resource spectra associated with non-redundant niche space, including thermal buffering and extended vertical microclimatic gradients.

(a) *Direct supports*

In terms of direct support for biodiversity, giant crowns and tree trunks provide physical substrate but also specific microhabitats for several taxa such as nearly continuous daylight sun-flecks above the forest canopy. For example, for epiphytes (Woods *et al.*, 2015), which represent more than one-third of all vascular plant species in some tropical forests (Nieder, Prosper, & Michaloud, 2001; Benzing, 2008). In general, although heliophile epiphytes exhibit low host-species specificity (Wagner, Mendieta-leiva, & Zotz, 2015), most species are strongly associated with very large trees, particularly large and highly illuminated crowns; i.e. several bark ferns, orchids and atmospheric bromeliads (Woods *et al.*, 2015; Gonzalez *et al.*, 2017). For instance, almost half of all bromeliad species occurring in Atlantic Forest of northeast Brazil are dwellers of the illuminated and desiccated crows supported by emergent tree species (Siqueira-Filho & Tabarelli, 2006). The largest tree individuals within a population also tend to be the oldest, and epiphyte abundance and diversity are therefore obviously expected to increase with tree size as a result of increasing habitat area and colonization time as host trees become larger and older. Indeed, the positive correlations between tree size and epiphyte abundance, biomass and diversity are widely reported for different tropical forest realms (Zotz & Vollrath, 2003; Woods *et al.*, 2015; Ding *et al.*, 2016; Gonzalez *et al.*, 2017). Using rigorous null models, however, Woods et al. (2015) tested the role of tree size on epiphyte assemblages and concluded that microhabitat heterogeneity also increases with tree size (e.g. wider variation of vapor pressure deficit from the inner to the outer crown), and that most epiphyte species are specialized on specific conditions and resources (e.g. canopy humus) provided exclusively by trees larger than 70 cm DBH. For instance, only 6% of epiphyte species (mostly bark ferns) were significantly associated with small trees, whereas 57% were associated with large trees (Woods *et al.*, 2015). Therefore, beyond mere physical support, large emergent trees amplify microhabitat heterogeneity thereby promoting more diverse epiphyte communities with abundant populations.

Colossal crowns and their huge bifurcations are essential platforms for nesting sites for several large raptors (Lewis, 1986; González & Vargas, 2011; Jenny, 2012), most of which are at risk of extinction (Bildstein *et al.*, 1998). For instance, the largest and rarest tropical eagle species on Earth, the Philippine Eagle (*Pithecophaga jefferyi*), rely on large emergent trees for nesting, as they provide natural platforms such as epiphytic ferns on their large high crowns (Lewis, 1986) which also provide a panoramic view for the eagles to scan the landscape. Due to increasing human pressure, including forest loss and selective logging, this species is on the brink of extinction and a conservation icon in the Philippines (Lewis, 1986). Another emblematic extant mega-raptor is the Harpy Eagle (*Harpia harpyja*), the largest Neotropical forest raptor (Jenny, 2012). Harpies nest on several species of emergent trees, virtually all of which are coveted by the logging industry (Alvarez-Cordero, 1996). Raptors are also important apex predators, thereby playing a key role in the top-down control of arboreal herbivore populations, such as sloths (Sergio *et al.*, 2008). It therefore remains unclear to what degree the collapse of mega-trees could lead to a trophic cascade in the absence of large canopy raptors.

Large trees also provide cavities that are essential for nesting and shelter of many vertebrate and invertebrate taxa (Gibbons & Lindenmayer, 2002; Cockle *et al.*, 2011a; Scheffers *et al.*, 2014), as many animal populations are limited by natural tree cavities (Newton, 1994; Cockle *et al.*, 2010). Nests of stingless bees (Apidae, Meliponini) in tropical rainforests are almost invariably (80-100%) found in branches, trunks and roots of large trees (>60 cm DBH), and nest density is typically correlated with the density of large trees (Eltz *et al.*, 2002, 2003; Samejima *et al.*, 2004). These studies also suggest that cavity-nesting stingless bees are limited by nest-site availability. For instance, the addition of artificial nest boxes increases nest density (Inoue *et al.*, 1993) and many colonies may be found within a same tree, particularly the largest specimens (Eltz *et al.*, 2003; Samejima *et al.*, 2004). Stingless bees are one of the most important groups of pollinator insects in neotropical forests, using a wide variety of floral resources (Momose *et al.*, 1998; Nagamitsu & Inoue, 2005). There are evidence that height partitioning may occur even within a same tree, with larger bees selecting the upper crowns for nesting (Kajobe, 2015), likely indicating competitive selection for higher cavities. Nest tree selection by stingless bees may still depend on the availability of resin for nest construction (Leonhardt & Blüthgen, 2009), which may only occur in large, late-successional trees (Samejima *et al.*, 2004).

In some temperate forests more than 40% of all birds and mammal species depend on cavity availability for nesting or roosting (Newton, 1994; Gibbons & Lindenmayer, 2002).

Tropical forests, however, host the greatest diversity of cavity-nesting birds, which account for a substantial component of the overall avian diversity, 678 species in the Neotropical region alone (Hoek *et al.*, 2017). For instance, cavity-nesting bird species account for 22% of the Atlantic Forest avifauna (Cockle *et al.*, 2011a). Yet the ecology of tree cavity supply, distribution and selection by birds and other vertebrates is at best embryonic in tropical forests compared to a vast analogous literature in temperate forests (but see Cockle *et al.*, 2011a).

In addition to larger, deeper cavities, mega-trees are also expected to be a favored resource for cavity-nesting birds because they can avoid both terrestrial and scansorial predators by selecting cavities in isolated crowns (Brightsmith, 2005; Cockle *et al.*, 2011a). Suitable avian nest cavities are more likely to occur in very large trees (>100 cm DBH), and nest density increases where artificial nest boxes are supplemented, indicating that cavity supply is limiting for cavity-nesting birds in tropical forests (Newton, 1994; Cockle *et al.*, 2010). This is particularly true for secondary (non-excavating) cavity-nesting birds, which rely on existing tree cavities and represent the most species-rich and most threatened group of cavity-nesting birds (Hoek *et al.*, 2017). This group preferentially selects large live trees with high cavities produced by wood decay, while excavators (i.e. primary cavity-nesting) tend to select smaller-girthed dead trees (“snags”) to construct their cavities (Cockle *et al.*, 2011a, 2012). Among secondary cavity-nesters, some have more specific requirements and are particularly suppressed by tree cavity scarcity. For instance, large tropical bird species such as falcons, are frequently found defending their nests against other cavity-nesting bird species (e.g. parrots; Cornelius *et al.*, 2008), as they depend on larger cavities with large openings, which represent a small fraction of the available tree-cavities in tropical forests (Boyle *et al.*, 2008). In Mesoamerica, for example, cavities used by Barred Forest Falcon (*Micrastur ruficollis*), Collared Falcon (*Micrastur semitorquatus*) and Laughing Falcon (*Herpetotheres* *cachinnans*), were all in very large (mean DBH > 95 cm) emergent trees, which represented only 5% of the surveyed trees (Gerhardt, 2004).

Amphibians and reptiles often benefit from temporary pools in cavities on large trees used as breeding sites. Uprooted large trees also generate the largest amount of spatial heterogeneity, including upland water bodies such as sizeable peccary wallows, which are critical sites for pond-breeding frogs in Neotropical forests (Gascon, 1991; Beck, Thebpanya, & Filiaggi, 2010). Additionally, the huge and complex structure of large tree forks provide essential shelter and foraging sites for other herpetofauna, particularly lizards (e.g. Vitt, 1991; Ellinger *et al.*, 2001).

Mega-tree cavities also form critical roosting habitat for bats, which play diverse ecological roles in tropical forests, including seed dispersal, pollination and predation (Kunz *et al.*, 2011). Bat foraging requirements are usually very general, but they have specific roosting requirements, which are essential for their survival and reproduction (Kunz & Lumsden, 2003). Tree cavities are one of the main roosting habitats used by tropical forest bats, especially those in the families Phyllostomidae and Emballonuridae in the Neotropics (Kunz & Lumsden, 2003). Furthermore, most species select large cavities in large-diameter emergent trees (Evelyn & Stiles, 2003; Kunz & Lumsden, 2003). Bat roosting sites located using radiotelemetry in Mexico were always in large trees (> 50 cm DBH) for a common frugivorous bat species (*Sturnira lilium*, Phyllostomidae), and fewer than 2% of all surveyed trees were larger than roosting sites. Gleaning faunivore bats, which account for ~ 20% of all bat species in Neotropical forests, are also highly restricted to very large trees in mature forests (Simmons & Voss, 1998). Selection of large-girthed trees occurs because they are more likely to host cavities with large internal volume. Emergents rising above surrounding canopy trees also provide reduced predation risk and the appropriate microclimate; for instance, higher solar radiation provides energetic benefits for bats (Kunz & Lumsden, 2003).The vertical forest canopy heterogeneity also determines the composition and diversity of arboreal vertebrate assemblages, so that higher-stature old-growth forests are associated with greater taxonomic and phylogenetic diversity (e.g. Martins *et al.*, 2017).

Several tropical forest primate species also select large emergent trees as secure sleeping sites, which is critical for their fitness, as they may spend over half of their lives at those natural shelters (Lutermann, Verburgt, & Rendigs, 2010; Phoonjampa *et al.*, 2010; Cheyne *et al.*, 2012). In particular, several gibbon species (Hylobatidae) usually overnight in the thickest, tallest, large-crowned emergent trees (Phoonjampa *et al.*, 2010; Cheyne *et al.*, 2012). As gibbons do not build nests, they are very vulnerable to predator attacks, including raptors, snakes and felids. By selecting large emergent trees as sleeping sites, primates not only avoid competition with other frugivores, but also minimize predation risk (Cheyne *et al.*, 2012). Moreover, mega-trees also provide essential and often super-abundant resources, including flowers, seeds and mature fruit pulp for many arboreal and terrestrial consumers (Dunn, Cristóbal-Azkarate, & Veà, 2009), and their vast crowns can accommodate large feeding aggregations and group sizes.

Finally, we briefly discuss the resource contribution of mega-trees to entire assemblages of forest frugivores (Terborgh, 1986ab; Peres, 2000; Shanahan & Compton, 2001; Diaz-martin *et al.*, 2014). Some large-crowned species in tropical forests (e.g. *Ficus* spp.) provide “keystone plant resources” (*sensu* Terborgh, 1986a) such as fruits, seeds and flowers that become available in large amounts during critical times of low resource availability along the annual cycle, thereby having a large, disproportionate effect on frugivores. For instance, only 12 plant species sustain up to 80% of the animal biomass during the period of resource scarcity at Cocha Cashu, Peru, thereby setting the carrying capacity of the forest for the frugivore community (Terborgh, 1986b). Several mega-tree species provide keystone resources, particularly in the Moraceae and Sapotaceae. Loss of such keystone resources — for example, via selective timber extraction — can lead to the functional collapse of whole forest ecosystems due to impacts on both lower and higher trophic levels (Johns, 1986; Terborgh, 1986b; Malhi et al. 2014).

(b) *Indirect supports*

The indirect contribution of mega-trees to biodiversity persistence encompasses forest microclimatic buffering, extended vertical microclimatic gradients and support for plant-animal interactions. Although mega-trees are often scattered at low densities in an otherwise more homogeneous forest canopy, they store a relatively large amount of aboveground forest biomass (Slik *et al.*, 2013; Lutz *et al.*, 2018) and break up the forest canopy by projecting their crowns well above the canopy (Clark & Clark 1996). This creates singularity in upper canopy conditions by enhancing structural complexity, but also impact the forest understorey, promoting cooler and wetter microclimate, and increasing water and nutrient resource availability (Manning, Fischer, & Lindenmayer, 2006; Hardwick *et al.*, 2015; Jucker *et al.*, 2018). Mega-trees therefore account for microclimatic buffering and extended vertical microclimatic gradients (Hardwick *et al.*, 2015; Jucker *et al.*, 2018), which benefit specialists such as the shade-tolerant flora and their attendants. This is particularly important in tropical forests where approximately one third of all woody plant species (from shrubs to subcanopy species) are shade-tolerant inhabiting forest understorey (Gentry, 1982) and many species operate near their thermal tolerance limits (Doughty & Goulden, 2008). Moreover, the diversity of many animal groups is vertically stratified in tropical rainforests, such as arthropods (Charles & Basset, 2005), birds (Chmel et al., 2016) and mammals (Vieira & Monteiro-Filho, 2003). Therefore, the collapse of the emergent layer may potentially lead to the complete reorganization of animal communities as some species move downwards and interact competitively with others.

By directly supporting several groups of plants and animals, mega-trees are indirectly connected to extensive food webs and plant-animal interactions. For example, epiphytes such as the tank bromeliads supported by the emergent forest layer (Ellwood & Foster, 2004; Benzing, 2008) host a diverse fauna, with different epiphyte species typically associated with different animal assemblages (Stuntz *et al.*, 2002b). Ellwood & Foster (2004) showed that a single large epiphyte can support an invertebrate biomass comparable to that of the entire tree crown in which they occur, which would double our estimates of invertebrate biomass in tropical forest canopies. Like large tree cavities, epiphytes can buffer extreme weather conditions, thereby providing “climate microrefuges” for several animal taxa (Stuntz, Simon, & Zotz, 2002a; Scheffers *et al.*, 2014). Although the importance of these *microrefuges* is more evident in temperate ecosystems with pronounced climatic variation, it is also critical in tropical forests where elevated temperatures can be detrimental for ectothermic fauna with low thermal tolerance (e.g. arthropods, frogs and lizards), particularly under future scenarios of climate change. Specifically, for several species microhabitat temperature buffering represents the only way to escape lethal conditions resulting from extreme climatic events (Scheffers *et al.*, 2014).

In sum, mega-trees can be described as “keystone structures” (*sensu* Tews *et al.*, 2004) by favoring multiple species and ecological groups, thereby having disproportionate effects on biodiversity persistence via the augmented structural heterogeneity and resource spectrum of an ecosystem. However, investigations on the direct and indirect roles of mega-trees for their dependent biodiversity remain embryonic. It is worth mentioning that forest canopies remain one of the least studied environments in all terrestrial biomes, and are often referred to as “the last biotic frontier” (Erwin, 1983) or a “black-box” (Nakamura *et al.*, 2017).

(2) Supporting ecosystem functioning and services for humans

(a) *forest productivity, aboveground biomass and carbon stocks*

Tropical forests account for one third of the productivity and one quarter of the carbon stock in the terrestrial biosphere (Bonan, 2008; Beer *et al.*, 2010). Beyond its clear importance for the control of climate changes (Houghton *et al.*, 2015), forest aboveground biomass (AGB) may be the main vegetation driver of several ecosystem processes (e.g. litter production and decomposition; see Lohbeck *et al.*, 2015 for an example on tropical secondary forests). Understanding the drivers of variation in AGB is thus key to predict ecosystem functioning and adequately manage ecosystems.

Forest productivity and AGB are driven both by direct effects of environmental conditions (e.g. rainfall, temperature) on tree growth/survival and by vegetation properties, including taxonomic (e.g. species richness), structural (e.g. basal area) and functional (e.g. wood density) attributes (Poorter *et al.*, 2015, 2017; van der Sande *et al.*, 2017). Tree species diversity may increase tropical forest AGB, probably through niche complementarity effects on resource use efficiency, but its effect is apparently limited to small spatial scales (~0.1 ha; Poorter *et al.*, 2015). On the other hand, forest structural attributes markedly determine variation in aboveground biomass at local (Poorter *et al.*, 2015), regional (Malhi *et al.*, 2006) and continental scale (Slik *et al.*, 2013). Specifically, tropical forest AGB tends to increase strongly with increasing average stem diameter, stand basal area and mega-tree density (Slik *et al.*, 2013; Poorter *et al.*, 2015). For instance, Slik *et al.*(2013) performed a pan-tropical analysis on the drivers of AGB variation across 120 lowland tropical forests, demonstrating that density of mega-trees (DBH >70 cm) explain *c*. 70% of the site-level variation in aboveground biomass. Furthermore, higher density of mega-trees is the sole cause of the higher AGB of forests in the Palaeotropics compared to Neotropical forests (Slik *et al.*, 2013).

Mega-trees have extensive and well-lit crowns, and thus continuously sequester carbon at high rates, making the largest contribution to forest productivity (Stephenson *et al.*, 2014). Formerly, it was thought that individual mass growth rate should declines with tree size, but Stephenson et al. (2014) analyzed almost 700,000 trees of 403 tropical and temperate species and showed that, despite the decline in leaf-level productivity, mass growth rate increases continuously with tree size, probably as a result of increasing total leaf area. To give an idea of the disproportional productivity of mega-trees, trees with 100 cm DBH add annually in average the mass equivalent of an entire tree of 10-20 cm DBH, from the same species (Stephenson *et al.*, 2014).

Although tropical mega-trees account for a small fraction of the overall tree abundance, they store a substantial portion of forest biomass, which explain it strong effect on AGB at different spatial scales (Lutz *et al.*, 2018). At continental scale, they accounted on average for only 1.5, 2.4 and 3.8% of stems with DBH >10 cm across forest sites in South America, Southeast Asia and Africa, respectively, but stored approximately 25, 40 and 45% of AGB in these respective regions (Slik *et al.*, 2013). Also, regional gradients in AGB may be explained by variation in the density of mega-trees. For instance, *c.* 60% of variation in AGB across Amazonia is explained by basal area (Baker *et al.*, 2004) and the higher AGB of forests in the Eastern in relation to Western Amazon probably result from the higher abundance of very large trees with DBH >100 cm. In this region, trees with DBH >60 cm account for less than 10% of the total tree density but store half of forest biomass (Sist *et al.*, 2014). At local scale, Brown *et al.* (1995) also found that only 3% of the trees (emergent and large canopy species) account for 50% of aboveground biomass in southwestern Amazon. Individual biomass increases exponentially with stem diameter, which explains the disproportional contribution of large trees to forest biomass in comparison with small trees (Poorter *et al.*, 2015). Finally, it is worth noting that the relative contribution of large trees to carbon stocks may be still underestimated, as their larger crowns with complex branching patterns are not taken into account by conventional estimations of forest biomass from general allometric equations (Malhi *et al*., 2018).

(b) *Altering resource dynamics and climatic conditions*

As suggested by the Metabolic Scaling Theory, the pool and magnitude of fluxes of resources (i.e. water, carbon and nutrients) are strongly influenced by variation in organismal size (see Enquist, Michaletz, & Kerkhoff, 2014). Thereby, the large amount of biomass (i.e. foliage, fruits, flower, litter) associated with mega-trees not only provide supporting for biodiversity but also determine patterns of ecosystem functioning from local to regional scale. For instance, species with larger woody surface area may store greater amounts of water under heavy rainfall (Herwitz, 1985), and deep rooting systems allow mega-trees to tap groundwater (Brum et al., 2019), thus potentially influencing hydrological regimes (Nepstad et al., 1994). Such features allow mega-trees to maintaining maximum rates of transpiration for a longer time daily (Goldstein *et al*., 1998). Specifically, in Panama rainforest trees, every 0.1 m^2 increase in basal sapwood area allow for an increment of 10 kg in their diurnal water storage capacity (Goldstein *et al*., 1998). Also, in trees from Amazon forest, daily transpiration rates ranged from 0.7 l for small understorey trees to 1180 l for mega-trees (Jordan & Kline, 1977).

The large root systems and extensive foliage of tropical mega-trees may also support continuous photosynthetic activity and distribution of deep water (among other resources) in periods of resource scarcity (Nespstad et al., 1994; Goldstein et al., 1998), potentially supporting a number of understorey tree species with shallow rooting depth, and thus avoiding ecosystem collapse. Moreover, the larger belowground carbon allocated by mega-trees largely control spatial variation in tropical rainforest soil respiration (i.e. efflux of CO2 from soil surface; Katayama et al., 2009). Thereby, tropical mega-trees may largely control ecosystem functioning by altering spatial-temporal patterns of resource availability, microclimatic conditions and regional rainfall regimes. Yet, to date our knowledge on the role of tropical mega-trees in controlling resource dynamics and climatic conditions is still very limited.

(c) *Cultural heritage*

We shall briefly mention that sacred trees are a frequent figure in many myths/cosmovision, religious beliefs, cultural practices and historical events through a myriad of both ancient and contemporary cultures or ethnic groups globally (Cusack, 2006). This immemorial phenomenon is not restricted to tree worship but also includes places in which the sacred tree is the central location for rituals, including weeding and rain making ceremonies, funerals (e.g. burial sites), parades, sacrifices, judgements or social gathering (Dafni, 2007). Frequently, sacred trees represent a crucial component of forest sacred groves (Gadgil, 2018). In other traditions, parts of a sacred tree are considered a sort of talisman (Dafni, 2007). Such a diverse relationship with sacred trees highlights the inspirational/spiritual feelings trees have triggered on human beings.

Many sacred trees refer to tropical mega-tree species such as the sacred Maya Ceiba or “Yaaxche” (*Ceiba pentandra*), a crucial element of the Mayan cosmovision by connecting the upper, middle, and underworlds (Zidar & Elisens 2009). This mega-tree species is still a dominating element of the emergent layer across forests from Amazonia to South Mexico. The baobab trees (*Adansonia* spp.) are sacred and a cosmovision element for several African cultures (Vieilledent *et al*. 2013) as well as magnificent sightseeing for tourists. It is worth mention the strangler *Ficus* species in India (*F. reliosa*, *F. benghalensis*), which start life as epiphytes but achieve the stature of mega trees (Kandari *et al*., 2014). The Buddha achieved the enlightenment beneath the crown of a fig tree (*Ficus religiosa*), today named as the Bodhi tree (Niroula & Singh 2015). Other mega tree species are involved in the Hinduism (Niroula

& Singh 2015) and comprehensive search across ethnographic literature is likely to reveal the existence of several tropical mega-tree species considered sacred as already done for temperate regions (Cusack 2011). In addition to the relevance for locals, several sacred trees, their groves and forests have attracted increasing tourism and pilgrimage, making this topic an issue on conservation strategies and sustainable development (Habernan, 2013, Vieilledent *et al*., 2013).

V. ECONOMIC VALUE OF MEGA-TREES

Tropical forests provide a myriad of products and services economically relevant, with timber, non-timber forest products and carbon sequestration/storage being the foremost, as tropical timbers support multibillion-dollar market (ITC/ITTO, 2002). Moreover, hundreds of millions of people across the tropics rely on forests and trees for everyday subsistence (FAO, 2018). Although these assets are provided by trees in general, mega-trees commonly present specific features that make them more attractive for logging (e.g. high wood density) and account for most of the biomass in tropical forests (Slik *et al.*, 2013; Lutz *et al.*, 2018). Therefore, they have a disproportionally high contribution to these resources, especially in timber and carbon markets, as follows.

(1) **Timber**

Logging of ancient mega-trees in old-growth forests (i.e. the forest premium) represents an irresistible attractive able to guarantee that any tract of mature forest experience logging before forest conversion to other land uses such as agriculture or pasture. Although figures on domestic use of mega-trees during colonial times are scarce, they supported the naval enterprise globally, as well as the urban infrastructure such as the colossal baroque churches and administrative buildings in old colonial cities (Tripati *et al.*, 2005; Bernal, Valente, &

Pissarra, 2011). Many old colonial capitals such as Havana, Salvador and Goa exhibited active shipyards supported by mega-trees such as teak (*Tectona grandis*), rosewood (*Dalbergia nigra*) and sisoo (*Dalbergia sissoo*) (Tripati *et al.*, 2005). Caravels and galleons have gone a long time ago, but hardwoods from almost extinct mega-trees can still be admired in old buildings of colonial capitals globally, such as staircases, massive wardrobes and tables made from rosewood and still part of the furniture in churches and monasteries in the Brazilian coast region (Bernal *et al.*, 2011).

From colonial time until nowadays, timber and wood products remain as the main source of income from tropical forests. In fact, many countries started their economic development in the aftermath of colonial independence by exploiting their natural stock of tropical timber, such as Indonesia (Ghazoul, 2016). Annual exports of primary and secondary wood products from tropical forests have exceeded US$20 billion in the first decade of 2000, with further increases as more countries focus their exports on higher-valued secondary wood products (FAO, 2018). This tropical timber trade is dominated by Southeast Asia with Dipterocarp large-tree species (i.e. emergent tress achieving over 80 m high) as the mainstay. During the 1980s tropical hardwoods from Southeast Asia formed the bulk of the export market from developing countries, accounting for 84% of the market, while only 14% came from Africa and 1% from Latin America (Laird, 1995). Such a protagonism has not changed along the years; for instance, more roundwood is harvested from Borneo alone than from Africa and the Amazon combined (Curran *et al.*, 2004). They contribute over 85% of Indonesia’s timber exports and generate as much as US$ 6 billion in annual export revenue, and Kalimantan island provided 60% of Indonesia’s exports (Ghazoul, 2016). It is their abundance in Asia’s tropical forests that makes timber harvesting so lucrative. In fact, Asian dipterocarp rainforests have the highest stature of any tropical forest, showing the contribution of mega-trees in the timber trade.

But the leading role of mega-tree in the tropical timber market is not a prerogative of Asia; it is a global pattern. From the 300 species with commercial value assembled in the Tropical Timber Atlas (Gérard *et al.*, 2017), 278 are tropical angiosperms, from which 256 (92%) are mega-tree species (i.e. DAP > 70 cm). Almost half of these species come from Africa (117 species, 46%), followed by Latin America (80, 31%) and Asia/Oceania (59 species, 23%). Most important families are Fabaceae (40 species), Meliaceae (10) and Sapotaceae (8) in Africa, Fabaceae (27), Lecythidaceae and Moraceae (both with 6 species) in Latin America, and Dipterocarpaceae (17), Fabaceae (8) and Myrtaceae (4) in Asia. Finally, 155 species (60%) of these species can be also considered hardwood (i.e. wood density > 0.7) demonstrating again the quality of mega-trees as timber. Just to show an example, the five most valuable timber commercialized in Brazil (*Tabebuia* sp., *Hymenaea courbaril, Astronium lecointei*, *Manilkara* sp. and *Dinizia excelsea*) are all big, hardwood trees with all species achieving over US$ 300 per m^3 of sawn wood (ITTO, 2018).

(2) **Non-timber forest products**

Non-timber forest products (NTFP) include a wide range of products (e.g. medicinal plants, fibers, resins, latexes, fruits, foods, construction materials, and bushmeat) that have been exploited by forest-dwelling communities for centuries, including both subsistence and commercial purposes. For example, the mega-tree Borneo camphor (*Dryobalanopsis aromatica*) has been traded by Arab merchants since the 6th century (Shiva & Jantan, 1998). Recent studies have provided evidences that some species from Amazon were domesticated and increased in density by pre-Columbian people at least 8000 years ago such as Brazil nut (*Bertholletia excelsa*) (Levis *et al.*, 2017).

Nowadays, NTFP generate large amounts of income across both local and regional markets of tropical countries in addition to domestic/subsistence use (Laird, 1995). For instance, NTFP market in Indonesia reached US$ 125,OOO,OOO/year in the early 1980s (de Jong & Mendelsohn, 1992). Mega-tree NTFP such as rosewood oil, chicle (*Manilkara zapota*), and Brazil nuts, are traded widely on the international market (Laird, 1995). NTFP explored from Asian mega-trees are also concentrated among dipterocarps, producing for instance resins, including oleoresins such as *Dipterocarpus cornutus*, *D. crinitus*, *D. kerrii* and *D. grandiflorus* used in Malaysia, and *Dipterocarpus alatus, D. turbinatus*, and D. *tuberculatus* in South Asia. It also includes the dammar resin (*Dipterocarpus javanica*), camphor waxy (*Cinnamomum camphora* but also *Dryobalanops aromatica*), and Iliipe nut and butter fat (a group of 15 species of *Shorea* mainly *S. macrophylla*, *S. stenoptera*, *S. mecistopteryx* and *S. aptera*) (see a review of dipterocarp NTFP, their use and threats in Ghazoul, 2016). Of these, dammar and Illipe nut and butter fat arestill widely marketed and continue to support localeconomies in Sumatra and Kalimantan (Ghazoul, 2016).

In the Latin America most of the major NTFP are also extracted from mega-tree species such as andiroba (*Carapa guianensis*), copaiba (*Copaifera langsdorffii*) rosewood oil (*Anibarosae odora*), and Brazil nut (*Bertholletia excelsa*). These species have supported a recent and fast-growing market of medicinal and cosmetic products, opening a new opportunity for the sustainable use of the Amazon forest (Klimas, Kainer, & Wadt 2012; Newton, Watkinson, & Peres 2012). For instance, 580 tons of copaiba oleoresin was produced only in the Brazilian Amazon in 2010, generating US$ 2,416,186 (IBGE 2010). We can also mention the cocoa butter (*Theobroma grandiflorum*), bacuri (*Platonia insignis*), cumaru (*Dipteryx odorata*), pequia (*Caryocar nuciferum and C. villosum*) and uchi fruits (*Endopleura uchi*), chicle (*Manilkara zapota*) and breu resin (*Protium* spp.), and the infusion extracted from barks of pau d’arco (*Handroanthus impetiginosus*) and jatobá (*Hymenaea courbaril*) among others (Laird, 1995; Shanley et al., 2011). In some countries such as Peru, Brazil and Ecuador, Amazonian NTFP yielded greater returns per hectare than timber extraction, cattle ranching, and plantation forestry (Peters, Gentry, & Mendelsohn, 1989; Balick & Mendelsohn, 1992; Grimes *et al.*, 1994). Among 335 timber species utilized in the Brazilian Amazon, one-third have been also valued for their fruits, medicinal properties, and/or gums and resins. In some cases, such as rosewood, non-timber values exceed timber values (Clay & Clement, 1993). For example, in 2007, Brazil produced more than 30,000 tons of Brazil nuts for sale, generating over US$ 23 million (IBGE, 2007).

African mega-trees also play an important role as NTFP. For instance, from 38 species used by people from Cameroon 12 are mega-trees such as African walnut (*Coula edulis*), erimado (*Ricinodendron heudelotii*), moabi (*Baillonella toxisperma*), inoi (*Poga oleosa*), panda (*Panda oleosa*) and divida (*Scorodophloeus zenkeri*) used as spices and condiments, bush mango (*Irvingia gabonenses*), onzabili (*Antrocaryon klaineanum*) andowui (*Hexalobus crispiflorus*) as fruits, resins collected from okoumé (*Aucoumea klaineana*) and medicines from alstonia (*Alstonia boonei*) and bubinga (*Guibourtia tessmannii*) (Dijk, 1999). Some of this species are used as both timber and NTFP as the okoumé, which yields a resin used to tapped prior to felling for timber and after that to make torches (Laird, 1995). In southern Cameroon, from 31 timber species exploited by the Dutch logging company, GWZ, 19 (representing 86% of total volume) are also used by local communities as NTFP (Laird, 1995; Dijk, 1999). Due to unsustainable exploitation, some of these NTFP extracted from mega-trees reach high prices in the international market as the bark of the African cherry (*Prunus africana*), which provides a compound used to treat prostate disorders (Waterman, 1994) exported to Europe and USA. As supplies have begun to diminish elsewhere, large quantities of *Prunus* bark have begun to be exploited from Equatorial Guinea for the lucrative export market of US$ 220 million/year (Sunderland & Obama, 1999).

All this show the extent of the potential contribution of mega-tree products other than timber to the economy of tropical countries. However, there exist few information on species used as NTFP and its commercial value as most of documents refer to local markets and do not consider quantitative measures of NTFPs natural production rates (de Jong & Mendelsohn, 1992). Therefore, there is a need to compile information on production and harvesting regimes, as well as its ecological impacts, in order to sustainably manage wild NTFPs.

(3) **Carbon market**

The main carbon pools in tropical forest ecosystems are the living biomass of trees (Gibbs *et al.*, 2007), with mega-trees responding for up to half of forest aboveground biomass (Slik *et al.*, 2013). Therefore, tropical forests and mega-trees have a central protagonism in the climate change debate and agenda. To avoid tropical forests carbon to be released into the atmosphere as carbon dioxide, the United Nations Framework Conventionon Climate Change (UNFCCC) created economic incentives to help facilitate reductions in emissions from deforestation and degradation, so-called ‘REDD’. The REDD concept is a proposal to provide financial incentives to help developing countries voluntarily reduce national deforestation rates and associated carbon emissions below a baseline. Countries that demonstrate emissions reductions may be able to sell those carbon credits on the international carbon market or elsewhere. Most of the key REDD decisions were completed by 2013, with the final pieces of the rule book finished in 2015 (with sustainable management of forests, conservation of forest carbon stocks and enhancement of forest carbon stocks constituting the "+" in ‘REDD+’).

As deforestation challenges the viability and future of the timber industry, in the past decade research interest has been spurred by the potential of forests to store carbon. Conservationists have sought to convince several stakeholders (policy makers and politicians) that carbon market is an opportunity to preserve remaining forest stands. Several countries have pursued the REDD+ agenda buoyed by commitments from some countries to finance carbon conservation through protection of natural forests. For instance, at the 2007 COP 13, in Bali, Norwegian government announced US$ 1 billion towards the Brazilian REDD+ initiative and US$ 500 million towards the creation and implementation of national-based, REDD+ activities in Tanzania. In addition, the United Kingdom pledged US$200 million towards the Congo Basin Forest Fund to aid forest conservation activities in Central Africa. In 2010 Norway signed a letter of intent with Indonesia to provide the latter country with up to US$1 billion. The United States has provided more than $1.5 billion in support for REDD+ and other sustainable landscape activities since 2010, the same occurring with Finland and Australia (for more details on REDD+ projects see the Voluntary REDD+ Database at http://www.reddplusdatabase.org/).

In synthesis, carbon market and protection of remaining tropical forest have a potential to inject billion of dollar into the economy of tropical countries and potentially drive tropical forests to sustainable use.

VI. THREATS TO TROPICAL MEGA-TREES

As a substantial proportion of tropical floras, the majority of mega-tree species exhibit narrow geographical distribution and thus can be naturally considered vulnerable to extinction (Hubbell *et al.*, 2008, Newbold et al. 2018). Just to give one example, at least 90 *Shorea* species (emergent dipterocarp trees) are endemic of the Borneo Island (Ghazoul, 2016). In addition to such a natural rarity**,** mega-tree species vulnerability can be summarized into four major threats: landscape modification (i.e. habitat loss, fragmentation and edge-effects), logging operations and climate change.

(1) Landscape modification

By far, habitat loss represents the major threat for tropical mega-trees since a substantial portion of species exhibit narrow geographical distribution and old-growth forests continue to be converted into human-modified landscapes (Lewis *et al.*, 2015). For instance, tropical forest cover in the Southeast Asia region is reduced by an average net rate of 1.6 million ha yr^{-1} (~0.6% yr^{-1}; Stibig et al. 2014), and this figure describes what has been experienced by the other major blocks of tropical forests. In average, tropical forest deforestation is around 1% per year (Achard et al., 2002; Hansen *et al.*, 2013), but deforestation is not a random process. Historically, deforestation has been concentrated into lowland forests, particularly across agriculturally suitable areas such as flat lands covering fertile soils. Deforestation trajectory experienced by the Atlantic forest, which has been reduced to ~12% of its original forest cover, is illustrative of this global trend: while lowland forests accounted for >90% of Atlantic original forest cover, this habitat represent <30% of the remaining habitat and a very limited proportion of the protected areas (Tabarelli *et al.*, 2010). As informed earlier, the low-land forests are the main habitat for mega-tree species globally (Corlett & Primack, 2011).

Habitat loss also implies habitat fragmentation and the consequent expansion of forest edges as old-growth forests are converted into human-modified landscapes: i.e. a collection of small forest fragments/remnants immersed into open-habitat matrix such as pastures or agricultural fields (Fischer & Lindenmayer, 2007). Forest edges tend to be more illuminated and exposed to wind turbulence, fires and chemicals coming from the matrix, i.e. abiotic edges effects (*sensu* Murcia, 1995). Thereby forest edges usually consist of more open and desiccated habitats as compared to interior forests and such edge-affected habitats can normally penetrate *c.* 300 m into the forest, but much more (2 – 3 km) where edge-related fires occur (Laurance *et al.*, 2018). As land use intensifies, human-modified landscapes progressively retain edge-affected habitats rather than forest interior or forest stands free of edge effects (Lewis *et al.*, 2015). For instance, more than 90% of the remaining Brazilian Atlantic forest is within 1 km of an edge (Haddad *et al.*, 2015). It includes second-growth or secondary forests following land abandonment in the case they consist of small forest fragments.

Edge-affected habitats are unsuitable for mega-trees due to a myriad of processes. Increased wind turbulence cause uprooting and adults can die by physiological stress (i.e. desiccation stress) along forest edges (Laurance *et al.*, 2000). In fact, the large height achieved by tropical mega-trees also makes them more prone to hydraulic failures, particularly in environments under extremely desiccated conditions (Brum *et al.*, 2019) such as forest edges (Laurance *et al.*, 2000). Accordingly, elevated tree mortality associated to edge effects can reach *c*. 300 meters inside forest (Laurance *et al.*, 2018). Moreover, mega-tree seedlings do not tolerate illuminated habitats and the competition with the proliferating light-demanding pioneer tree species (Benítez-Malvido & Martínez-Ramos, 2003; Santo-Silva *et al.*, 2013). Thus, small remnants and forest edges (i.e. edge-affected habitats) lack mega-trees and forest emergent layer (Laurance *et al.*, 2006; Oliveira, Santos, & Tabarelli, 2008; Santos *et al.*, 2008). This is compatible to the idea that edge effects drive the remaining forest to intermediate or even early-successional stages, in which mega-trees, particularly shade-tolerant species, are not expected to occur (Tabarelli *et al.*, 2008). Additionality, edge-affected habitats are more prone to experience fire and available evidence suggest that mega-trees are more sensitive, although the underlying mechanism are still poorly understood (Barlow *et al.*, 2003). It is true that some tree species benefit from human disturbances and even proliferate in human-modified landscapes (the '*winners*' sensu Tabarelli, Peres, & Melo, 2012). This is the case of tree species benefited by illuminated habitats, such as pioneer or light-demanding canopy species. Although many large trees can be considered large-pioneer species (*sensu* Turner, 2001), others filters associated to forest edges, such as increased wind turbulence, prevent mega-tree species proliferation in human-modified landscapes (Laurance *et al.*, 2000, 2006; Oliveira *et al.*, 2008; Santos *et al.*, 2008).

Most of the threats mentioned here referred to vulnerability of adults. However, mega-tree species are potentially threatened by other process such as limited pollination and seed dispersal as do many tropical tree species depending on sensitive pollinators and seed dispersers such as hummingbirds, large bees and frugivorous vertebrates (Cordeiro & Howe, 2001; Caughlin et al., 2015; Neuschulz et al., 2016). Human-modified landscapes tend to be progressively “empty” (Redford, 1992) and in landscapes dominated by small forest fragments, lack of long-distance seed dispersal may be fatal for successful recruitment of some ecological groups; e.g. shade-tolerant, large-seeded mega-tree species (Melo, Dirzo, & Tabarelli, 2006; Costa et al., 2012). For instance, a substantial proportion of tropical mega-tree species bear large seeds dispersed by medium- to large-bodied vertebrates, including primates, large-gaped birds and terrestrial mammals such as tapirs and large rodents (da Silva & Tabarelli, 2000; Muller-Landau & Hardesty, 2005). Such recruitment bottlenecks have been documented for particular cases, but we are still far of achieving a comprehensive perspective on how they threat mega-tree species persistence. In synthesis, human-modified landscapes dominated by edge-affected habitats are unsuitable habitats for most of large trees and the forest emergent layers as already demonstrated for some tropical landscapes in the Amazonian and Atlantic forest (Joly, Metzger, & Tabarelli, 2014 Laurance *et al.* 2018).

(2) Logging

Logging represents a serious threat for commercial tropical tree species because (1) logging usually targets trees ≥ 50 cm DBH, (2) timber production is based on the exploitation of native forests rather than tree plantations, and (3) a substantial proportion of logging is done illegally, what implies the harvest of all large stems and consequently the local elimination of the reproductive individuals (Cannon, Peart, & Leighton, 1998; Shima *et al*., 2018).

Annually, around 1 billion cubic meters of wood from over 300 tropical tree species are commercialized, particularly from Southeast Asia and South America (ITTO, 2002, 2014). Available estimates inform between 27-50 million cubic meters of wood from commercial timber species being extracted every year in the Amazon region, part of it from protected areas (Asner *et al.*, 2005). Accordingly, several mega-tree species used in the timber market have been officially declared threatened of extinction such as *Bertholettia excelsa*, *Dinizia excelsa* and *Cedrela* spp. (Steege *et al*., 2015). In fact, the timber market has historically operated in the boon-collapse scheme and any region covered by tropical forest is now able to offer a list of mega-tree species, which were overexploited in the past until population decline or collapse. We mention here dozens of species that were once commercialized and now are not available any more due to the collapse of native populations. In the lack of commercial exploitation many mega-tree species might recover their populations, but population collapse due to logging may precede forest conversion to other land uses or forest degradation (Shima *et al*., 2018).

(3) Climate change

Climate change can directly affect mega-tree species in the case they represent increased frequency of severe droughts (Phillips *et al.*, 2010; Bennett *et al.*, 2015; Brum *et al.*, 2019); i.e. the case in many tropical regions (Dai, 2012; Boisier *et al.*, 2015). Global-scale analyses have documented greater mortality among large trees across tropical forests, potentially due to higher physiological vulnerability to water stress (Phillips *et al.*, 2010; Bennett *et al.*, 2015), particularly soft-wood species and those requiring moist habitats; i.e wet-affiliated taxa (Greenwood *et al*., 2017; Esquivel-Muelbert *et al.*, 2019). Large crowns above forest canopy are more exposed to high solar radiation and vapor pressure deficits, turning more challenging to maintain a positive carbon balance as water availability reduces and evaporative demand increases. Additionally, mega-trees grow slower as exposed to droughts, i.e. reduced growth rate (Bennett *et al.*, 2015). This is in accordance with the prediction of lower wood production/forest productivity in tropical forests experiencing slightly drier/warmer conditions or severe droughts (Feeley *et al.*, 2007; Brando *et al.*, 2008). Temperature-water related declines on productivity might be compensated by increased CO2, but the impact of such fertilization on mega-trees is still poorly known (but see Esquivel-Muelbert *et al*., 2019).

Indirectly, climate change can threat mega-trees via the association between droughts, tree mortality and forest fires. This is particularly the case of severe droughts associated with El Niño Southern Oscillation (ENSO) in the Amazon region. Droughts cause habitat desiccation and increased mortality among mega-trees, which in turns largely increment the amount of dead biomass and forest inflammability; i.e. feedback looping connecting drought, tree mortality and forest fire (Nepstad *et al.*, 2007). Positive synergisms between logging, ENSO-related drought and increased mortality of mega-trees (standing dead trees) has been documented in Borneo (Slik, 2004). Other potential climate-change related impacts on mega-trees includes the proliferation of lianas and the increased tree mortality it causes (Phillips *et al.*, 2002). On the other hand, it has been argued that climate change and CO2 fertilization may favor some mega-tree species (Esquivel-Muelbert *et al*., 2019). However, it does not mean that such winners are able to persist in human-modified landscapes.

Finally, we shall mention that all documented threats to mega-trees so far result from the common trajectory experienced by tropical forests globally since agriculture/cattle raising intensified: the conversion of old-growth forests into human-modified landscapes dominated by edge-affected habitats (see Melo *et al.*, 2013). Briefly, logging of the forest premium is followed by habitat loss and fragmentation for the establishment of crops fields or pastures;

land-use intensification progressively reduces forest remnant size and drive them towards edge-affected habitats with high vulnerability to experience forest fires (Barlow *et al*. 2016). In the Atlantic forest region 15 million hectares of degraded lands (i.e. low productivity pastures) have been mapped and assigned to future forest restoration actions (Rodrigues, Isernhagem, & Brancalion, 2009). At old-frontiers degraded landscapes or commodity-devoted field predominate and this tragedy is expected to persist until the opportunity costs imposed by tropical forest remains elevated. Such forest trajectory towards degraded landscapes (i.e. reduced old-growth/edge-affected habitat ratio) due to the synergisms and concomitant occurrence of human disturbances has been advocated for a long time such as the forest die-back (Nepstad *et al*. 1999), and forest secondarization (Tabarelli *et al*. 2008); two threatening scenarios for most of the mega-tree species, particularly forest dependent species, now exposed to the climate change powerful drivers.

VII. SYNTHESIS AND A WAY FORWARD

We have just started to investigate the complex and multiple-patch role played by mega-tree species on biodiversity persistence, provision of ecosystem services and proper livelihood for forest-dependent people globally. As a stimulating exercise we would assume that the relative biomass supported by mega-tree species represent a proxy in terms of foliage, fruits, flower, litter and microhabitats plant attendants are connected to. It implies that the bulk of tropical biodiversity is in fact mega-tree dependent and it represents a pivotal working hypothesis to be tested.

Despite such limited knowledge it is clear that large tree species represent a substantial portion of tropical tree flora, with a disproportional contribution for biodiversity persistence as a multitude of taxa are associated to them directly or indirectly. Moreover, they have supported the tropical timber market historically, and provide invaluable ecosystem services and goods that are relevant commercially or for better livelihood of traditional populations; i.e. protection of tropical cultural heritage.

Protecting this resource is challenging as threats to large tree species do not operate isolated and result from an historical process that is gaining speed globally and rapidly: old-growth forest conversion towards human-modified landscapes. Climate changes adds new threats (i.e. severe droughts) to the already declining mega-tree populations in human-modified landscapes. Furthermore, it represents a potent threat for some mega-tree species considered until recently as living in “safety” by inhabiting patches of old-growth forests either at protect areas or in the last remote forests.

This is an alarming perspective, since the most promising approaches for protecting tropical biodiversity rely on the protection of old-growth forest blocks such as biodiversity corridors and its derivations (e.g. biodiversity-friendly landscapes; Melo *et al.*, 2013). Evidence continues to accumulate and reinforce the notion that old-growth forests represent irreplaceable habitats for uncountable large-tree species (i.e. forest-dependent species) and that strategies such as land-sharing (*sensu* Fischer *et al*., 2014) can be incorporated as complementary tool. However, severe droughts and cascades associated to CO2 fertilization can condemn large tree species on remote areas as they apparently favor other ecological groups. Similar to several mountain floras, for some mega-tree species there is no place to go anymore although our knowledge about climate change impacts on tropical forests has just started to develop.

In this perspective, the future of mega-tree flora depends on our ability of protecting large blocks of old-growth forest and their vulnerability to climate changes, particularly severe droughts. Locally, it implies the persistence of forest cover at regional level in order to guarantee some key functions such as rainfall interception, storage and evapotranspiration (Jordan & Kline, 1977; Herwitz, 1985; Goldstein *et al*., 1998), which can reduce the impact of droughts by ameliorating the regional climate and prevent widespread forest fires (Barlow *et al*., 2003; Lawrence & Vandecar, 2015). We are back to biodiversity corridor approach but in this case the matrix can consist of productive forests.

Globally, climate changes must be mitigated and protection of mega-tree species represent another claim for this. Both local and global demands could be tacked by establishment of productive (i.e. multiple-use) forest landscapes combining forestry and provision of global relevant services (services market). Local initiatives towards productive forest landscapes, the cornerstone tool for protecting mega-tree species, are already in course (e.g. forest for people; Larson *et al*., 2010), but is still limited in the tropics (García-Fernández, Ruiz-Pérez, & Wunder, 2008) as it face challenges relative to governance conditions, in the involvement of multiple stakeholders in the planning process, and in adjusting traditional practices to formal forestry regulations (Guariguata, Sist, & Nasi, 2012). However, it must be improved and scaled up rapidly as agribusiness moves to the last pieces of old-growth forest globally and human-modified landscapes continues to be degraded (Laurance *et al.*, 2014; Lewis *et al.*, 2015). Instruments such as REED+ and payments for ecosystem services could be explicitly integrated for supporting productive forest landscapes. Such approach represents an economic, political, technological and a social challenge as protecting tropical forests still pose an elevated cost of opportunity that few stakeholders are prone to pay. The future of mega-tree species, tropical forests and human-well-being are deeply interconnected and productive forest landscapes are likely to bring unanticipated benefits for future generations.

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Table 1. Summary of key direct and indirect support to biodiversity provided by mega-tree species in tropical rainforest, including driving processes, benefited taxa or ecological groups, and associated ecosystem services.

	Structures/Resources	**Support type**	**Taxa/Ecological groups benefited**	**Ecosystem functions & services**
Direct support	Large emergent crowns and forks	Nesting sites	Large-bodied raptors (e.g. Falconiformes)	Top-down control
		Roosting sites	Bats, birds, lizards, primates	Pollination, seed dispersal, top-down control, pest control
		Unique microhabitat conditions and resources (e.g. canopy humus)	Epiphytes	Carbon sequestration, biomass retention
	Tree cavities	Nesting sites	Birds, stingless-bees	Pollination, seed dispersal

		Microrefuges to extreme microclimatic conditions	Arthropods, frogs, lizards	Pathogens population control
	Uprooting - Temporary or permanent upland pools	Breeding sites, peccary wallows	Peccaries, amphibians, reptiles	Pathogens population control
	Masting flowering/fruits	Abundant food resources in critical times of low resource availability ("keystone resources")	Whole communities of frugivores and pollinators	Pollination, seed dispersal
Indirect support	Large trunks with emergent crowns	Microclimatic buffering	Shade-tolerant flora and their attendants	Carbon sequestration and storage
		Extended vertical physical support and microclimatic gradients	Microclimate-specialist species, whole-community	Maintaining trophic structure, preventing of

cascading extinctions and community collapse

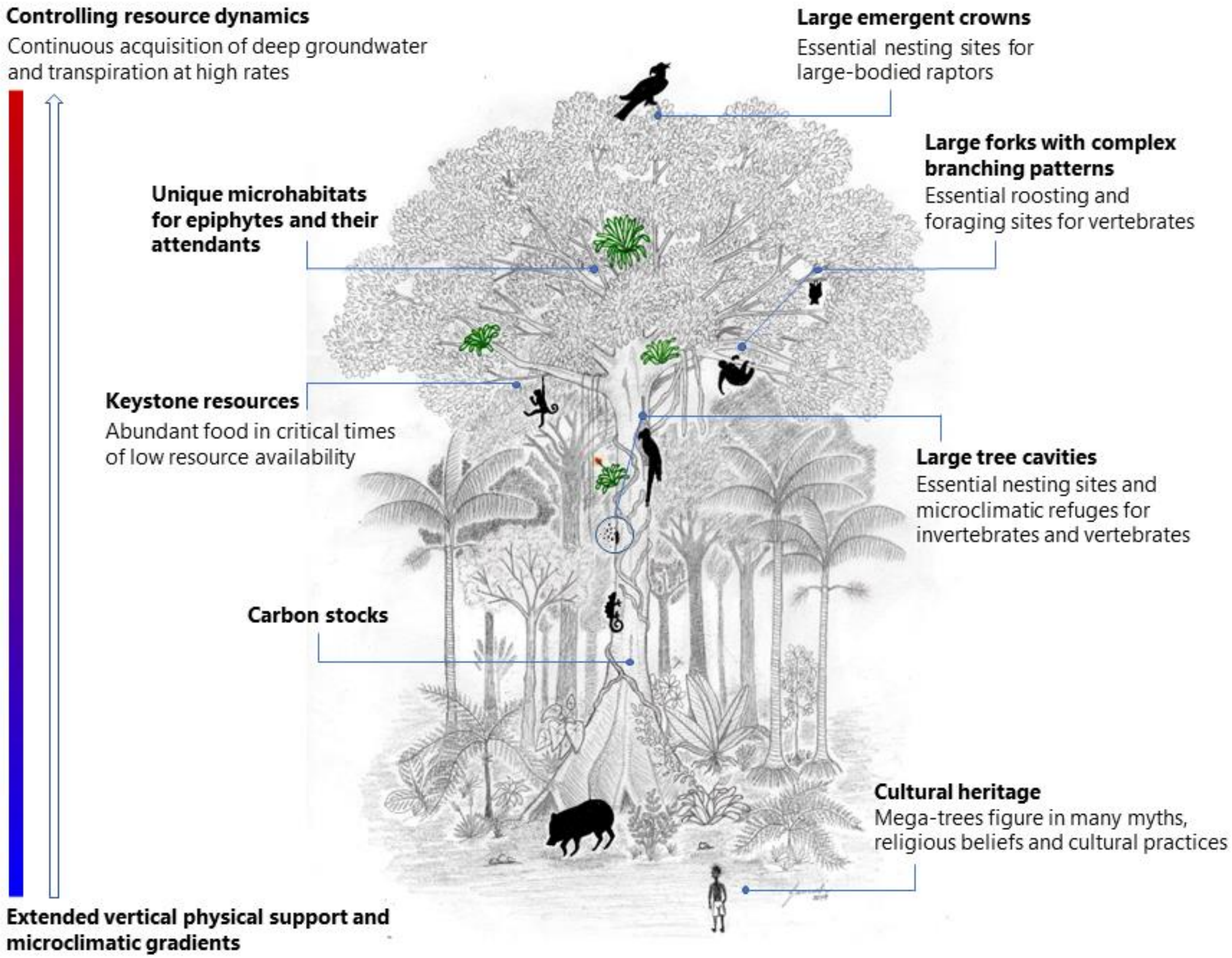

Figure 1. Schematic illustration of key structures and associated functions provided by tropical mega-trees.

CONCLUSÕES

Espécies de árvores em florestas neotropicais apresentam uma ampla gama de estratégias funcionais de regeneração e uso-de-recursos, que determinam seu sucesso e abundância de acordo com condições ambientais, disponibilidade de recursos e distúrbios em múltiplas escalas espaciais. Regionalmente, floras neotropicais apresentam espectros similares de variação em atributos funcionais, mas são dominadas por espécies com estratégias contrastantes. Isto sugere que embora a distribuição de espécies de árvores possa se extender por condições menos favoráveis, suas abundâncias são fortemente restringidas por fatores biogeográficos ou climáticos. Especificamente, floras mais ao norte da distribuição de florestas neotropicais tendem a ser dominadas por espécies com estratégias de uso-de-recursos mais aquisitivas, associadas a rápidas taxas de crescimento; enquanto que floras em direção ao sul são gradualmente dominadas por estratégias mais conservativas, associadas a tolerância a estresses abióticos. De fato, tem-se demonstrado que regiões mais ao norte da distribuição de florestas neotropicais têm sofrido distúrbios mais frequentes historicamente, além de em geral apresentarem maior precipitação anual, o que em conjunto deve explicar a maior dominância relativa de plantas com estratégias de rápido crescimento, adaptadas a distúrbios. Condições climáticas contemporâneas explicam em grande parte variações regionais, com o aumento em dominância de espécies com atributos mais aquisitivos (i.e., menor densidade foliar e caulinar) e sementes pequenas em ambientes potencialmente mais produtivos (i.e., maior evapotranspiração potencial) e com maior sazonalidade de temperatura. Estes atributos, no entanto, atingem valores máximos em baixas latitudes, particularmente na região Amazônica, provavelmente devido à estabilidade geológica e climática desta região, que deve favorecer estratégias lentas, associadas a menores taxas de crescimento e mortalidade, e maior estabilidade de processos ecossistêmicos.

Apesar desses padrões gerais, há uma ampla variação na composição e diversidade funcional de assembleias de árvores em cada região. Tal variação é em parte explicada pela estrutura de paisagens locais, no entorno imediato de remanescentes florestais. Especificamente, a redução da cobertura florestal em escala de paisagem tende a alterar fortemente a composição e/ou diversidade funcional de assembleias de árvores. Apesar de grande variação entre atributos e regiões quanto à direção, magnitude e escala dos efeitos, um pequeno conjunto de atributos, que em geral co-variam entre espécies, tende a responder de forma relativamente consistente a mudanças na estrutura de paisagens. Esses atributos têm relações bem estabelecidas com a capacidade de plantas recrutarem e sobreviverem em ambientes sob limitação de recursos, particularmente luz e nutrientes. Assim, o “gargalo ecológico” para a persistência de espécies de árvores em paisagens tropicais fragmentadas parece depender da capacidade de recrutamento e sobrevivência em condições abióticas impostas por efeitos de borda, à medida que a cobertura florestal é reduzida em escala de paisagem e consequentemente áreas afetadas por tais efeitos são expandidas. A perda de habitat em escala de paisagem atua, portanto, como uma força chave na organização de assembleias de árvores, filtrando grandes histórias-de-vida em paisagens tropicais fragmentadas.

Por sua vez, assembleias de árvores em florestas sazonalmente secas, na Caatinga, são principalmente organizadas em função de gradientes ambientais naturais, de precipitação e fertilidade de solos. Neste ecossistema, tem-se demonstrado que perturbações antrópicas estão mais relacionadas a como populações humanas usam recursos naturais do que com processos de desmatamento, devido às condições de pobreza que impedem empreendimentos lucrativos em larga escala. Enquanto outros estudos têm reportado declínios na diversidade funcional devido à crescente dominância de estratégias aquisitivas com a intensificação de perturbações antrópicas crônicas, na paisagem de Caatinga estudada neste trabalho, perturbações (i.e., extração de madeira e pressão de pastejo) têm importância secundária na organização de assembleias de árvores. Isto provavelmente se deve à ampla variação, em escala de paisagem, de condições ambientais naturalmente impostas por gradientes de precipitação (~ 500 a 1000 mm anuais) e fertilidade, que agem como forças predominantes. Esses dois fatores interagem entre si e determinam a abundância relativa de espécies de acordo com combinações específicas, ou “síndromes de atributos”. Especificamente, síndromes associadas à estratégia de evitar estresses hídricos através da produção de tecidos espessos e pouco densos, capazes de armazenar água e assim manter alto potencial hídrico sob escassez de água, aumentam em prevalência em ambientes sob menor precipitação anual, mas com maior capacidade de retenção de água nos solos. Por outro lado, o aumento da precipitação média anual leva à emergência e dominância de duas estratégias de tolerância a estresses hídricos. Ambas possuem alta densidade de madeira, mas se distinguem quanto a atributos foliares, sendo mediadas por condições edáficas que determinam maior dominância de atributos foliares conservativos em solos relativamente férteis. Embora o aumento em dominância de estratégias mais aquisitivas sob maior disponibilidade de recursos (i.e., água e nutrientes) constraste com padrões comumente observados em outros ecossistemas, isto pode ser interpretado no caso específico de florestas sazonalmente secas, representando diferentes estratégias de conservação de água, que co-ocorrem na escala de paisagem mas predominam em situações específicas de acordo com suas combinações de atributos. Esses resultados demonstram que os impactos de mudanças climáticas neste ecossistema devem depender de como padrões de chuva co-variam no espaço com outros fatores ambientais, como a fertilidade e a capacidade de retenção de água dos solos.

Finalmente, eu concluo que um grupo ecológico específico em florestas tropicais úmidas, as grandes árvores emergentes ou "mega-árvores", desempenham funções ecológicas desproporcionais em magnitude e algumas insubstituíveis, mas são particularmente ameaçadas por processos contemporâneos operando em escala local (e.g. extração seletiva de madeira), regional (e.g. perda e fragmentação florestal) e global (mudanças climáticas). Como a biomassa aumenta em escala exponencial com o aumento em altura e diâmetro de árvores, mega-árvores são raras localmente mas retêm mais da metade da biomassa vegetal em florestas tropicais, controlando ciclos e estoques de carbono e nutrientes. A biomassa desproporcional de mega-árvores pode também ser traduzida em termos de folhagem, flores, frutos, serapilheira e microhabitats que suportam grande parte da biodiversidade em florestas tropicais. Alguns suportes físicos à biodiversidade são providos exclusivamente por mega-árvores, como microhabitats associados a imensos troncos e copas iluminadas que ultrapassam o dossel florestal com complexos padrões de ramificação. De fato, alguns grupos de plantas (e.g. epífitas) e animais (e.g. aves) em florestas tropicais dependem de microhabitats providos exclusivamente por mega-árvores, como cavidades com grandes aberturas para nidificação. Adicionalmente, mega-árvores sustentam comunidades de herbívoros, polinizadores e frugívoros, provendo recursos alimentares essenciais em períodos anuais críticos; e indiretamente amplificam o espaço de nicho, com o tamponamento microclimático e a ampliação de gradientes microclimáticos. Mega-árvores têm também grande valor econômico, sustentando historicamente o mercado de madeira, e mais recentemente uma série de produtos não-madeireiros essenciais para a subsistência ou economia de populações tradicionais. No entanto, mega-árvores seguem uma trajetória de declínio em florestas tropicais. Alguns dos atributos que explicam a sua relevância também determinam a sua vulnerabilidade, como maiores alturas e troncos com madeira densa. Estas características determinam maior mortalidade desse grupo diante de secas intensas que promovem falhas hidráulicas, bem como menor recrutamento e sobrevivência em habitats de borda com ventos, incêndios e condições secas e iluminadas; além de lhe tornarem alvo principal em operações de extração de madeira. A conservação de biodiversidade e serviços ecossistêmicos em florestas tropicais depende, portanto, da manutenção de grandes blocos de floresta e matrizes menos hostis em paisagens produtivas com usos múltiplos, e da nossa capacidade de mitigar os efeitos de futuras mudanças climáticas, particularmente secas severas.

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