PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

ECOLOGIA DE METAPOPULAÇÕES E METACOMUNIDADES DE BROMÉLIAS ATMOSFÉRICAS

CLEBER JULIANO NEVES CHAVES

Orientador: Davi Rodrigo Rossatto
Co-orientadora: Clarisse Palma da Silva

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CLEBER JULIANO NEVES CHAVES

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutor em Ecologia e Biodiversidade.

Orientador: Davi Rodrigo Rossatto
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AUTOR: CLEBER JULIANO NEVES CHAVES
ORIENTADOR: DAVI RODRIGO ROSSATTO
COORIENTADORA: CLARISSE PALMA DA SILVA

Aprovado como parte das exigências para obtenção do Título de Doutor em ECOLOGIA E BIODIVERSIDADE, especialidade: Biodiversidade pela Comissão Examinadora:

Prof. Dr. DAVI RODRIGO ROSSATTO
Departamento de Biologia Aplicada a Agropecuária / UNESP - Faculdade de Ciências Agrárias e Veterinárias - Jaboticabal / SP

Prof. Dr. FLAVIO NUNES RAMOS
Instituto de Ciências da Natureza / UNIFAL - Universidade Federal de Alfenas / MG

Prof. Dr. MARCUS ALOIZIO MARTINEZ DE AGUIAR
Departamento de Física do Estado Sólido e Ciência dos Materiais - Instituto de Física Gleb Wataghin / UNICAMP - Universidade Estadual de Campinas - SP

Prof. Dr. TADEU DE SIQUEIRA BARROS
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

Profa. Dra. MARINA CORREA CORTES
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

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“Everything was fermenting, growing, rising with the magic yeast of life. The joy of living, like a gentle wind, swept in a broad surge indiscriminately through fields and towns, through walls and fences, through wood and flesh.”

Boris Pasternak – *Dr. Zhivago*

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PREFÁCIO

Esta tese foi concebida no início do declínio de uma 'fase de ouro' da ciência brasileira. E como todo declínio, este veio como um banho de água fria para muitos de nós, jovens pesquisadores, que, pela própria juventude e pouca vivência da história nacional, acreditávamos que a 'fase de bonança' não seria apenas uma fase. Não por falta de aviso de pesquisadores seniores, há que se ressaltar aqui. Durante os cinco anos que se seguiram da minha aprovação no doutorado do Programa de Pós-Graduação em Ecologia e Biodiversidade (PPGEB) da Unesp de Rio Claro (quatro anos e meio, desde a minha matrícula), eu e muitos colegas/amigos vimos e vivemos o progressivo corte de verbas para a ciência em todo o território nacional (Fig. 1). A euforia de antes se reduziu a uma fuga de grandes pesquisadores para fora do Brasil ou para centros científicos nacionais mais consolidados. O próprio PPGEB, criado em 2013, que agrupava renomados nomes de diversas áreas da Ecologia e tinha o potencial para ser uma grande referência nacional na área, sofreu com o esvaziamento de professores para outros centros e com diversos mestrandos e doutorandos sem bolsa por meses ou até anos. Um corte de verba também foi vivido por mim, durante o doutorado. Mesmo recebendo uma bolsa da FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo), esta não me foi renovada e acabei recebendo por menos tempo do que esperava. Não desconsiderando a minha extrema posição privilegiada na ciência brasileira, visto que recebi a provável melhor bolsa de doutorado do país, o seu corte me custou mudanças abruptas no planejamento da presente tese e nos planos de vida seguintes a ela. O que até então estava sob controle, acarretou numa ansiedade desnecessária para o final de uma importante fase para todo pesquisador e culminou num tumor de testículo. Nada de mais, no frigir dos ovos (com o perdão do trocadilho), mas não recomendo.

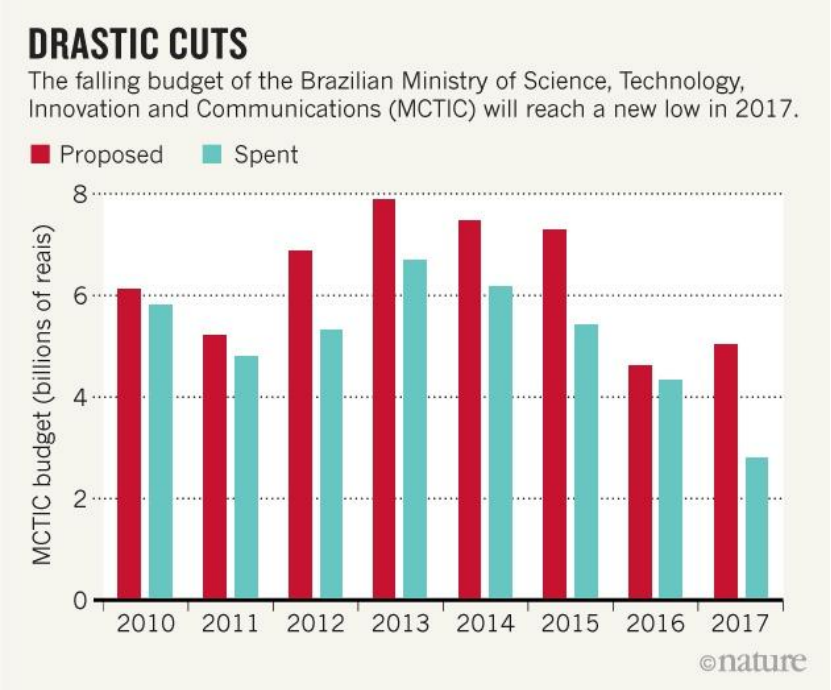

Figura 1. Ascensão e queda do orçamento previsto e gasto pelo Ministério da Ciência, Tecnologia, Inovação e Comunicações (MCTI) de 2010 a 2017. Fonte: Nature website (doi: 10.1038/nature.2017.21766). Meu doutorado se iniciou em 2014.

Figura 2. Diferentes tipos de ambientes e substratos de comunidades epífitas dominadas por bromélias atmosféricas. Nas fotos estão retratadas comunidades formadas por *Tillandsia recurvata*, *T. tricholepis* e *T. pohliana*. Elas estão por todos os lados!

Indo ao enfoque desta tese, motivo pelo qual fez você, leitor, chegar aqui, ela trata de plantinhas diminutas que geralmente passam desapercebidas pela maioria de nós: as bromélias atmosféricas. Se você é brasileiro, latino-americano *(si habla portugués*), ou mesmo sul-estadunidense (*if you can speak portuguese*), provavelmente já viu essas plantinhas amontoadas sobre árvores, postes e fios das cidades e campos (Fig. 2). Elas estão por quase todos os lados. Com algum espírito investigativo e olhando mais para o alto, você vai reparar que elas não estão distribuídas de forma uniforme pelas árvores, postes e fios, por exemplo. Certas árvores hospedam bem mais delas do que outras. Mas por quê? Antes de tentar responder, só tome cuidado para não tropeçar no meio-fio, cair num bueiro aberto, ou atravessar uma avenida movimentada sem olhar o tráfico. Esse mesmo espírito acometeu meu orientador Davi Rossatto, nos idos de 2013, e a mim mesmo, logo em seguida. Bastante atrasados, se considerarmos que essas questões vêm acometendo a outros pesquisadores desde o século XIX.

Devo confessar que, mesmo estudando ecofisiologia de bromélias-tanque durante o meu mestrado e em parte da minha graduação, as bromélias atmosféricas nunca haviam me interessado muito, afinal, 'elas não têm tanque'. A ideia de trabalhar com elas veio depois do final do meu mestrado na UFMG (Universidade Federal de Minas Gerais), quando meu até então orientador, José Pires, me falou que Davi havia acabado de aprovar um projeto no CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) para trabalhar com *Tillandsia*s – o principal gênero das bromélias atmosféricas – em Jaboticabal (SP), onde ele está lotado pela UNESP. Davi também tinha acabado de se credenciar no programa da pós de Rio Claro. Como eu ainda estava empolgado em estudar bromélias, pensei, "por que não?". O projeto de Davi gravitava em torno da ecofisiologia de espécies de *Tillandsia*, mas, com o convívio com colegas ecólogos, e pelo 'eco' da ecofisiologia me instigar mais do que o restante do termo, acabei deixando um pouco de lado o que havia aprendido no mestrado para embarcar em um mundo que pouco havia estudado até então, a ecologia de comunidades. Em Rio Claro, longe do meu orientador, acabei sendo 'pescado' por Clarisse Palma, para ficar em seu laboratório, ao invés da até então vazia sala de alunos do programa de pós-graduação. Clarisse é uma grande pesquisadora que trabalha com evolução e genética de populações e que orientava minha parceira, Bárbara Leal, que embarcou comigo de Belo Horizonte para Rio Claro, para fazermos o doutorado juntos. O que começou como uma gentileza, rendeu, além de uma boa amizade com Clarisse, uma parceria e sua co-orientação.

Como estudar bromélias atmosféricas, ecologia de comunidades, ecofisiologia e genética de populações mantendo um mínimo de coesão que uma tese exige? Bem, a abstração de epífitas formando populações e comunidades em árvores distintas não é exatamente uma ideia nova. A saída foi então recorrer à ideia de comunidades de bromélias atmosféricas interligadas pela dispersão de suas sementes, formando metacomunidades epífitas. A teoria das Metacomunidades de Leibold et al. (2004) serviu de elo de ligação para todas essas ideias aparentemente díspares e como fio condutor

para as novas perguntas que foram aparecendo. Uma dessas perguntas começou a ser desenvolvida durante o meu estágio-sanduíche na *Technische Universität Dresden* (Alemanha), com Uta Berger. Uta é uma grande cientista e parceira de Volker Grimm e Steven Railsback, duas 'celebridades' da modelagem baseada no indivíduo (IBM). Foi Uta quem me possibilitou fazer, sem custos, um dos melhores cursos da área, lecionado por ela, Volker, Steven e Robert Schlicht. Esse foi, sem dúvida, o ponto alto do meu estágio-sanduíche e o melhor curso que fiz na vida (Fig. 3). O período com Uta serviu para eu aprender, quase do zero, sobre IBMs, repensar ideias e direcionar esforços no desenvolvimento de um modelo que, até então, era apenas um devaneio limitado à minha cabeça, mas que acabou se fundindo com o tema de Clarisse para se tornar o último capítulo desta tese.

Figura 3. Participantes do 11th Summer School in Individual- & Agent-based modelling, em Holzhau (Alemanha). Eu sou o segundo ao fundo, da direita para esquerda (em pé), Uta Berger está em pé ao lado da escada, à esquerda. À direita da escada encontram-se Steven Railsback e Voker Grimm. Foto oficial de divulgação.

Os quatro capítulos que compõem esta tese estão, em maior ou menor grau, relacionados a cada um dos quatro paradigmas, ou arquétipos, listados por Leibold et al. (2004; Leibold and Chase 2018). Todos eles estão em inglês e no formato de artigos, pois foram escritos visando publicações internacionais. Mas a Introdução Geral e as Considerações Finais estão em português, para trazê-los à realidade brasileira. A Introdução Geral, em específico, traz um mínimo arcabouço teórico dos diferentes temas nos quais esta tese se baseia e que pode ser auxiliar na sua compreensão. Tal arcabouço foi desenvolvido durante esses quatro anos e meio de doutorado, com uma constante e crescente aquisição de conhecimento acerca dos mais variados temas da ecologia. Estou certo que muito fiz e muito aprendi, mas que tudo isso não passa de uma pincelada frente a toda riqueza de conhecimento que hoje se forma continuamente acerca desses temas. Caberá agora a você, leitor,

avaliar se esta tese é ou não do seu agrado. Que essas páginas lhe tragam boas ideias e uma agradável leitura.

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O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001, do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) - Código de Financiamento 471756/ 2013-0 e da Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) - processos 2016/04396-4 e 2017/01559-2). O apoio concedido na forma de financiamento de projeto e de bolsas de doutorado e doutorado sanduíche por essas agências foi fundamental para o desenvolvimento desta tese. Esta tese tornou-se possível também graças aos recursos computacionais disponibilizados pelo Núcleo de Computação Científica (NCC/GridUNESP) da Universidade Estadual Paulista (UNESP).

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RESUMO GERAL

Bromélias atmosféricas são cerca de 300 espécies do gênero *Tillandsia* que geralmente compõem o grupo de epífitas vasculares dominante das porções mais altas e externas dos dosséis florestais do continente americano. Diversas adaptações à dessecação fizeram com que essas plantas fossem conhecidas como o caso mais extremo de epifitismo vascular, chegando a formar abundantes comunidades em árvores de ambientes antropizados e se fixassem até mesmo em substratos artificiais, como postes e fios. Por serem formadas em diferentes árvores, vistas como manchas de habitat, envoltas por uma matriz inóspita para epífitas, comunidades epífitas, como as dominadas por bromélias atmosféricas, são consideradas como um 'sistema ideal' para o estudo empírico de metacomunidades. Sob a teoria 'guarda-chuva' das Metacomunidades, tratamos a cada capítulo desta tese de temas como ecologia funcional, genética de populações, modelagem ao nível individual (IBM) e ecologia de espécies invasoras, para compreender padrões naturais de distribuição e coexistência entre espécies de bromélias atmosféricas. A estruturação desta tese foi guiada de acordo com os paradigmas da teoria de metacomunidades de Leibold et al. (2004). No primeiro capítulo abordamos a influência da heterogeneidade do dossel na abundância e distribuição de bromélias atmosféricas em um ambiente antropizado com múltiplos agrupamentos funcionais arbóreos. No segundo capítulo testamos a influência de atributos arbóreos na formação de metacomunidades de bromélias atmosféricas em múltiplas escalas e como esses efeitos são influenciados pelo aumento ou redução da conectividade entre comunidades locais, resultantes de diferentes densidades arbóreas regionais. No terceiro capítulo testamos possíveis interações positivas e negativas entre três espécies de bromélias atmosféricas com grande sobreposição de nicho e averiguamos como essas interações se refletem na coexistência natural entre elas. No quarto capítulo testamos a estruturação genética de uma metapopulação de *Tillandsia recurvata* (L.) L. e descrevemos sua dinâmica espaço-temporal através de modelagens baseadas no indivíduo (IBM). Concluímos, ao longo dos quatro capítulos, que a estruturação de metacomunidades epífitas dominadas por bromélias atmosféricas depende do grau de heterogeneidade e conectividade entre suas comunidades locais. Especificamente, a formação desses sistemas está relacionada à combinação dos diferentes atributos arbóreos locais que compõem o dossel e à densidade arbórea regional.

PALAVRAS-CHAVE: Bromélias, ecologia de comunidades, epífitas, genética de populações, interações entre espécies, metacomunidades

GENERAL ABSTRACT

Atmospheric bromeliads are a group of ca. 300 species of *Tillandsia* genus, which usually is the dominant group of vascular epiphytes in upper and outer canopy layers of American forests. Many drought adaptations made these plants be known as the extremest case of vascular epiphyte, forming abundant communities on trees of anthropic environments and attaching even to abiotic substrates, as posts and wires. Due to their distribution on distinct trees, seen as habitat patches in an inhospitable matrix, epiphytic communities are regarded as 'ideal systems' for the empiric study of metacommunities. Under the Metacommunity Theory, we deal in each chapter of this thesis with topics such as functional ecology, population genetics, individual-based modelling (IBM), and ecology of weeds, to understand natural patterns of distribution and coexistence among species of atmospheric bromeliads. The structure of this thesis is according the paradigms of Metacommunity Theory of Leibold et al. (2004). In the first chapter, we address the influence of canopy heterogeneity on the abundance and distribution of atmospheric bromeliads in an anthropic environment with multiple functional groups of trees. In the second chapter, we test the influence of tree traits on the assembling of metacommunities of atmospheric bromeliads in multiple scales and whether these effects are affected by the increase or reduction on the connectivity of local communities, arising from distinct regional tree densities. In the third chapter, we test possible positive and negative interactions among three atmospheric bromeliad species with highly overlapping niches and investigate whether these interactions are reflected on their natural coexistence. In the fourth chapter, we tested the genetic structure of a *Tillandsia recurvata* (L.) L. metapopulation and described its temporal-spatial dynamics through the IBM. We concluded, in the course of the four chapter, that the structure of the epiphytic metacommunity dominated by atmospheric bromeliads depends on the heterogeneity degree and connectivity among their local communities. Specifically, the assembling of these systems is related to the local combination of distinct tree traits comprising the canopy and the regional tree density.

KEY-WORDS: Bromeliads, community ecology, epiphytes, metacommunities, population genetics, species interactions

INTRODUÇÃO GERAL

A construção desta tese foi, desde a concepção de seu projeto, pensada de uma forma interdisciplinar, visando a utilização de diferentes abordagens do estudo de ecologia de comunidades e populações. Sob a teoria 'guarda-chuva' das Metacomunidades (Leibold et al. 2004), tratamos a cada capítulo de temas como ecologia funcional, genética de populações, modelagem ao nível individual (IBM) e ecologia de espécies invasoras para compreender padrões naturais de distribuição e coexistência entre espécies epífitas (bromélias atmosféricas, em específico). Devido à grande interligação entre tais temas, nenhum deles é muito aprofundado, porém uma breve síntese dos tópicos centrais da tese é dada a seguir.

DE METAPOPULAÇÕES A METACOMUNIDADES

O termo 'metapopulação' foi criado por Levins (1969) para descrever as dinâmicas temporais de 'uma população de populações' de uma espécie. Segundo ele, populações podem ser definidas como um conjunto de indivíduos que interagem entre si durante um tempo de vida finito. Metapopulações, por sua vez, são sistemas nos quais populações locais estão conectadas pela dispersão de indivíduos de diversas gerações (Hanski & Gilpin 1991). O termo tem origem na noção geral de estrutura hierárquica da natureza e na abstração de paisagens formadas por redes de manchas de habitats interligadas pela dispersão entre populações locais (Hanski & Gaggiotti 2003). Da mesma forma que as dinâmicas de populações locais são definidas pelas taxas de nascimento e morte de seus indivíduos, os processos de extinção e estabelecimento de novas populações em ambientes propícios ao seu estabelecimento (i.e. *turnover*) definem, de modo geral, as dinâmicas de metapopulações (Hanski & Gilpin 1991).

Se duas ou mais espécies coexistem em ambientes interligados, elas formam uma comunidade de metapopulações, ou uma metacomunidade. Metacomunidades podem ser vistas como redes compostas por comunidades ligadas entre si pela dispersão (Wilson 1992). De modo geral, metacomunidades são formadas em duas escalas: uma escala regional maior, composta por várias escalas locais menores e potencialmente heterogêneas conectadas pela dispersão (Leibold and Chase 2018). Possíveis interações entre espécies geralmente ocorrem nas escalas menores, mas a coexistência local e regional delas será também um resultado da dispersão e heterogeneidade espacial (Ricklefs 1987; Leibold and Chase 2018). Além da escala, a ecologia de metacomunidades se difere da ecologia de comunidades tradicional pelo reconhecimento explícito da dispersão e heterogeneidade (McGill 2010; Vellend 2010; Leibold and Chase 2018). A interação desses três fatores resulta nos padrões de ocorrência e coexistência de espécies que nós observamos na natureza. Uma das tentativas de se entender os padrões de composição de espécies em comunidades locais se baseia em quatro modelos [ou paradigmas] conceituais indissociáveis que incluem alguns dos mais importantes fatores da ecologia de comunidades (e.g. seleção de nicho, dispersão, estocasticidade,

processos de extinção-colonização; Leibold et al. 2004; Holyoak et al. 2005; Leibold and Chase 2018):

(SS) "*species-sorting*" (heterogeneidade ambiental) – pressupõe uma heterogeneidade ambiental que seleciona espécies com capacidades de crescimento e estabelecimento diferenciadas para cada mancha de habitat (Leibold and Chase 2003);

(ME) "*mass-effect*" (fonte-dreno) – pressupõe que as manchas de habitat são interconectadas pela dispersão frequente de comunidades maiores, formadas em ambientes com menores taxas de extinção (i.e. fontes), para comunidades menores, formadas em ambientes com maiores taxas de extinção (i.e. dreno; Mouquet and Loreau 2003);

(PD) "*patch-dynamic*" (competição-dispersão) – pressupõe que as espécies que coexistem em manchas de habitats ambientalmente homogêneas exibem diferentes taxas de dispersão que levam a *trade-offs* relacionados a suas estratégias de vida (e.g. colonizadores X dominantes; Loreau and Mouquet 1999);

(NT) "*neutral-model*" (estocasticidade) – pressupõe que as espécies não diferem na exploração de recursos e que a formação de comunidades se deve exclusivamente à estocasticidade relacionada à demografia, colonização, extinção e dispersão entre comunidades locais (Hubbell 2001).

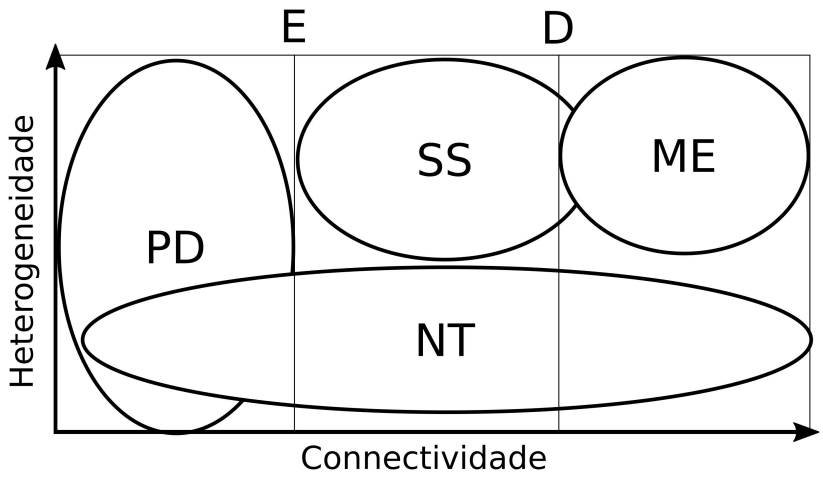

Figura 1. A importância dos quatro paradigmas da teoria de metacomunidades (Leibold et al. 2004) em relação à heterogeneidade e conectividade entre comunidades locais (Figura adaptada de Leibold and Chase 2018). À esquerda de E, as comunidades são limitadas pela dispersão. À direita de D, as comunidades possuem um excesso de dispersão.

A importância de cada um desses paradigmas pode ser disposta em dois eixos relacionados ao grau de heterogeneidade e conectividade entre comunidades locais (Fig. XX; Leibold and Chase 2018). Enquanto a baixa heterogeneidade entre manchas de habitat aumenta o efeito da estocasticidade (NT), a diferenciação dos efeitos de SS, ME e PD, sob alta heterogeneidade, dependerá do grau de conectividade entre as comunidades locais (Fig. 1). Por outro lado, cada um dos paradigmas possui diferentes premissas acerca de processos locais (utilização de recursos, interações biológicas, estocasticidade demográfica, deriva) e regionais (heterogeneidade ambiental, dispersão; Leibold and Chase 2018) e a interação de tais processos molda a estrutura de metacomunidades que podem ser classificadas de acordo com a distribuição e coexistência de suas espécies (e.g. tabuleiro de xadrez, aninhado e randômico; Leibold and Mikkelson 2002).

A maioria dos estudos teóricos considera metacomunidades como sistemas discretos, onde processos locais ocorrem dentro de manchas de habitat definidas e a dispersão entre elas ocorre através de uma matriz inóspita. Estudos empíricos, no entanto, são muitas vezes realizados em sistemas naturais distribuídos em paisagens onde a matriz é habitável ou inexistente, ou se restringem a sistemas clássicos (e.g. arquipélagos, sistemas de lagos, poças de água, bacias hidrográficas). Apesar de pouco estudadas, comunidades epífitas formadas em diferentes árvores também podem ser concebidas como um sistema discreto de metacomunidades, onde cada árvore é vista como uma mancha de habitat imerso em uma matriz completamente inóspita (Burns 2007; Burns and Zotz 2010). Apesar de comunidades epífitas poderem ser vistas como um 'sistema ideal' para o estudo empírico de metacomunidades (Burns 2007), o entendimento da complexidade e particularidade desses sistemas é vital para se entender como eles são moldados pelos diferentes fatores e paradigmas que compõem a teoria de metacomunidades.

EPÍFITAS

Epífitas (*epí* = sobre, *phytón* = planta), de modo geral, são plantas que nascem e se desenvolvem em cima de outras sem prejudicá-las (ver Mirbel 1815; Benzing 1990). Este grupo vegetal engloba diferentes tipos de plantas, desde algas aquáticas, hepáticas e musgos até frondosas bromélias que abrigam microcosmos nos tanques de água formado pelo entrelaçamento de suas folhas (i.e. fitotelmas; Kitching 2000). No entanto, diferentemente das epífitas aquáticas que necessitam apenas de adaptações para agarrarem-se a outras plantas, a história da ocupação de ambientes epifíticos terrestres envolveu diversos desafios relacionados à polinização e dispersão de propágulos, ao estabelecimento de juvenis e, principalmente, ao suprimento de água e nutrientes (Lüttge 1989). Uma vez que ambientes epifíticos terrestres estão mecanicamente desacoplados do solo, a falta de ligação direta com um reservatório constante de água é o principal fator limitante para a colonização dos dosséis florestais (Lüttge 1989; Zotz and Bader 2009; Benzing 2012). Por esse mesmo motivo, epífitas são tidas como um dos grupos vegetais mais vulneráveis aos atuais distúrbios antrópicos e às mudanças climáticas (Benzing 1990).

Epífitas, representam 9% de todas as plantas vasculares (Zotz 2013), sendo 55% delas nativas das Américas (Benzing 2012). Em florestas neotropicais, em especial, as epífitas são a forma de vida mais diversa, abrangendo cerca de 50% da flora vascular local e até 15% de sua biomassa total (Hofstede et al. 1993; Foster 2001). É principalmente nesses ambientes que as epífitas possuem um maior papel ecológico, abrigando outros organismos e tendo uma função vital na hidrologia e no fluxo de nutrientes florestal (ver Benzing 1990, 2000, 2012; Zotz and Bader 2009). Dessa forma, qualquer impacto negativo advindo da grande vulnerabilidade de epífitas às mudanças ambientais pode afetar consideravelmente outros componentes dos ecossistemas em que elas estão inseridas.

De mecanismos para estocar água em tecidos suculentos à plantas revivescentes, a limitação

hídrica típica do ambiente epifítico foi contornada por diversas adaptações surgidas em plantas vasculares (ver Benzing 2012). Dosséis vegetais são formados por troncos, galhos e coberturas foliares com características distintas que levam ao cruzamento de diferentes gradientes de luz, temperatura, humidade e suprimento nutricional (Zotz 2016). Essa heterogeneidade de habitats nos dosséis vegetais vai muito além de sua limitação hídrica e levou à seleção de espécies epífitas com diferentes necessidades fisiológicas. A variação vertical na composição de espécies ao longo de dosséis florestais, por exemplo, é um fato continuamente reportado na literatura (e.g. Pittendrigh 1948; Ruiz-Cordova et al. 2014). Esses estudos mostram que as porções superiores dos dosséis são, geralmente, habitadas por plantas mais tolerantes à dessecação, e as porções mais inferiores são habitadas por plantas mais tolerantes ao sombreamento .

BROMÉLIAS ATMOSFÉRICAS

Bromélias atmosféricas geralmente compõem o grupo de epífitas vasculares dominante das porções mais altas e externas dos dosséis florestais do continente Americano (e.g. Pttendrigh 1948; Ruiz-Cordova et al. 2014). Esse grupo abrange cerca de 300 espécies do gênero *Tillandsia* L. (Benzing 2012) e se originou entre 5 e 10 milhões de anos a partir de modificações heterocrônicas (i.e. quando organismos adultos exibem as características juvenis de seus ancestrais; Haeckel 1875) de bromélias-tanque que habitavam paisagens áridas da porção norte da cordilheira dos Andes (ver Benzing 2012). Devido a isso, tais plantas passaram a apresentar tamanhos reduzidos e raízes que raramente se desenvolvem além da sua função de fixação mecânica na planta hospedeira (Benzing 2012). Isso, somado a características como suculência foliar, metabolismo fotossintético CAM (*Crassulacean Acid Metabolism*), folhas cobertas por tricomas, que absorvem água e nutrientes diretamente da atmosfera (resumido por Benzing 2012), e até mecanismos de transporte hídrico extra-foliar (Herppich et al. 2018), fez com que as bromélias atmosféricas fossem conhecidas como, possivelmente, o caso mais extremo de epifitismo vascular (Benzing 2012). Tantas adaptações contra a dessecação fez com que elas dispensassem plantas hospedeiras e se fixassem até mesmo em substratos artificiais, como postes e fios de eletricidade, se espalhando em diversas paisagens antrópicas (e.g. Puente and Bashan 1994; Wester and Zotz 2010; Benzing 2012).

Tillandsia recurvata (L.) L.

Conhecida por diversos nomes (e.g. *ball-moss*, *Jamaican ball moss*, *musgo de bola*, *heno de bola* e *galinita*) que refletem sua ampla distribuição no continente Americano – desde a Argentina até o sul dos Estados Unidos (Smith and Downs 1977; Global Biodiversity Information Facility: http://www. gbif.org) – *Tillandsia recurvata* está entre as espécies de bromélias atmosféricas mais abundantes e conhecidas popularmente. Tal fato se deve à sua grande capacidade de colonização de paisagens antrópicas, onde é capaz de formar populações de milhares de indivíduos em árvores, postes, cercas e até fios elétricos (e.g. Puente and Bashan 1994). *Tillandsia recurvata* se destaca das

outras bromélias atmosféricas por ser a mais xerófita das epífitas tropicais e subtropicais (Biebl 1964) e, talvez, a planta com maior capacidade adaptativa do ocidente (Foster 1945), pelo seu ciclo de vida rápido, auto-fecundação espontânea e intenso crescimento vegetativo por clonagem, que lhes confere o aspecto típico de 'bola' (Soltis et al. 1987; Smith et al. 1989; Orozco-Ibarrola et al. 2015; Chilpa-Galván et al. 2018).

Ao contrário de outras epífitas, *T. recurvata* é apontada como beneficiada pelos distúrbios antrópicos e pelas mudanças climáticas atuais (e.g. Caldiz et al. 1993; Guevara-Escobar et al. 2011), que estão levando a um rápido aumento de sua distribuição geográfica (McWilliams 1992). A rápida capacidade de colonização de novas áreas fez com *T. recurvata* se tornasse um conhecido elemento de paisagens antrópicas, atraindo o interesse de pesquisadores de diversas áreas do conhecimento que identificaram desde sua ação antiangiogênica (Lowe et al. 2012, 2014) até o seu uso como bioindicadora (Smodiš et al. 2004; Bermudez et al. 2009). Por outro lado, isso também fez com ela seja considerada danosa para plantas ornamentais e nativas. Em um estudo feito por Birge (1911), no Texas (EUA), por exemplo, o autor relata que era "do conhecimento local que as *ball moss* retiram gradualmente a vida de suas hospedeiras". Claver et al. (1983), por sua vez, reportou que as populações de *T. recurvata* tiveram "um rápido crescimento nos últimos 10 a 15 anos que causou sérios danos às florestas e plantas ornamentais do entorno de La Plata (Argentina)", as classificando como uma 'planta daninha epífita' (*epiphytic weed*). Tal concepção estimulou o desenvolvimento de diversos técnicas visando o combate ao seu crescimento, incluindo o uso de herbicidas (e.g. Caldíz and Beltrano 1989; Kaplan 2004; Aguilar-Rodriguez et al. 2016). De fato, apesar de não ser uma planta parasita, alguns estudos indicam que grandes populações de *T. recurvata* podem chegar a competir por luz com os ramos de suas hospedeiras, modificar suas cascas e até afetar, por alelopatia, o crescimento de suas plântulas ou de outras epífitas (e.g. Valencia-Diaz et al. 2012; Flores-Palacios et al. 2015; Aguilar-Rodriguez et al. 2016). Apesar da ação direta de *T. recurvata* sobre suas hospedeiras ainda carecer de investigações aprofundadas, esses estudos demonstram a grande capacidade oportunística da espécie para colonizarem rapidamente áreas antropicamente perturbadas.

ESTRUTURA DA TESE

A estruturação desta tese foi guiada de acordo com os paradigmas da teoria de metacomunidades de Leibold et al. (2004). Os temas de cada capítulo são brevemente colocados a seguir em conjunto com os paradigmas da teoria mais abordados por eles (ver siglas):

Capítulo 1 – paradigma SS – Neste capítulo utilizamos o ambiente antropizado de um campus de universidade (UNESP / FCAV em Jaboticabal, SP) que possui plantações de árvores de diferentes tipos funcionais (e.g. *Eucaliptus*, *Pinus*, ipês) como um 'laboratório' para detectar possíveis preferências na ocorrência e abundância de bromélias atmosféricas.

Capítulo 2 – paradigmas SS, ME e NT **–** Neste capítulo buscamos compreender o efeito da combinação de diferentes atributos arbóreos da formação de metacomunidades de bromélias atmosféricas em múltiplas escalas (variação funcional individual, distribuição no dossel, seleção de hospedeiro, abundância, diversidade funcional e composição de espécies). Buscamos também desvendar como esses efeitos são influenciados pelo aumento ou redução da conectividade entre comunidades locais, resultantes de diferentes densidades arbóreas regionais.

Capítulo 3 – paradigma PD – Diferentemente dos capítulos anteriores, neste capítulo deixamos de desconsiderar as espécies de bromélias atmosféricas e buscamos, através de levantamentos em campo e experimentos, medir a sobreposição de seus nichos, testar possíveis interações positivas e negativas e averiguar como essas interações se refletem na coexistência natural entre elas.

Capítulo 4 – paradigma NT – Para excluirmos os efeitos da heterogeneidade ambiental e preferências de nichos, o foco deste capítulo passou de metacomunidades para metapopulações. Em um grupo de árvores de espécies aparentadas e com idades similares, testamos, através de marcadores genéticos e modelagem IBM, a estruturação populacional em escala fina de *Tillandsia recurvata* e descrevemos sua dinâmica espaço-temporal. O enfoque em apenas uma espécie nos permitiu explorar mais o caráter oportunístico de uma das bromélias atmosféricas mais abundantes e amplamente distribuídas do continente americano.

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CAPÍTULO I

HOST TRAIT COMBINATIONS DRIVE ABUNDANCE AND CANOPY DISTRIBUTION OF ATMOSPHERIC BROMELIAD ASSEMBLAGES

Cleber J. N. Chaves[1]; Júlio C. Dyonisio[2]; Davi R. Rossatto[1,2]

[1] Programa de Pós-graduação em Ecologia e Biodiversidade, Universidade Estadual Paulista (UNESP), Instituto de Biociências, 13506-900 Rio Claro, Brazil; [2] Universidade Estadual Paulista (UNESP), Faculdade de Ciências Agrárias e Veterinárias, Departamento de Biologia, 14884-900 Jaboticabal, Brazil

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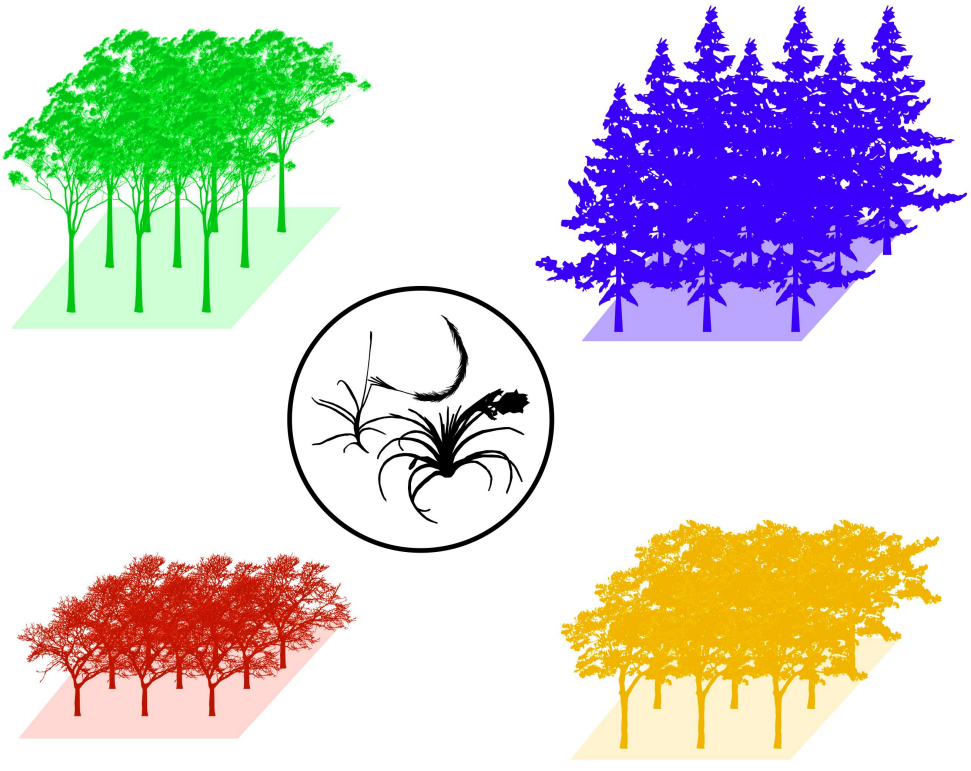

ABSTRACT

Epiphytes are strongly dependent on the conditions created by their host's traits and a certain degree of specificity is expected between them, even if these species are largely abundant in a series of tree hosts of a given environment, as in the case of atmospheric bromeliads. Despite their considerable abundance in these environments, we hypothesize that stochasticity alone can not explain the presence and abundance of atmospheric bromeliads on host trees, since host traits could have a greater influence on the establishment of these bromeliads. We used secondary and reforested seasonal forests and three distinct silvicultures to test whether species richness, phylogenetic diversity and functional diversity of trees can predict the differential presence, abundance, and distribution of atmospheric bromeliads on hosts. We compared the observed parameters of their assemblage to null models and performed successive hierarchic partitions of the variance of abundance and distribution of the assemblage to detect the influence of multiple traits of the tree hosts. Our results do not indicate direct relationships between the abundance of atmospheric bromeliads to phylogenetic or functional diversity of trees, but instead indicate that bromeliads occurred on fewer tree species than expected by chance. We distinguished functional tree patterns that can improve or reduce the abundance of atmospheric bromeliads, and change their distribution on branches and trunk. While individual tree traits are related to increased abundance, species traits are related to the canopy distribution of atmospheric bromeliad assemblages. A balance among these tree functional patterns drive the atmospheric bromeliads assemblage of the forest patches.

KEYWORDS**:** Atmospheric bromeliads, canopy ecology, epiphyte assembling, functional ecology, host preference, phorophyte, *Tillandsia.*

INTRODUCTION

About 9% of vascular plant diversity (near 30,000 species) are mechanically dependent on other plants (Benzing 1990; Zotz 2013), and for this reason are important elements of many ecosystems, particularly in the neotropics. Thus, the epiphytic assemblages provide a remarkable system to evaluate species-specific interactions in plants, since their hosts are capable to facilitate or difficult their fixation and reproduction (Callaway et al. 2002; Steel and Wilson 2003, Wagner et al. 2015). Given the particularity of each host tree and the niche differences of epiphytic species, a certain degree of specificity is expected between them; i.e. the exclusive occurrence of an epiphyte species on a single host species (ter Steege and Cornelissen 1989; Tremblay et al. 1998). Although a strict host tree specificity, or a completely random host tree selection are rare, many works reported the existence of host preference (i.e. a greater abundance of a epiphyte species on a few host species; e.g. ter Steege and Cornelissen 1989) and host limitation (i.e. a concentration of individuals of a epiphyte species on a few host species as a result of limiting factors of the other tree species; e.g. Vergara-Torres et al. 2010) in epiphyte communities.

In both host preference or host limitation scenarios the host traits play a crucial role on epiphyte assemblage and distribution, since each host tree species offers a specific combination of phenological patterns, architectural traits and bark characteristics that provide a wide spectrum of epiphyte habitats (Zotz and Schultz 2008; Benavides et al. 2011). Traits of hosts can propitiate or limit the presence of epiphytes: for example; larger trees have greater available surface and more complex structures to receive epiphyte seeds (e.g. Benzing 1990; Bernal et al. 2005; Flores-Palacios and Garcia-Franco 2006; Laube and Zotz 2006; Benavides et al. 2011); trees with rough and furrowed barks can increase seed establishment and improve water absorption (e.g. Callaway et al. 2002; Cascante-Marín et al. 2009; Wagner et al. 2015); and deciduous canopies can facilitate the establishment of more drought-adapted species and limit the success of shade-adapted species (e.g. Cardelus 2007; Einzmann et al. 2015). Thus, tree species that are functionally similar and/or phylogenetically related could host similar epiphyte species.

An example of highly drought-specialist epiphytes are the atmospheric bromeliads, a group composed mainly by species of the *Tillandsia* genera (Bromeliaceae) (Benzing 2012). These plants are often small, absorb water and nutrients almost entirely from aerosols through their squamous leaves (Martin and Schmitt 1989), require high light irradiances, and have a CAM metabolism (Benzing 1981; Benzing 1990). Thus, they are found profusely on drier habitats such as dry forests (e.g. Benzing 2000; Flores-Palacios 2015; Reyes-García et al. 2008), appearing even in outer canopies of wet forests (e.g. Pittendrigh 1948; Johansson 1974; Griffiths and Smith 1983; Einzmann et al. 2015). Atmospheric bromeliads can also be largely abundant on trees of

anthropogenic transformed habitats, such as silviculture forests, and even on abiotic substrates, such as telephone wire cables and power lines (e.g. Martin et al. 1986; Wester and Zotz 2010; Benzing 2012). This creates an assumption that these plants should be able to colonize any substrate (Callaway et al. 2002; Wester and Zotz 2010), but their abundances will probably be fostered by substrates that optimize or limit their growth and reproduction (Bernal et al. 2005; Valencia-Diaz et al. 2010; Vergara-Torres et al. 2010). Furthermore, the atmospheric bromeliad preferences could be hampered in an environment with many tree species with distinct facilitator and limiter characters, since it is probable that some traits of a tree, such as crown shape or leaf area, can affect the hosting ability of its neighbor trees.

Here we used patches of secondary and reforested tropical forests to test if species richness, phylogenetic relatedness, and functional diversity of trees (not only the hosts) can predict the differential presence and abundance of atmospheric bromeliad assemblages on trees. Additionally, we tested which combination of functional traits of the trees of those patches, adding up the trees from three distinct silvicultures (*Pinus elliottii*, *Eucalyptus* spp. and *Tabebuia* spp.), could: (1) facilitate or limit the establishment of atmospheric bromeliads and (2) predict their distribution on tree hosts (i.e. if individuals attach more to the branches or to the trunk of the trees). Finally, we assessed how the presence or absence of these trait combinations in all studied vegetation patches will affect the whole atmospheric bromeliad assembly. We hypothesize that stochasticity alone cannot explain the presence and abundance of atmospheric bromeliads on host trees, since the assumed microclimatic conditions influenced by host traits may have a greater influence on the establishment and growth of atmospheric bromeliads.

METHODS

Study site

We performed this study during November 2013 in five vegetation patches differing in species composition at Faculdade de Ciências Agrárias e Veterinárias (FCAV), UNESP, Jaboticabal – SP, Brazil (48°17'S, 21°14'W) **[see SUPPORTING INFORMATION**]. This region has a smooth and wavy relief, about 600 m.a.s.l., and a typical tropical climate (Souza et al. 2003), with an annual rainfall around 1,420 mm (historic average between 1971-2000). Our chosen vegetation patches were two diverse forests (mixed-species): a semi-deciduous secondary forest (SF) and a semi-deciduous forest reforestation patch (RP); and three different silviculture forests: a *Eucalyptus* sp. patch (EP), a *Pinus elliottii* patch (PP) and a *Tabebuia* sp. (Bignoniaceae) grove (TP). The atmospheric bromeliad composition measured on silviculture patches can be attributed to a single functional tree pattern, once, unlike the mixed species patches (secondary and reforested forest patches), each of them represents an isolated functional group of trees. According with FCAV

historical records, these patches were planted around 1979-1980, with no management thereafter. In each of these vegetation patches we randomly assembled five 10 x 10 plots to describe vegetation composition and distribution on canopy (Table S1). All vegetation patches are spaced less than 1 km apart; thus in our study area the supply and interchange of propagules among vegetation patches can be very high, which makes the disjoint distribution and abundance patterns of atmospheric bromeliads among trees probably caused by their host preferences.

Data collection

We identified the species and measured trunk diameter at breast height (DBH) and height of each studied tree individual found in each plot. Additionally, we measured the leaf area index (LAI) of each studied plot taking hemispheric photographs with a CI-110-24P-ID (CID Bioscience Inc., Camas, WA, USA). Functional traits related to the capability to host epiphytes (i.e. deciduousness, bark type, peeling capability, heliophyte or esciophyte, and presence of thorns and needles; classification based on Lorenzi and Gonçalves 2011) were assessed for each tree species, consulting the literature (Lorenzi et al. 2009; Lorenzi 2011; Lorenzi 2014a; Lorenzi 2014b). On each tree, of each plot, we counted and identified all atmospheric bromeliads identifying where they were located (i.e. trunk or branches) **[see Supporting Information]**.

The distribution of atmospheric bromeliad assemblage on tree canopies

To analyze the distribution of atmospheric bromeliad assemblages on tree canopies (AB_{dst}) we employed the followed metric: $AB_{dst} = A_{trunk}/A_{total}$. Where A_{trunk} represents the atmospheric bromeliad abundance at the trunk and A_{total} the total abundance in each host tree. Thus, the closer AB_{dst} is to 1, the more relative abundance of atmospheric bromeliads a tree has on its trunk, and the closer AB_{dst} is to 0, the more relative abundance of atmospheric bromeliads a tree has on its branches. An AB_{dst} closer to 0.5 implies a relative balance between the atmospheric bromeliad abundances on trunk and branches.

Statistical Analysis

To test the differences of atmospheric bromeliad abundance (AB_{abund}) and distribution on tree canopies (AB_{dst}) among vegetation patches (i.e. EP, PP, TP, RP, and SF; see 'Study sites' section above, for abbreviations), we used general linear models (GLMs) and analysis of variance (ANOVA), followed by pairwise means comparisons, using chi-square values for Poisson (count data) and Binomial (proportion data) types of distribution (Crawley 2002). To test the relationship of AB_{abund} and AB_{dst} with tree richness, tree functional diversity (FD and Fdi; Petchey and Gaston

2006; Cianciaruso et al. 2009), and tree phylogenetic diversity (PD; Faith 1992), we fit simple linear models and tested them also with ANOVA.

To test if host tree species richness, phylogenetic diversity (PD; Faith 1992), and functional diversity (FDi; Cianciaruso et al. 2009) of the vegetation patches with diverse tree species (RP and SF) are less, greater or equal to the expected by chance (see Laube and Zotz 2006b), we randomized all atmospheric bromeliad individuals raised on all tree hosts of each vegetation types. Then we calculated the species richness, PD, and FDi (see the functional dendogram in Online Resource 1) of host trees on the random draw. We repeated this process 10,000 times, on a specific R language script [**see SUPPORTING INFORMATION**], generating a null model with a 95% confidence interval for each of the parameters that were used to compare to the observed values.

To test if the pool of host tree species raised on both RP and SF have a random phylogenetic structure, we compared the observed phylogenetic structure (correlation between co-occurrence and phylogenetic distance) to patterns expected under a null model (1,000 runs, shuffling phylogeny tip labels), based on Schoener's index of co-occurrence (Cavender-Bares et al. 2006). In addition, to test if the pool of host tree species of RP and SF are phylogenetically under-dispersed (i.e. if atmospheric bromeliads attach to trees of more restricted phylogenetic groups), we randomized 1,000 times their data matrix abundances (maintaining the tree species occurrence frequencies) and compared the observed phylogenetic diversity (i.e. phylogenetic species variability, richness, evenness and clustering; Helmus et al. 2007) with the null model obtained. To calculate the phylogenetic parameters we constructed a phylogeny (Online Resource 2) with all tree species through the mega phylogenetic tree of phylomatic software (R20120829; phylodiversity.net/phylomatic) **[see Supporting Information]**.

In order to detect which of the functional traits of trees were more important and how they interact to explain the observed variation in atmospheric bromeliad abundance (AB_{abund}) and distribution on tree canopies (AB_{dst}), we constructed data trees through successive hierarchic partitions and 1,000 randomizations (to test the significance) of all data using: (1) non-host and host trees for AB_{abund}, and (2) only the host trees for AB_{dst} [**see SUPPORTING INFORMATION**]. We did so once this second analysis used the percentage of atmospheric bromeliad distribution on each tree canopy and, thus, needed that they hosted at least one of those epiphytes. The same procedure was repeated with the subsequent groups generated by the most significant variable until no significant partition could be observed, pulling out all variables that already had explained the variance of the previous partitions. To split groups when the most explanatory variable was quantitative, we divided the data into two groups by their median. With the resulting data tree we traced how the traits of trees interact to increase or decrease the abundance and structuring of

atmospheric bromeliad assemblage. Additionally, we determined which patterns of interactions among functional traits of trees (Host patterns) are more prone to: (1) host larger numbers (higher than 400) of atmospheric bromeliads (named here as "Best Hosts"); (2) host fewer numbers (less than 10) of atmospheric bromeliads (named as "Worst Hosts"); (3) host more than 90% of atmospheric bromeliads on the trunk (named as "Trunk Hosts"); (4) host more than 90% of atmospheric bromeliads on the branches (named as "Branches Hosts").

The relationships among the assignment of each tree to each Host pattern were tested through GLMs. The correlations among these assignments were grouped in only one variable, through a Principal Component Analysis (Hill and Smith 1976) of (1) all trees and (2) only the host trees, to test relationships of the Host patterns with, respectively, (1) AB_{abund} and (2) AB_{dst}, through GLMs. Finally, we performed an Euler diagram to observe if some species have tree individuals assigned to different Host patterns and if some species have tree individuals assigned exclusively to a single Host pattern. All the analyses were performed on R software 3.1.2 (R Core Team 2014), through "vegan", "picante", "rich", "FD", "ade4", "phytools", "hier.part", and "venneuler" packages (Dray and Dufour 2007; Kembel et al. 2010; Wilkinson 2011; Revell 2012; Walsh and Mac Nally 2013; Laliberté et al. 2014; Oksanen et al. 2015).

RESULTS

Atmospheric bromeliad species and differences among vegetation patches

We found four species of atmospheric bromeliads at our patches of sampled vegetation: *Tillandsia recurvata*, *T. pohliana, T. tricholepsis*, and *T. loliacea* **[see Supporting Information]**. *Tillandsia recurvata* was the most abundant species (Table 1), representing more than 80% of the atmospheric bromeliads found in our study area (57.6% at EP; 82.1% at TP; 69.7% at PP; 81.5% at RP; 52.5% at SF).

The *Tabebuia spp.* patch (TP) had by far the greatest atmospheric bromeliad abundance by host ($\chi^2 = 52609$, df = 4, $p < 0.001$; see Fig. 1A and also Online Resource 1), which was distributed primarily on branches ($\chi^2 = 97.14$, df = 4, $p < 0.05$; Fig. 1B). On the other hand, the trees of *Eucalyptus* sp. patch (EP) presented the lowest average number of atmospheric bromeliads by host ($p < 0.05$; Fig. 1A) with all of them attached to the trunk (Fig. 1B). We found no statistical significant relationships of AB_{abund} and AB_{dst} with species richness, functional diversity, or phylogenetic diversity of the trees ($p > 0.05$). While almost all trees of TP and PP served as host for atmospheric bromeliads, more than 60% of trees in reforestation patch (RP) and secondary forest (SF) showed no epiphytes (Online Resource 3).

Tree species richness, phylogenetic and functional diversity on atmospheric bromeliad assembly

Based on 95% confidence intervals, the host species richness in the reforestation patch (RP) and secondary forest (SF), as well the functional diversity (FDi) of SF, were lower than expected by chance (Fig. 2). However, the phylogenetic diversity (PD) of both vegetation patches and functional diversity (FDi) of RP were similar to null models (Fig. 2). The host tree species raised on RP and SF have a random phylogenetic structure, since we observed no difference between the observed phylogenetic structure and the null model. Furthermore, the phylogenetic species diversity (i.e. phylogenetic species variability, richness, evenness and clustering) of RP and SF also showed a random or even an over dispersed phylogenetic structure (based on 95% confidence intervals; Table 2).

Functional patterns of the host trees affecting bromeliad assembly

We found that the deciduousness of the host was the major determinant of the variance explanation in our successive hierarchic partition of the AB_{abund} (24.4%, $z = 3.76$, $p < 0.05$): deciduous trees had higher atmospheric bromeliad abundance, while semi-deciduous trees had lower abundance (Fig. 3A). For AB_{dst}, bark type played the major role in explaining variance (26.1%, $z = 8.74$, $p < 0.05$): trees with reticulated bark showed higher abundances of atmospheric bromeliads on branches and trees with smooth bark possessed higher abundance on the trunk (Fig. 3B). However, the great interaction of deciduousness and bark type with other variables showed that distinct traits combination can generate similar AB_{abund} and AB_{dst} values. For instance, semi-deciduous trees showed similar atmospheric bromeliad abundance than evergreen trees with needles or deciduous trees with high LAI and DBH values.

According to the functional trait interactions demonstrated by our model, the Best Hosts were those trees with: (1) deciduous behavior and DBH lower than 154 cm (AB_{abund} = 423.3 on average); and (2) deciduous behavior and DBH higher than 154 cm, with grooved bark and growing under an LAI lower than 1.65 (AB_{abund} = 594.0 on average; Fig. 3A). In contrast, the Worst Hosts were: (1) semi-deciduous trees (AB_{abund} = 3.57 on average); (2) evergreen trees, without needles (AB_{abund} = 2.44 on average); and (3) deciduous trees, with a DBH higher than 154 cm, and under an LAI higher than 1.65 (AB_{abund} = 6.5 on average; Fig. 3A). Considering the position that bromeliads preferably occupy on the host, the named Branches Hosts were those trees with: (1) reticulated barks (AB_{dst} = 0.04 on average) and (2) grooved barks, height lower than 7.9 m, and under an LAI lower than 1.31 (AB_{dst} = 0.02 on average; Fig. 3B). Finally, the named Trunk Hosts were: (1) trees with smooth barks (AB_{dst} = 0.99 on average); (2) trees with flaky bark, needles, DBH lower than

367 cm, and under an LAI lower than 1.54 (AB_{dst} = 0.96 on average); and (3) trees with grooved bark, height higher than 7.9 m, and without thorns (AB_{dst} = 1.0 on average; Fig. 3B).

The *Tabebuia* spp. patch (TP) showed the higher proportions of trees assigned as Best Hosts (almost 80%; Fig. 4A). All trees of *Eucalyptus* sp. patch (EP), and nearly 80% of reforestation patch (RP), were assigned as the Worst Hosts (Fig. 4B). Nearly 30% of host trees of TP, and 20% of RP and secondary forest (SF) were assigned as Branches Hosts (Fig. 4C). All host trees of EP and nearly 30% of *Pinus elliotti* patch (PP), RP, and SF were assigned as Trunk Hosts (Fig. 4D).

The first principal component of PCA using all host and no-host trees explained 47.5% of variance of the assignment of each tree to each Host pattern; and the first principal component of PCA with only tree hosts explained 51.9% of this variance (Table 3). Both were significantly related to AB_{abund} (χ^2 = 220.97, df = 1, $p < 0.001$) and AB_{dst} (χ^2 = 93.68, df = 1, $p < 0.001$; Table 3), however the contribution of each host tree pattern showed an opposite effect on abundance and canopy distribution. While the assignment of trees to the patterns "Best" and "Branches Hosts" was related to the increase of abundance of atmospheric bromeliads and the relatively higher abundance on branches, the assignment of trees to the patterns of Worst and Trunk Hosts were correlated to the decrease of abundance and the occurrence of bromeliads on trunks (Table 3).

We observed that trees assigned as Trunk Hosts are unlikely to be assigned as Best Hosts (χ^2 = 49.88, df = 1, $p < 0.001$; Fig. 5A) and likely to be assigned as Worst Hosts (χ^2 = 71.62, df = 1, $p < 0.001$; Fig. 5B), and more trees assigned as Best Hosts were likely to be also assigned as Branches Hosts than the trees unassigned to this pattern (χ^2 = 31.28, df = 1, $p < 0.001$; Fig. 5C). No relationships were found among trees assigned as Worst and Branches Hosts (χ^2 = 1.69, df = 1, p = 0.194; Fig. 5D). Many species of trees assigned as Worst Hosts also had individuals assigned to the other Host patterns (30 species; Fig. 6). Only those species of trees assigned as Branches Hosts had no individuals assigned as Trunk Hosts (Fig. 6). Each Host pattern had no more than 23% of exclusive species (i.e. trees assigned to only one Host pattern; Fig 6).

DISCUSSION

We were able to provide evidence that stochasticity alone cannot explain the presence and abundance of atmospheric bromeliads on host trees. As observed for other epiphytes and even for *Tillandsia* spp. (Burns 2007; Reyes-García et al. 2008; Silva et al. 2010; Sáyago et al. 2013), we found clusters of atmospheric bromeliads on fewer tree species than expected by chance [**see SUPPORTING INFORMATION**]. Thus, only a few species in the pool of trees of mixed-species forests could have specific traits that can create a habitat for atmospheric bromeliad establishment,

growth and reproduction, which in turn can increase their abundance. However, as recorded by Silva et al. (2010) for other epiphyte groups, we did not find a phylogenetic signal on the host species selection, which means that its facilitating or limitating traits are not phylogenetically conserved.

Following the small number of studies reporting host preferences of atmospheric bromeliads (e.g. Reyes-García et al. 2008; Flores-Palacios et al. 2015), our results suggest that their occurrence are related to tree traits responsible for increasing light exposition into the canopy (see Reyes-García et al. 2008; Einzmann et al. 2015); such as deciduousness, low leaf area index (LAI) and the presence of needles (in comparison with the broad leaves of many angiosperm trees). These preferences are related to drought adaptation of some epiphytes (Einzmann et al. 2015), a key characteristic of atmospheric bromeliads (Benzing and Renfrow 1971; Benzing 1990; Hietz 1997; Bernal et al. 2005). In this study, we report impressive abundances of *Tillandsia* spp. on trees presenting such traits (more than 2,600 individuals on a single tree) [**see SUPPORTING INFORMATION**]. This singular host preference shows not only the high reproductive capability of these plants, but also their considerable ability to overcome a hard canopy filter to epiphytism (see Einzmann et al. 2015), comparable to the pioneer role of early successional species (e.g. Horn 1974). This comparison could also be reinforced by the higher abundance of atmospheric bromeliads on deciduous trees with lower trunk diameter (DBH) – because they are more prone to lose branches (e.g. Zimmerman and Olmsted 1992) – requiring them to complete a full life cycle in a small amount of time (Sarmento Cabral et al. 2015). Similar results were observed for some *Tillandsia* species (Zimmerman and Olmsted 1992), but are not expected in other epiphytes (e.g. Yeaton and Gladstone 1982; Hietz and Hietz-Seifert 1995; Zotz 1999; Laube and Zotz 2006a), since they show more abundance on large trees due to the greater bark area, longer time for colonization and greater heterogeneity in microhabitats (e.g. Benzing 1990; Laube and Zotz 2007; Zotz and Schultz 2008; Woods et al. 2015).

The intricate interaction among the tree functional traits, and its architecture (e.g. Malizia 2003), can elevate or decrease its hosting capacity. For instance, in a study with *Tillandsia recurvata*, Bernal et al. (2005) found that in scrubland vegetation (trees with height up to 4m) this species preferred large host trees, when comparing tree species with similar architecture. On one hand, this argument can explain the greater abundance of atmospheric bromeliads found on larger individuals of *Pinus elliottii* (an evergreen tree with needles; see Fig. 3A). However, it cannot explain the incredible abundance on *Tabebuia* spp., which are smaller and thinner trees. *P. elliottii* trees are more prone to house atmospheric bromeliads on their trunk (see Fig. 3B), since such trees

are taller than *Tabebuia* spp., thus providing more trunk surface for epiphytic establishment (see Flores-Palacios and Garcia-Franco 2006; Benzing 2008; Izuddin and Webb 2015).

The bark types of trees have been associated with the epiphyte preferences of hosts (Steege and Cornelissen 1989; Benzing 1990; Castro Hernández et al. 1999; Bernal et al. 2005; López-Villalobos et al. 2008; Vergara-Torres et al. 2010; Wagner et al. 2015), but we show that for atmospheric bromeliads this trait is more related to their distribution on hosts canopies rather than abundance. Trees with smooth barks house more atmospheric bromeliads on trunk, and trees with more ridged and furrowed barks house more atmospheric bromeliads on branches (Fig. 3B). Thus, these epiphytes may have a preference for smooth barks (although not directly affecting their abundance), since young branches of rough bark trees are often smoother (e.g. Everhart et al. 2009; Ranius et al. 2009). This is an interesting result for epiphytes, since smooth barks have a non-adequate surface for their attachment. However, that does not seem to be a problem for atmospheric bromeliads, which are capable of colonizing even telephone wires. Furthermore, the preference for smoother bark is probably due to its lower water-holding ability and its resulting drier micro environment (Chomba et al. 2011; Wagner et al. 2015). Moreover, the drier conditions of the branches and their higher dew formation, as they are in an outer canopy position (see Freiberg 1997; Graham and Andrade 2004; Wagner et al. 2013; Woods et al. 2015), also explain the nesting of atmospheric bromeliads on the branches of trees with rough barks. These results suggests, once more, the preference of atmospheric bromeliads for the likely xeric conditions provided by some tree traits.

When we analyzed all possible interactions of tree functional traits, we were able to discern distinct functional patterns of trees that are more prone to optimize or limit the fixation of atmospheric bromeliads. The higher similarity within distinct patterns of the “Best Hosts” and “Branches Hosts” (i.e. these patterns are more nested on Figs. 3A-B) and the dissimilarity within the patterns of the “Worst Hosts” and “Trunk Hosts” (i.e. the patterns are more scattered on Figs. 3A-B) are noticeable. For instance, a deciduous tree that could host large abundances of atmospheric bromeliad, could also host very few individuals when presenting a high DBH or LAI. Therefore, the proportion of trees assigned as Best and Branches Hosts were lower than the other two patterns, in our sampled vegetation patches (except in TP). These results, as observed in other studies with *T. recurvata* and other epiphytes, suggest a strong host limitation of atmospheric bromeliad assemblies, on both monocultures (EP and PP) and mixed-species patches (RP and SF) (Tremblay et al. 1998; Bernal et al. 2005; Vergara-Torres et al. 2010; Flores-Palacios et al. 2015).

The balance among the proportions of Best, Worst, Trunk, and Branches Hosts determines the atmospheric bromeliad abundance and canopy distribution in communities. The more trees are

assigned as Best or Branches Hosts – or the less trees are assigned as Worst or Trunk Hosts – the more atmospheric bromeliads will be attached on the trees of a given vegetation patch and the greater the proportion of atmospheric bromeliads attaching on their branches. For instance, the *Tabebuia* spp. patch (TP), which showed the higher proportion of Best and Branches Hosts, showed the greatest abundance of atmospheric bromeliads, which were nested primarily on branches. By contrast, the opposite results were observed on *Pinus elliotti* patch (PP), in which all trees were assigned as Worst and Trunk Hosts. On the other hand, the vegetation patches composed by multiple species of trees (RP and SF), assigned both to Best and Branches Hosts as to Worst and Trunk Hosts, showed few atmospheric bromeliads, which were almost equitably spread between trunk and branches. This result can be due to a reduction and scattering of xeric habitat on diverse forests, since their trees are able to exploit canopy space more efficiently than monocultures (Pretzsch 2014; Jucker et al. 2015) and could create new niches for other epiphyte types.

Given the greater amount of substrate on branches compared to trunks of many trees (Whittaker and Woodwell 1967; Ruiz-Cordova et al. 2014) and the differential host capacity of each of these crown partitions, our results highlight that to demonstrate host preferences of epiphytes it is not enough to count their differential abundance on each tree. For instance, a tree could house a small amount of atmospheric bromeliads just because it has a small amount of substrate with great host capability (e.g. on its trunk), not because overall it is a bad host. Such a statement can be based on the fact that 80% of trees with traits related to low abundance of atmospheric bromeliads (assigned as Worst Hosts) are also more prone to host them on their trunk (i.e. also assigned as Trunk Hosts), and the trees with traits related to great abundance (assigned as Best Hosts) have more chances to nest atmospheric bromeliads on their branches (i.e. also assigned as Branches Hosts), compared to those without this pattern (i.e. unassigned as Branches Hosts). Furthermore, many of tree species that were assigned as Trunk Hosts have the ability to self-pruning their branches (as *Pinus elliottii* and *Eucalyptus sp.*; e.g. Mäkinen and Colin 1999; Smith et al. 2006). So, the atmospheric bromeliads only can be fixed and increase their abundance on their trunks.

According to our results, the majority of tree species must be seen as a potential unpleasant host for atmospheric bromeliads, since almost 90% of tree species had individuals assigned as Worst Host. However, individual trait combinations of a tree, as well as its interaction with the neighborhood (i.e. being shaded or changing its crown shape), can increase its host capability. In this way, individual traits of each tree are more influential in explaining differential abundance of atmospheric bromeliads. This explains why the assemblages of atmospheric bromeliads had a reduced and clumped abundance on some tree species of the diverse forests and varied widely

among distinct silvicultures. Extrapolating this preference pattern to other groups of epiphytes, it becomes clear that, for conservation of epiphytic diversity, we must not only preserve the diversity of tree species, but also maintain the individual abundances by species. On the other hand, species-specific traits, such as bark type or presence of thorns, may play an important role on the distribution of atmospheric bromeliads within the crown of a host tree, since no species had individuals assigned as both Branches and Trunk Hosts. So, if a tree has individual traits that make it a good host, it will be its species traits that will determine where in its crown the atmospheric bromeliads will be nested, a condition which, as stated before, will be reflected in the atmospheric bromeliad's total abundance.

CONCLUSION

The assembly of atmospheric bromeliad species is not stochastic, but rather, is mainly determined by a set of host trait combinations that increase the xeric conditions of epiphytic niche on different crown partitions. A balance of trees assigned to functional patterns can facilitate or limit the epiphyte's abundance and distribution. In order to detect general patterns of host preference, more studies grouping epiphyte individuals by ecological functionality, instead of using a single or all raised epiphytes species, will be essential. This approach may be more powerful and enlightening in elucidating the forces governing their assemblage.

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CONTRIBUTIONS BY AUTHORS

C.J.N.C. carried out the data analysis and writing; J.C.D. helped in fieldwork; D.R.R. conceived the study design, carried out fieldwork and writing.

CONFLICTS OF INTEREST

No conflicts of interest.

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TABLES AND FIGURES

Table 1. Abundances of atmospheric bromeliad species found on each vegetation patch.

Vegetation Patch	*Tillandsia recurvata*	*Tillandsia pohliana*	*Tillandsia tricholepsis*	*Tillandsia loliacea*
Eucalyptus sp.(EP)	76	40	7	9
Tabebuia spp. (TP)	15,927	207	336	207
Pinus elliottii (PP)	570	159	17	72
Reforestation (RP)	44	5	0	5
Secondary forest (SF)	52	40	4	3
Total	16,669	451	364	296

Table 2. Comparison between the observed and the randomized (95% confidence interval) phylogenetic structure of the host trees of reforestation patch (RP) and secondary forest (SF) with its conclusive inference on distinct phylogenetic diversity metrics. PSV: Phylogenetic Species Variability. PSR: Phylogenetic Species Richness. PSE: Phylogenetic Species Evenness. PSC: Phylogenetic Species Clustering.

Metric	Vegetation patch	Null model quantiles 2.5%	Null model quantiles 97.5%	Observed	Phylogenetic Structure
PSV	RP	0.741	0.914	0.831	random
	SF	0.702	0.765	0.717	random
PSR	RP	2.585	3.777	3.754	random
	SF	2.134	2.962	3.585	overdispersed
PSE	RP	0.651	0.869	0.757	random
	SF	0.508	0.718	0.635	random
PSC	RP	0.151	0.372	0.284	random

SF	0.267	0.364	0.386	overdispersed

Table 3. Relationships between the abundance (AB_{abund}) and distribution of atmospheric bromeliads (AB_{dst}) with the first component of PCA, done with the presence/absence of trees assigned to each Host pattern (Best, Worst, trunk, and Branches). The table also shows the weight of which the presence of trees assigned as each Host pattern does on the first component of PCA and the percentage of its explained variance.

	PC1 Scores				Explained	Slope	R^2
	Best	Worst	Trunk	Branches	Variance (%)		
AB_{abund}	-0.977	0.358	0.696	-1.154	47.5	-1.31^{***}	0.446^{***}
AB_{dst}	-0.941	0.551	0.702	-1.325	51.9	2.57^{***}	0.525^{***}

*** $p < 0.001$.

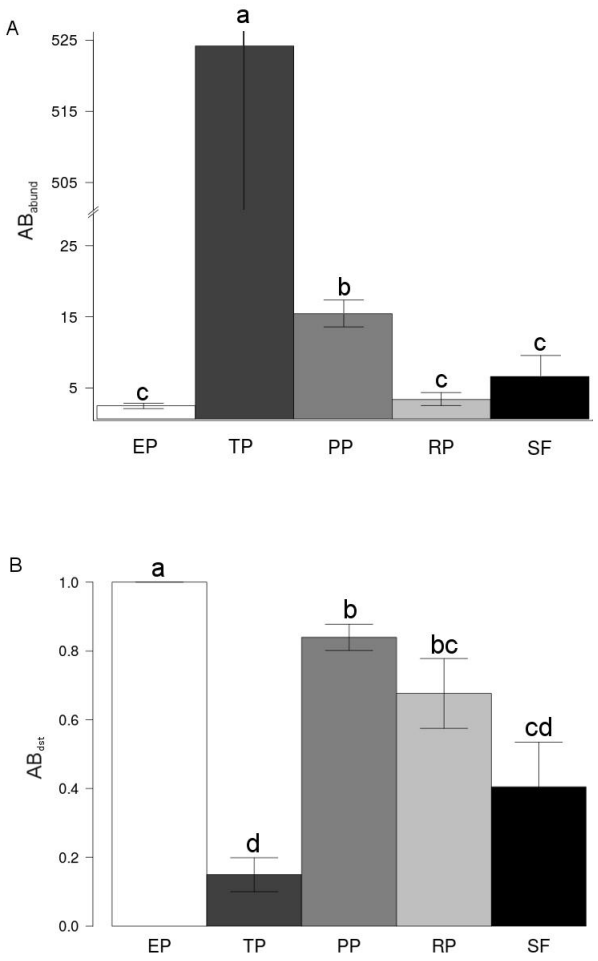

Figure 1. (A) Abundance (AB_{abund}) and (B) distribution on tree canopies (AB_{dst}) of atmospheric bromeliads assemblage along the tree hosts) of *Eucalyptus* sp. patch (EP), *Tabebuia* spp. patch (TP), *Pinus elliottii* patch (PP), reforestation patch (RP), and secondary forest (SF). The closer AB_{dst} to 1, more abundance of atmospheric bromeliads on trunk, and the closer AB_{dst} to 0, more abundance on branches. Vertical bars indicate standard error of means. Same letters indicate statistical similarity between vegetation patches according to Tukey test ($p = 0.05$).

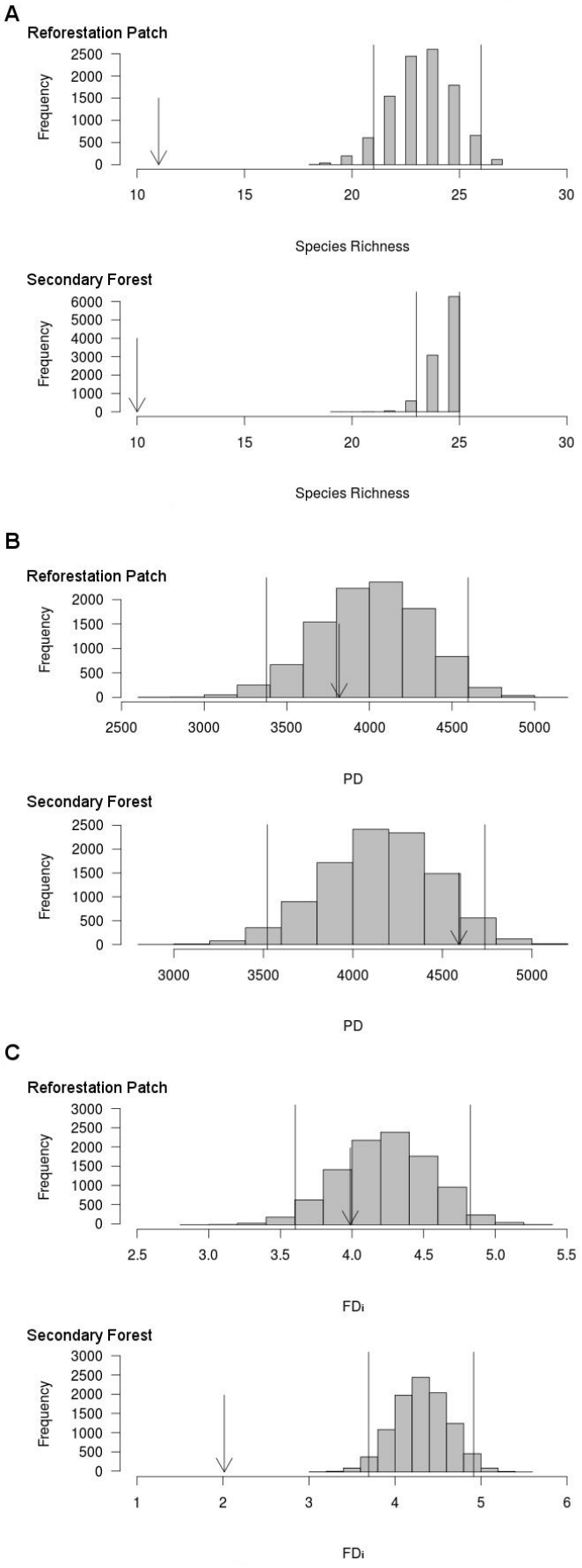

Figure 2. Histograms of (A) tree species richness, (B) phylogenetic diversity (PD) and (C) functional diversity (FDi) of atmospheric bromeliads on each sampled tree on reforestation and secondary forest patches. The vertical lines delimit the 95% confidence intervals of the obtained null models. The vertical arrows point the observed values of each index.

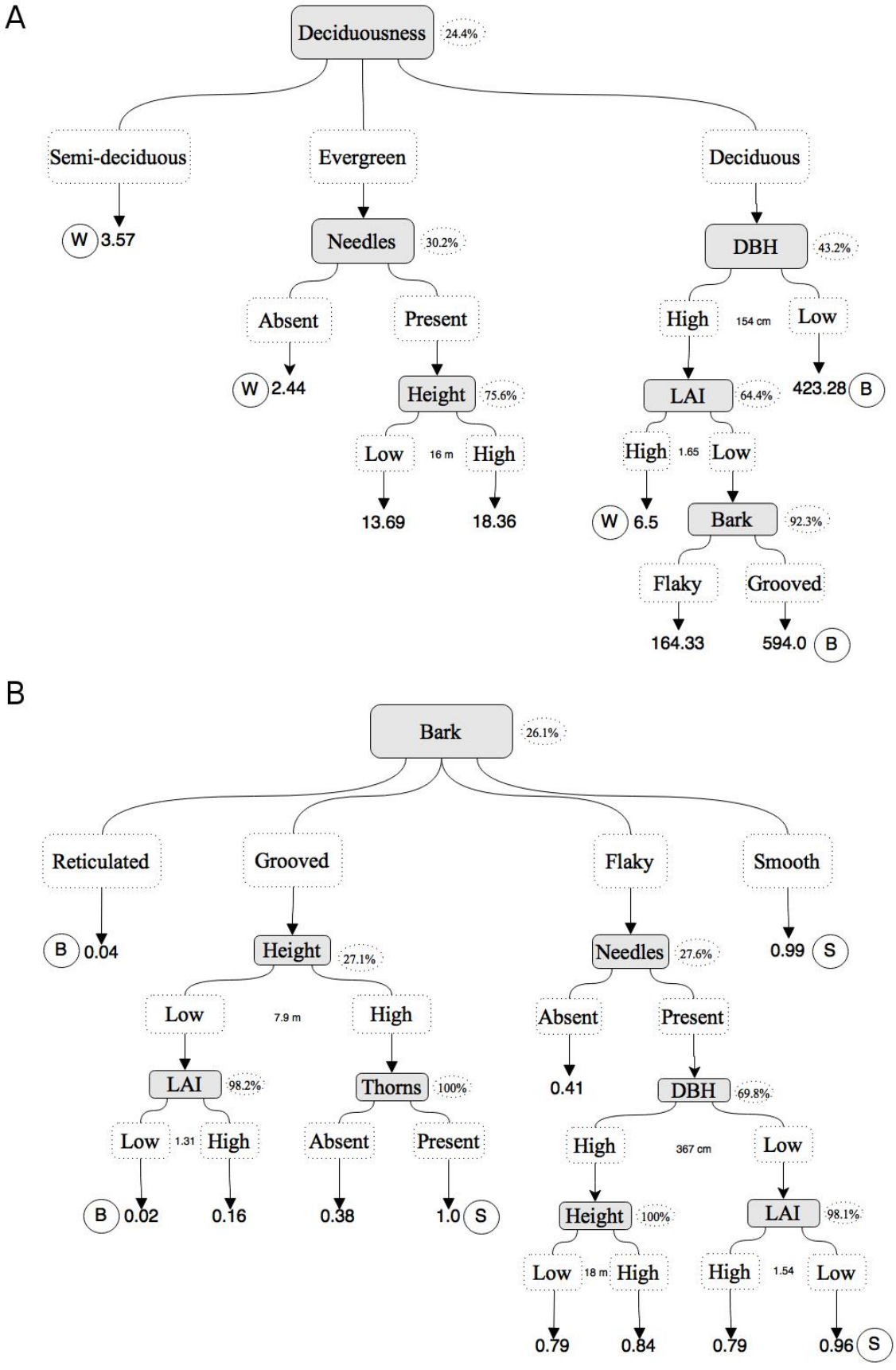

Figure 3. Data trees of the successive hierarchic partitions for (A) abundance (AB_{abund}) and (B)

distribution on tree canopies (AB_{dst}) variances, showing the tree traits interactions. The gray rectangles represent a trait that best explained the variance of a group formed by a previous hierarchic partition (when preceded by an arrow). White and dotted rectangles represent the groups formed by the most explanatory trait (just above). White and dotted ellipses show the explanation percentage of the most explanatory trait. Values between some of the white and dotted rectangles represent the median value of quantitative traits, on which the groups were formed. The values appointed by the last arrows are the mean of AB_{abund} (on figure A) and AB_{dst} (on figure B) of the groups formed by the traits interactions of all significant hierarchic partition. The circles appoint the patterns of traits interactions which were named as Best, Worst, Branches, or Trunk Hosts (specifically B and W, on figure A; or B and S, on figure B).

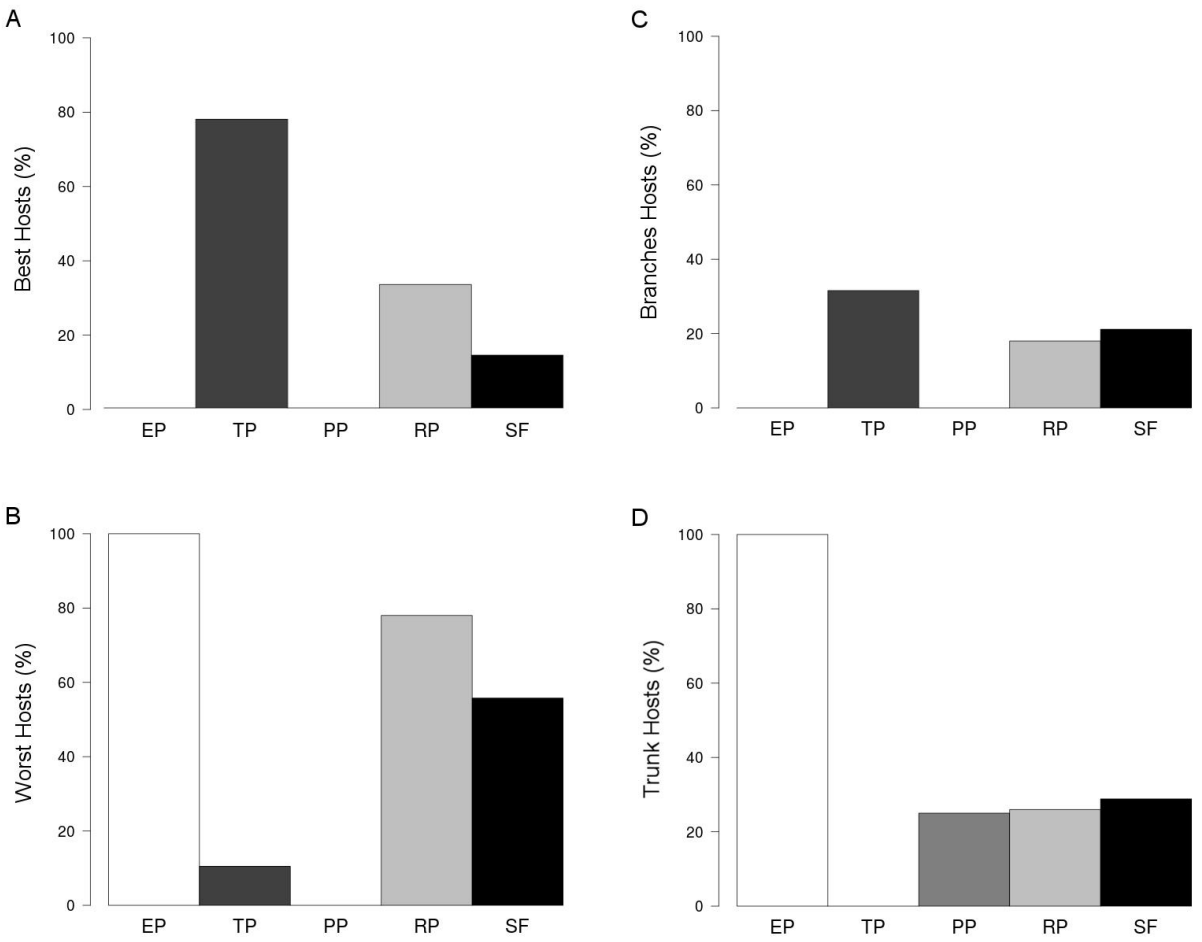

Figure 4. Percentage of trees assigned as (A) Best, (B) Worst, (C) Branches, and (D) Trunk Hosts in *Eucalyptus* sp. patch (EP), *Tabebuia* spp. patch (TP), *Pinus elliottii* patch (PP), reforestation patch (RP), and secondary forest (SF).

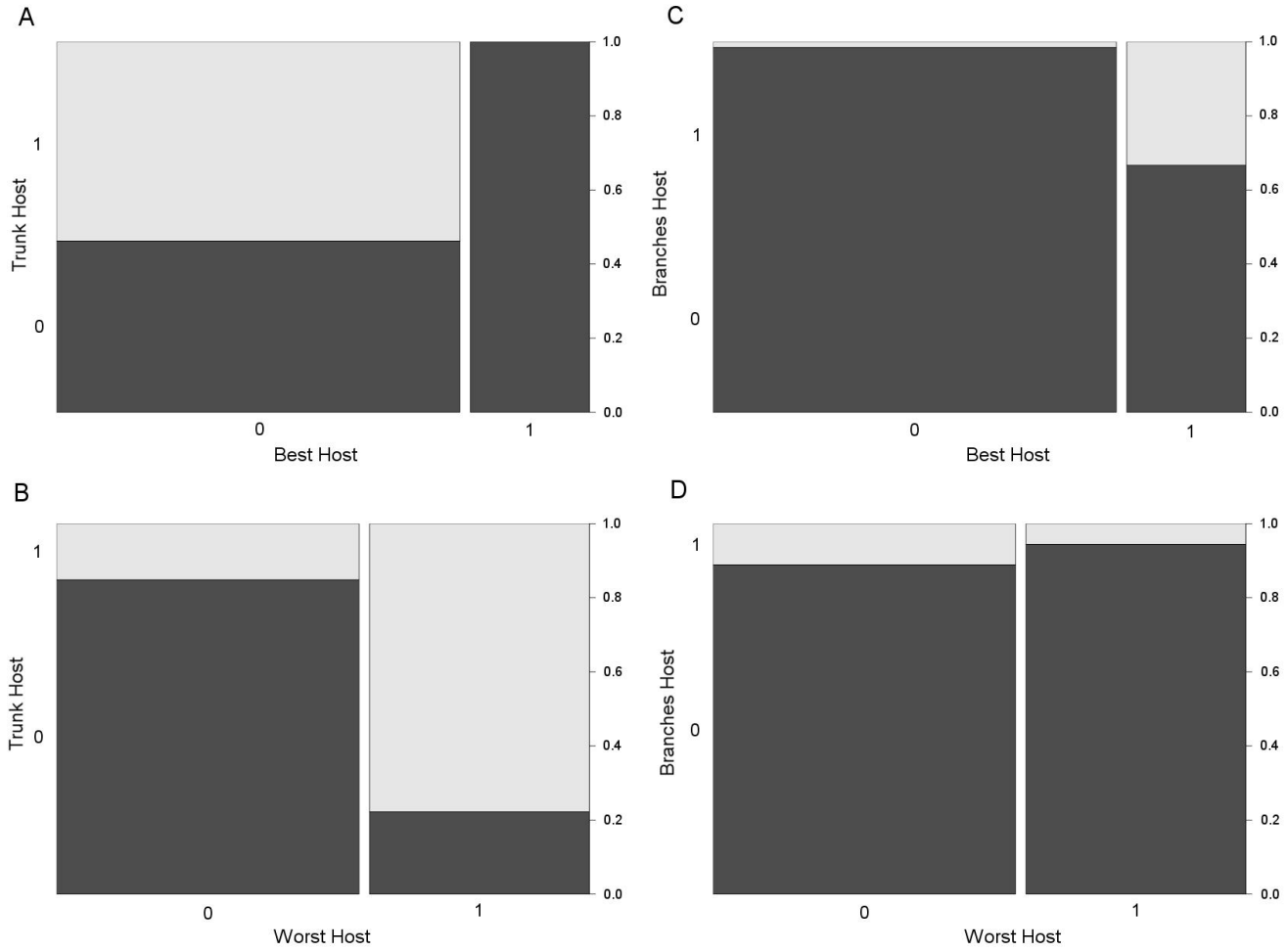

Figure 5. The frequencies of trees assigned as Trunk (y-axis of A and B) and Branches Hosts (y-axis of C and D) which were also assigned as Best (x-axis of A and C) and Worst Hosts (x-axis of B and D). 0 and 1 represent the trees which were unassigned and assigned to each specific Host pattern. The columns widths represent the frequencies of trees assigned (1) and unassigned (0) as Best or Worst Hosts. The gray and black colors represent the frequencies of trees assigned (1) and unassigned (0) as Trunk or Branches Host. Only the relationship showed on D had no significance ($p > 0.05$).

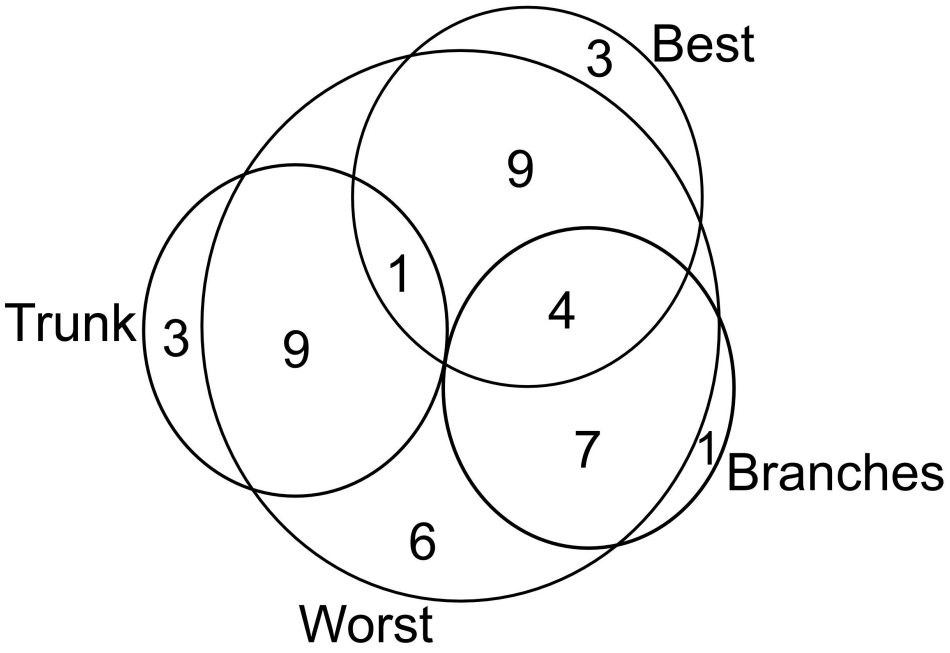

Figure 6. Euller diagram showing the number of tree species with individuals assigned to only one host pattern, and the number of tree species with have individuals assigned to more than one host pattern (intersections).

CAPÍTULO II

TREE DENSITY VARIATION IMPLIES DISTINCT EFFECTS OF TREE TRAITS AS ENVIRONMENTAL FILTERS FOR ATMOSPHERIC BROMELIADS

Cleber J. N. Chaves[1]; Davi R. Rossatto[1,2]

[1] Programa de Pós-graduação em Ecologia e Biodiversidade, Universidade Estadual Paulista (UNESP), Instituto de Biociências, 13506-900 Rio Claro, Brazil; [2] Universidade Estadual Paulista (UNESP), Faculdade de Ciências Agrárias e Veterinárias, Departamento de Biologia, 14884-900 Jaboticabal, Brazil

Correspondence

Cleber J. N. Chaves: cleberchaves@gmail.com

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ABSTRACT

- Epiphytic assemblages are one of the most interesting cases of metacommunities, as trees can constitute discrete habitat patches and their traits act as environmental filters for local epiphytic communities. In view of metacommunity theory, increasing tree densities should increment the overall habitat amount and reduce the dispersal limitation among isolated epiphytic communities. However, atmospheric bromeliads (ABs) are a wind dispersed group of epiphytes that are profusely found in dry and anthropic environments of the New World that commonly have low tree densities and stronger wind flows.
- Here, we studied the interaction between tree traits and varying tree densities driving community assembling of ABs. We investigated the influence of tree traits at multiple scales of community assembling of ABs, from the direct relationships between tree-AB traits and AB distribution along the canopy, to host selection, individual abundance, functional diversity, and species composition.
- We sampled twelve plots along a tree density gradient. For each plot, the environmental factor grouped tree density, LAI (leaf area index), and functional distance from the source tree, whereas the spatial factor grouped euclidean distance from source tree and number of host trees.
- Our results show the prevalence of distinct functional groups of trees according to tree densities variation, which distinctly impact interactions between trees and epiphytes. Under lower tree densities, individual tree traits have putative stronger effects on AB fitness, which induces them to preferentially establish in specific canopy positions, establish on preferential hosts, and increase their abundance, supporting smaller communities under suboptimal conditions. Higher tree densities, on the other hand, reduces the effect of individual tree traits by enhancing dispersal limitation.

- Our results demonstrate the importance of host tree traits for the assembly of epiphytic communities, even for groups with an apparently ubiquitous distribution in some landscapes, as atmospheric bromeliads. Further studies with other epiphytic groups could provide more detailed insights into tree-epiphyte interactions.

Keywords

Epiphytes, canopy, host-specificity, landscape ecology, mass-effect, neutral theory, metacommunities, *Tillandsia*

INTRODUCTION

The niche concept is the oldest and most accepted theory explaining patterns of distribution, abundance, co-occurrence, and interaction of species. A species niche is a multi-dimensional space where biotic and abiotic interactions allow species birth rates to be greater than or equal to death rates (Grinnel 1917; Hutchinson 1957; Leibold 1995; Chase & Leibold 2003). The Niche Theory is based on a deterministic perspective, in which the differential niches of each species allow them to co-exist and constitute ecological communities. In contrast, the Neutral Theory is based on a stochastic model arguing that argues that species differences do not drive population dynamics, but the main drivers of ecological patterns in natural communities are the extinction-speciation balance, ecological drift, and dispersal limitation (Hubbell 2001).

Ecologists have agreed that the assembly of any community is within a continuum between deterministic and stochastic perspectives, which are often circumscribed to the local and regional scales, respectively (MacArthur & Levins 1964; Tilman 2004; Leibold & Mc Peek 2006; Vellend et al. 2014). Indeed, dispersal of propagules among communities has a major role on linking both local (e.g. species interactions and microclimatic conditions) and regional processes (e.g. landscape, geology, and biome) that determine community assembly (Leibold & Chase 2018). Reducing dispersal limitation among communities, for instance, should increase the importance of local environmental factors (Leibold & Chase 2018), but a massive dispersal lead to an opposite effect (i.e. mass effect; Loureau & Mouquet 1999; Moquet & Loreau 2003). On the other hand, a strong dispersal limitation, caused by a reduced regional species pool can lead to the assembly of colonizing species that respond more to spatial than to environmental factors, regardless potential dispersal limitations among local communities (Leibold & Chase 2018).

The explicit recognition of dispersal as an important driver of community assembly, in addition to spatial and regional factors, is in the core of metacommunity theory (Leibold & Chase 2018).

Metacommunities are, in general, defined as a set of communities linked by dispersal of multiple interacting species (Wilson 1992; Leibold et al. 2004). Epiphytic communities are a good, although understudied, example of discrete metacommunities, in which each tree constitutes a discrete patch of habitat surrounded by a harsh matrix (Southwood & Kennedy 1983; Burns & Zotz 2010; Löbel & Rydin 2009; Mondragón, Valverde & Hernández-Apolinar. 2015). In this system, the canopy three-dimensional heterogeneity should drive the assembly of local epiphytic communities (e.g. Löbel & Rydin 2010; Chaves, Dyonisio & Rossatto 2016). Under this perspective, the environmental filter played by tree traits combinations selects individuals and species able to tolerate conditions along the canopy. Therefore, we should be able to detect a relationship between tree traits combinations with individual morphophysiology (e.g. Löbel and Rydin 2009; Burns and Zotz 2010; Krah et al. 2018), canopy distribution (e.g. Pittendrigh 1948; Ruiz-Cordova, Toledo-Hernández & Flores-Palacios 2014; Mondragón, Valverde & Hernández-Apolinar 2015; Woods et al. 2015), and composition of epiphytic communities (e.g. Dislich & Mantovani 2016; Köster, Nieder & Barthlot 2017). Conversely, landscape structure in which epiphytic metacommunities take place (e.g. anthropic pressures and geographic barriers) could act as a regional factor, limiting regional species pool for local community assembly and reducing tree traits' importance (e.g. Cardós, Martínez, Aragón & Ellis 2018).

Despite limiting regional species pool, landscape features could also affect the overall metacommunity structure (e.g. Resetarits, Cathey & Leibold 2018). Landscapes with increasing tree densities, for instance, should increment the overall habitat amount and minimize the dispersal limitation among local epiphytic communities. However, local persistence and dispersal among local communities can be limited by denser forests when communities are primarily composed by drought tolerant and wind-dispersed species (see Nathan, Horn, Chave & Levin 2002). Atmospheric bromeliads (hereafter "ABs") are one of the greatest specialized cases of epiphytism (Benzing 2012), on which a combination of features, such as reduced body, wind dispersal seeds, CAM photosynthesis and hairy

and succulent leaves have allowed their dominance in dry and anthropic environments (e.g. Medina 1974; Zotz & Hietz 2001; Crayn, Winter & Smith 2004). These environments often have low tree densities and strong wind flows that likely increase AB seed dispersal distances and reduce dispersal limitations (Nathan, Horn, Chave & Levin 2002). Under such conditions, a massive dispersal of seeds from huge communities can also reduce the effect of tree traits on communities composition (i.e. "mass-effect"; e.g. Loureau & Mouquet 1999; Mouquet & Loreau 2003). The role of tree traits as an environmental filter on AB communities should therefore vary according with a tree density gradient.

In this study, we investigate the relative contribution of the environmental filter performed by tree traits on the assembling of AB communities under distinct tree densities. For this, we encompass multiple scales of the community assembling of ABs, from individual morphophysiology and canopy distribution, to species composition and environmental dispersal. We hypothesized that tree traits have a stronger effect under moderate dispersal limitation, but it is overtaken by mass-effect underpinning lower dispersal limitations. Since AB communities are often species poor, regional dispersal limitations should also have a great effect on their assembly.

MATERIAL AND METHODS

Study areas and sampling strategy

We performed the study in three Cerrado-Atlantic Forest natural transitional sites located in southeast Brazil: Assis Ecological Station, S22.5961 W50.3783 (1,760 ha.); Itirapina Ecological Station, S22.2229 W47.8532 (2,300 ha.); and Pedregulho Ecological Station, S20.2565 W47.4588 (2,070 ha.). Within each site, we selected two areas with scattered trees with none or little tree crown overlapping (tree densities less than or equal to 0.05 trees.m^{-2}), and two areas with high canopy coverage (tree densities higher than 0.20 trees.m^{-2}). We considered that the most abundant local

community acts as the main source of propagules for the metacommunity. Therefore, for each sampled area, we randomly searched for a tree hosting the largest abundance of ABs (hereafter referred as 'central tree') and designed a circular plot around it. To sample a similar number of trees within each sample density, we used circular plots with different radii. At high-density areas, we established a 6 m radius plot (shaded plots), and at low-density areas, we established a 20 m radius plot (exposed plots).

Host trees and atmospheric bromeliads traits

Within each sampled plot, all trees greater than 10 cm in diameter at breast height (DBH) were identified; nine individual tree traits were measured, and an additional six species traits were determined from the literature (Table 1). We also measured leaf area index (LAI) at 1 m from the ground (using the CI-110-24P-ID – CID Biosciences canopy analuzer); and determined AB composition and abundance. In exposed plots we determined LAI as the average among five distinct measures by plot. We randomly collected five individuals of each AB species hosted on each tree and measured five functional traits and four traits related to their canopy position (Table 2). As trees height are up to 18 m (average of ca. 8 m), we could easily sampled all AB individuals by trimmer and count their abundance from the ground, using binoculars. For further information on how field measurements were performed, see Tables 1 and 2.

Individual morphophysiology and canopy position

We adopt an approach based on Fourth-Corner Analysis (Legendre, Galzin & Harmelin-Vivien 1997) to test the effect of host tree traits on individual ABs morphophysiological traits, as well asthe relationships between both types of traits under distinct tree densities. This analysis usually relate species traits to environment using species vs. site, environment vs. site, and species vs. trait matrices, to test whether any given species trait is significantly correlated (positively or negatively) to each environmental variable (Legendre, Galzin & Harmelin-Vivien 1997, Leibold & Chase 2018). We

included LAI values as a measure of shading degree of each tree crown and assumed that host tree traits are part of environmental variables. We then tested pairwise correlation between host traits and individual-specific AB traits using ordinary functions on R software (R Core Team 2017).

We also tested the correlation among host tree traits, AB canopy position traits and tree density. For this, we grouped the variance on host tree traits and on AB canopy position traits in two principal components (PCs) each . Given that we had qualitative and quantitative traits, we performed an analysis that mix an ordinary Principal Component Analysis (PCA) to Multiple Correspondence Analysis (MCA) using *PCAmixdata* R package (Chavent, Kuentz, Labenne, Liquet & Saracco 2017, R Core Team 2017).

Host selection, individual abundance, and functional diversity

To define spatial and environmental factors driving metacommunity assembling, we assumed that: (I) tree functional traits are associated to their ability to host epiphytes, playing the role of environmental filters (e.g. Chaves, Dyonisio & Rossatto 2016); (II) central trees are the main source of seeds for each sampled metacommunity; (III) more trees hosting ABs implies more habitat patches available for new epiphytic communities. By assuming such conditions, the AB abundance on the central trees were considered as a potential mass-effect, resulted from the combinations of spatial and environmental factors. In each plot, we defined the spatial factor as the effect of the Euclidian distance between each tree and the central tree, and the number of trees hosting ABs, once they are not directly related to trees' functional traits. Additionally, we defined the environmental factor as the effect of leaf area index (LAI) and functional distance between each tree and the central tree within each plot. The functional distance grouped all functional traits measured in each tree (see Table 1) in a single variable (i.e. Gower distance; Gower 1971).

We split the individual and joint contribution of spatial and environment factors, highlighting the specific contribution of mass-effect (AB abundance on the central trees) on the variance of local

community composition, host selection (i.e. presence/absence of AB), AB abundance, and local functional diversity. To encompass these distinct faces of functional diversity, we used the *FD* R package (Laliberté, Legendre & Shipley 2014, R Core Team 2017) to calculate the following indexes at the individual-level of AB community: (i) average functional distance among AB individuals (AFD; using Gower distance); (ii) Functional Richness (FRic; Villéger, Mason & Mouillot 2008); Functional Divergence (FDiv; Villéger et al. 2008); Functional Evenness (FEve; Villéger, Mason & Mouillot 2008); and Functional Dispersion (FDis; Laliberté & Legendre 2010).

Species composition

To partition the variation on species composition of local communities, we adopted the method described by Peres-Neto, Legendre, Dray, and Borcard (2006), using the *Vegan* R package (Oksanen et al. 2017, R Core Team 2017). The variation on site (i.e. each tree) vs. species matrix were examined in relation to both site vs. environment (i.e. tree traits) and site vs. space matrices using adjusted R-*squared* in a Redundancy Analysis (RDA). This method gives us the fraction of the total variation on species composition that is explained individually and conjointly by the environmental and spatial factors (Peres-Neto, Legendre, Dray, & Borcard 2006).

Spatial and environmental dispersal

To evaluate whether the central tree within each plot act as a source for the metacommunity, we tested if the remaining communities appear closer and/or on functionally similar trees, in both areas under low and high tree densities. For this, we randomized 1000 times AB individuals on trees within each plot using the *Vegan* R package (Oksanen et al. 2017, R Core Team 2017). This method can distinguish whether each sampled metacommunity has a spatial and/or environmental over- or under-dispersion pattern. Therefore, we performed the analysis only using AB individuals from trees other than the central trees, because we assume that AB dispersion starts on the center of each plot and

spread over the plot. In each randomization, we calculated the following measures with the random host trees, using the *FD* R package (Laliberté, Legendre, & Shipley 2014, R Core Team 2017): (i) average functional (i.e. Gower distance) and (ii) euclidian distances from the central tree of each plot; (iii) FRic; (iv) FDiv; (v) FEve; and (vi) FDis. To control the effect of distinct regional tree diversities on each studied site, we compared the observed values to the null models dividing both values to what is expected when all trees sampled in each plot hosts AB individuals (i.e. V_{obs} or V_{rand} / V_{all}; where V_{obs}, V_{rand}, and V_{all} are, respectively, the observed values, random values, and the values found for all trees in the plot). We then tested if the observed values are lower, equal, or higher than expected by chance (CI of 95%). Spatially and environmentally over- and under-dispersion were indicated by measures higher and lower than expected by chance, respectively. We determined the spatial dispersion based on the Euclidian distance from the central tree, and the environmental dispersion by an index summarizing the complex nature of functional diversity, which is based on the sums of dispersion for all calculated functional diversity indexes (i.e. average functional distance from the central tree, FRic, FDiv, FEve, and FDis). This index ranges from -1 to 1, with (I) values equal to -1 meaning that all functional indexes are under-dispersed, and communities occur only on functionally similar trees; (II) values equal to 1 meaning that all functional indexes are over-dispersed, and communities occur in more disparate trees; (III) and values equal to 0 meaning that all indexes show a random pattern and trees' functional traits are not important for AB communities, or that the values of functional indexes are nullifying each other.

RESULTS

Plots description

Tree densities varied between 0.0056 and 0.0509 trees.m^{-2}, for exposed plots, and between 0.2122 and 0.3714 trees.m^{-2}, for shaded plots. Trees within exposed of open plots showed, in average,

greater circumferences at breast height (CBH) and crown volumes (57.3 cm and 74.3 m^3, respectively) than trees within shaded plots (35.7 cm and 37.8 m^3, respectively; see Table 3). The average CBH and crown volume were even greater for trees hosting atmospheric bromeliads (ABs) in open plots (69.6 cm and 126.1 m^3, respectively; see Table 3). In total, we found 384 trees, of which 140 hosted 3130 ABs from four species: *Tillandsia recurvata* L.; *T. loliacea* Mart. ex Schult.f.; *T. pohliana* Mez; and *T. tricholepis* Baker (Table 3). The most abundant AB species was *T. tricholepis*, but *T. recurvata* was the only species occurring in all sampled plots (Table 3). The three most frequent tree species were *Pouteria ramiflora* Radlk., *Copaifera langsdorffii* Desf., and *Dalbergia miscolobium* Benth., which appeared, respectively, 32, 28, and 24 times at the studied sites. Nevertheless, *P. ramiflora*, *Anadenanthera falcata* Speg., and *Maytenus aquifolia Mart.* were the three most frequent AB hosts, appearing 20, 18, and 13 times, respectively.

We found the vast majority of AB individuals on the central trees of both exposed and shaded plots, as expected for 'source communities' in a metacommunity system. The remaining AB individuals occurred almost regularly over euclidean distance classes from the plot center (Fig. 1A-B). On the other hand, AB individuals from shaded plots were less regularly distributed across functional distance classes of trees (compared to the central trees) than those sampled in exposed plots (Fig. 1C-D). Trees showed a Gaussian-shaped distribution of functional distance classes in both exposed and shaded plots (Fig. 1C-D).

Individual morphophysiology and canopy position

We observed almost the same number of significant relationships among tree host traits and AB traits in plots under low and high tree densities, and almost no significant relationships changed its signal under distinct tree densities (Fig. 2). Furthermore, we detected distinct tree-AB traits relationships under distinct tree densities. LAI, for instance, was the tree trait most related to AB traits under high tree density, showing the strongest predictive power for the number of AB ramets (r^2 =

0.382; Fig. 2). Under low tree density, however, LAI had only a weak significant relationship with this same variable ($r^2 = 0.036$; Fig. 2).

The first two principal components of tree traits grouped together 33.4% of variance, and the first two principal components of traits of AB position in canopy group together 37.5% of variance. The first two principal components of tree traits variance are significantly related to the principal components of AB position variance (Fig. 3A-B). The first component of host traits variance is also significantly related to tree density (Fig. 3C). According to such analysis, taller trees with larger and less shaded canopies, larger bark areas, and rougher bark, have the tendency to occur in areas under low tree densities and to host ABs at the bottom of their trunk (Fig. 3A and C). In turn, shorter and semi-deciduous trees with taller crowns and peeling barks tend to host ABs on boughs (i.e. larger branches) and at greater altitudes (Fig. 3B).

Host selection, individual abundance, functional diversity, and species composition

Under low tree density, tested variables explained the largest part of the observed variance on host selection, while only half of variance is explained by such variables under high tree density (Fig. 4). When we exclude the regional effect, the relative individual contribution of the environmental factor (i.e. the tree traits) on host selection, AB abundance and AFD is, in general, greater than space and mass-effect factors (Fig. 5). However, the total contribution of environment (i.e. independent + conjoint contributions) explained more of the variance of tested variables under low tree density than space, while the opposite prevailed for almost all variables under high tree density (Fig. 5).

The environmental factor contributed to most of all explained variance on composition of local AB communities, but both environmental and spatial factors didn't shared explained variance (Fig. 6). The regional effect (i.e. the sampling location) explained the largest part of the variation in many of the tested variables, contributing to almost all explained variance on host selection and FRic under high

tree density and to the largest part of the explained variance on AFD, under low and high tree densities (Fig. 5).

Spatial and environmental dispersal

All plots under low tree densities showed spatial and environmental dispersal patterns, varying between under- and over-dispersion, with no clear tendency (Fig. 7). Half of the high tree densityplots showed a random environmental dispersal, but a single plot of them showed a non-random spatial pattern (Fig. 7). Nevertheless, high tree density plots with no random environmental dispersal had greater deviations from the null model with increasing tree density (from 0.2 to 0.6), and the plot with highest tree density showed the greatest environmental dispersion pattern (Fig. 7).

DISCUSSION

Studies have shown that the environment is generally the main factor driving species composition of local assemblies within metacommunities (e.g. Cottenie 2005; Leibold & Chase 2018). Our study shows that communities dominated by atmospheric bromeliads (AB) are not an exception to these general assumption. However, we suggest a novel approach drawing on biotic variables (i.e. tree traits) as an important component of the environmental factor. Our approach shows that tree traits has indeed a significant effect on local epiphytic communities of ABs, although this effect varies according to tree densities. Our results also show that dispersal limitation among communities affect host selection, AB abundance, functional diversity, and species composition. We claim that considering multiple scales of community assembling, from individual morphophysiology to species composition and environmental dispersion, is important to increase our understanding about the assembling of such metacommunities, which are composed by few close-related species, and many individuals/species.

Our results reinforce the view that tree traits act as environmental filters for epiphytic communities, been directly related to both individual traits and canopy position of epiphytes. The

combination of tree traits define a mosaic of habitats with distinct levels of suitability along the canopy, thus selecting specific features of epiphytes and resulting on their differential distribution (Benzing 1990; Mondragón, Valverde & Hernández-Apolinar 2015; Chaves, Dyonisio & Rossatto 2016). Nevertheless, our study shows that higher tree densities may weaken the environmental filter performed by individual tree traits. Furthermore, varying tree densities also select distinct functional groups of trees that interact distinctly with epiphytes, with a potential effect on epiphytes fitness and on preferential establishment of such plants on specific canopy positions. These results point out the base of how the landscape structure, here quantified in terms of tree density, changes the effect of tree traits on the assembling of epiphytic communities.

Although the environmental factor has a major contribution on explaining community assembling of atmospheric bromeliads under low tree densities, some of our findings also suggest an additional role of mass-effect under such conditions. Indeed, we detected a small difference between environmental and spatial contributions on some variables (host selection, AB abundance, and AB FDiv). Moreover, our results show a spatial suppression of the environmental contribution, when comparing their individual and joint effects, and an environmental and spatial dispersal of AB individuals, suggesting a joint influence of both space and environment. Some studies have already indicated mass-effect as an important driver of communities assembling (see Cottenie 2005; Peres-Neto, Legendre, Dray, & Borcard 2006; Leibold & Chase 2018). Under lower tree densities, large communities inhabiting trees with better conditions may contribute to the maintenance of smaller communities in trees with suboptimal conditions through massive seed dispersal events. Conversely, under extremely low tree density, we found a single AB individual attached to sampled trees other than the source (central tree), suggesting a spatial limitation under such condition.

Under high tree density, in contrast, we showed that the spatial factor contributes more than the environmental factor for the variance of all but two variables: species composition and functional

evenness. Such greater relative contribution has been rarely reported in literature (Leibold & Chase 2018), and can be comparable to those findings on tree communities that shaped the basis of neutral theory (Hubbell 2001; Condit et al. 2002). Indeed, under higher densities, the environmental filtering exerted by individual tree traits may be reduced, and the joint effect of overlapping trees have an increased importance. The increasing overlap of tree crowns also intensify the limitation for seeds dispersed by the wind, which reduces the dispersal distances among communities (Nathan, Horn, Chave & Levin 2002). Accordingly, our results indicated that the plot showing the highest tree density have the greatest environmental over-dispersion, although we cannot exclude regional effects at this locality (e.g. greater tree diversity). In fact, no plot showed extremely high tree densities and this result could be related to a regional effect at this locality (e.g. greater tree diversity). Finding AB communities under such conditions is challenging due to the huge spatial limitation to wind seed dispersal of seeds into these environments (Nathan, Horn, Chave & Levin 2002).

CONCLUSIONS

Here, we demonstrate how tree traits drive ABs community assembling by affecting directly their morphophysiology and fitness, shaping their distribution in the canopy, and influencing host selection, individual abundance, and species and functional composition. Our study also shows that varying tree densities, and contrasting crown overlapping, can limit or boost propagules exchanges among local communities in this metacommunity system, reducing the relative contribution of individual tree traits. Our results are relevant considering that our target system, atmospheric bromeliads, are very common and abundant among vascular epiphytes in the Neotropics, constituting communities even in abiotic substrates, such as bare rock surfaces and electric wires (e.g. Martin & Schmitt 1986; Wester & Zotz 2010; Benzing 2012). Further studies with other epiphytic groups could provide more detailed insights on tree-epiphyte interactions, and on the relative importance of tree traits on the assembling of these communities.

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AUTHORS' CONTRIBUTIONS

- CJNC and DRR developed the conceptual and methodological foundation of this study, designed the field study and coordinated field data acquisition;
- DRR identified host trees species;
- CJNC conducted statistical analyses and wrote the first draft;
- CJNC and DRR contributed to the subsequent drafts.

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TABLES AND FIGURES

Table 1. Tree traits measured in this study with their units, specificity level and source of achievement (literature or reference for field measurement).

Trait	Unit	Specificity level	Source
Deciduousness	Deciduous, Semi-deciduous, or Evergreen	species	Lorenzi 2002
Habitat preference	Heliophyte, Mesophyte, or Generalist	species	Lorenzi 2002
Succession stage preference	Pioneer, Secondary forest, Climax, or Generalist	species	Lorenzi 2002
Biome preference	Cerrado or Atlantic Forest	species	Lorenzi 2002
Soil water-status preference	Hygrophytic, Xerophytic, or generalist	species	Lorenzi 2002
Bark peeling	present/absent	species	Observations
Height	m	individual	From the ground up the tallest point of the crown
Trunk height	m	individual	From the ground up to the first branch
Trunk slope	degrees	individual	Relative to the ground
Circumference at breast height (DBH)	cm	individual	Field measurements
Roughness	cm	individual	Field measurements (see Pérez-Harguindeguy et al. 2016)
Bark area	m^2	individual	Field measurements (see Ruíz-Cordova et al. 2014)
Crown volume	m^3	individual	Field measurements (see Chilpa-Galván et al. 2013)
Bark dry weight	mg	individual	Field measurements
Bark SI (Succulence Index)	units	individual	Field measurements (see Ogburn and Edwards 2012)

Table 2. Atmospheric bromeliads' traits measured on up to five individuals of each species hosted on each sampled tree, showing their Unit, Class and Description.

Trait	Unit	Class	Description
Ramets number#	units	Functional	Vegetative reproduction capacity
Height of the highest ramet	cm	Functional	High radiation stress or growth rate
Fruit number	units	Functional	Sexual reproduction capacity
Succulence Index (Leaf SI)	units	Functional (see Ogburn and Edwards 2012)	Water storage capacity
Leaf Area	mm^2	Functional	High radiation or drought stress
Attachment altitude	m	Canopy location	-
Substrate	Twig (< 5cm*), branch (5cm* < x < 20cm*), bough (> 20cm*), upper trunk**, lower trunk**, and trunk base**	Canopy location	Which portion of tree host it is located
Substrate degree	degrees	Canopy location	-
Periphery	units	Canopy location (see Zotz 1997)	How deep inside canopy it is located

* diameter measure

** upper or lower half of the trunk (up to the first branching), disregarding the first meter from the ground (trunk base)

Shoots originated by sympodial vegetative growth (Benzing 2012)

Table 3. Number of trees and atmospheric bromeliads sampled in each plot with their coordinates, tree density and type.

Locality	Plot center		Plot type	Tree density (trees/m²)	Trees					Atmospheric bromeliads				
	Lat	Long			CBH (cm)	Height (m)	Crown volume (m³)	Total	AB hosts	*T. recurvata*	*T. loliacea*	*T. pohliana*	*T. tricholepis*	Total
Assis	-22.60652	-50.38682	Open	0.0056	164.0	14.0	403.4	7	2	1	0	10	0	11
Assis	-22.57310	-50.40942	Open	0.0072	85.3	6.9	249.9	9	7	252	88	0	0	340
Itirapina	-22.24901	-47.82413	Open	0.0342	75.5	7.3	66.6	43	41	101	0	121	1567	1789
Itirapina	-22.20485	-47.90319	Open	0.0509	63.3	11.1	125.6	64	7	24	0	0	4	28
Pedregulho	-20.25652	-47.45878	Open	0.0095	41.4	6.3	43.8	20	17	239	267	4	0	510
Pedregulho	-20.25416	-47.45829	Open	0.0358	43.2	4.1	6.2	45	10	127	49	8	0	184
Assis	-22.59608	-50.37830	Closed	0.3006	46.8	7.9	64.8	34	5	10	0	0	0	10
Assis	-22.59805	-50.36922	Closed	0.3537	33.0	4.3	10.1	40	2	23	0	0	0	23
Itirapina	-22.22290	-47.85324	Closed	0.2387	28.7	4.5	7.2	27	15	57	0	6	92	145
Itirapina	-22.22018	-47.85147	Closed	0.2564	40.6	10.3	41.3	29	12	1	0	16	1	18
Pedregulho	-20.25620	-47.45881	Closed	0.2122	38.0	6.6	54.2	24	6	3	8	0	0	11
Pedregulho	-20.25728	-47.45828	Closed	0.3714	29.7	7.0	42.7	42	16	16	23	22	0	61
		Total						384	140	854	435	187	1664	3130

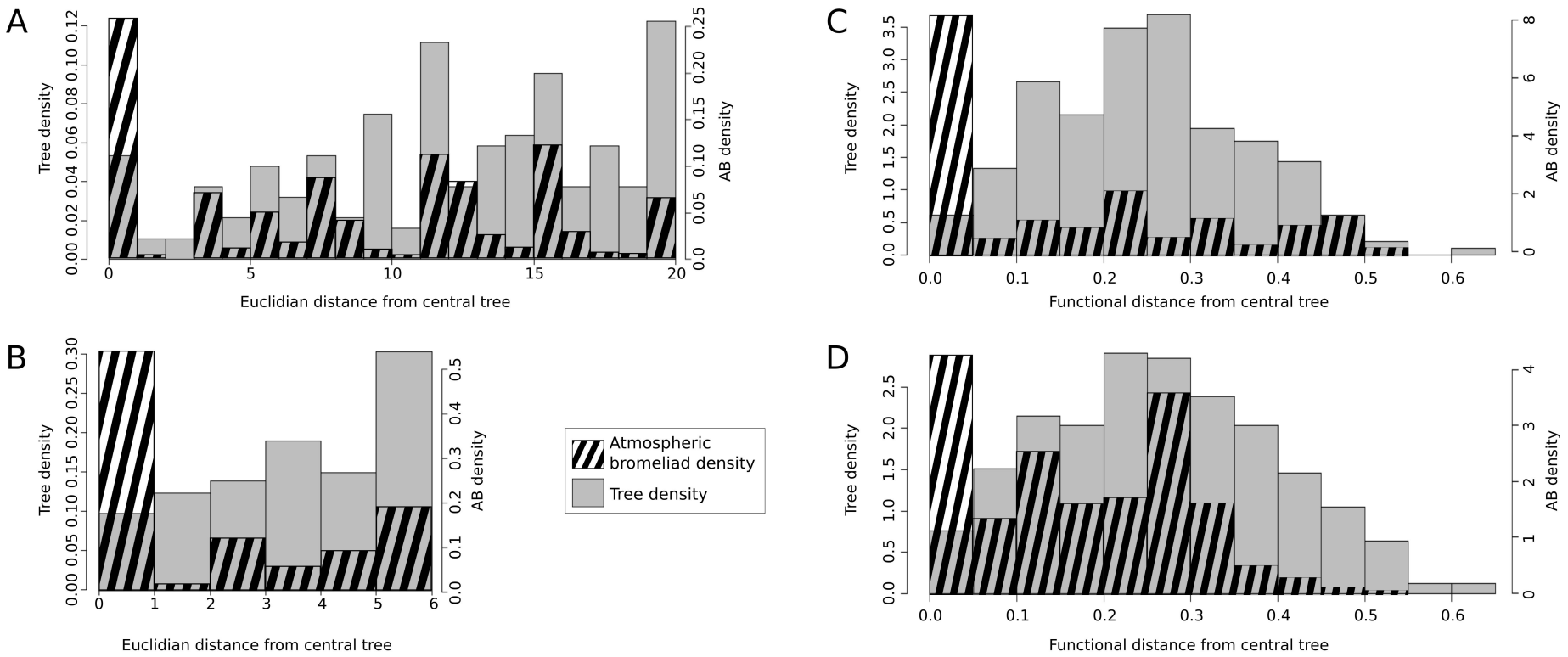

Figure 1. Histograms showing the distribution of trees and atmospheric bromeliads in exposed (A and C) and shaded plots (B and D) according to their euclidian (A nad B) and functional distances (C and D) from the central tree of each plot.

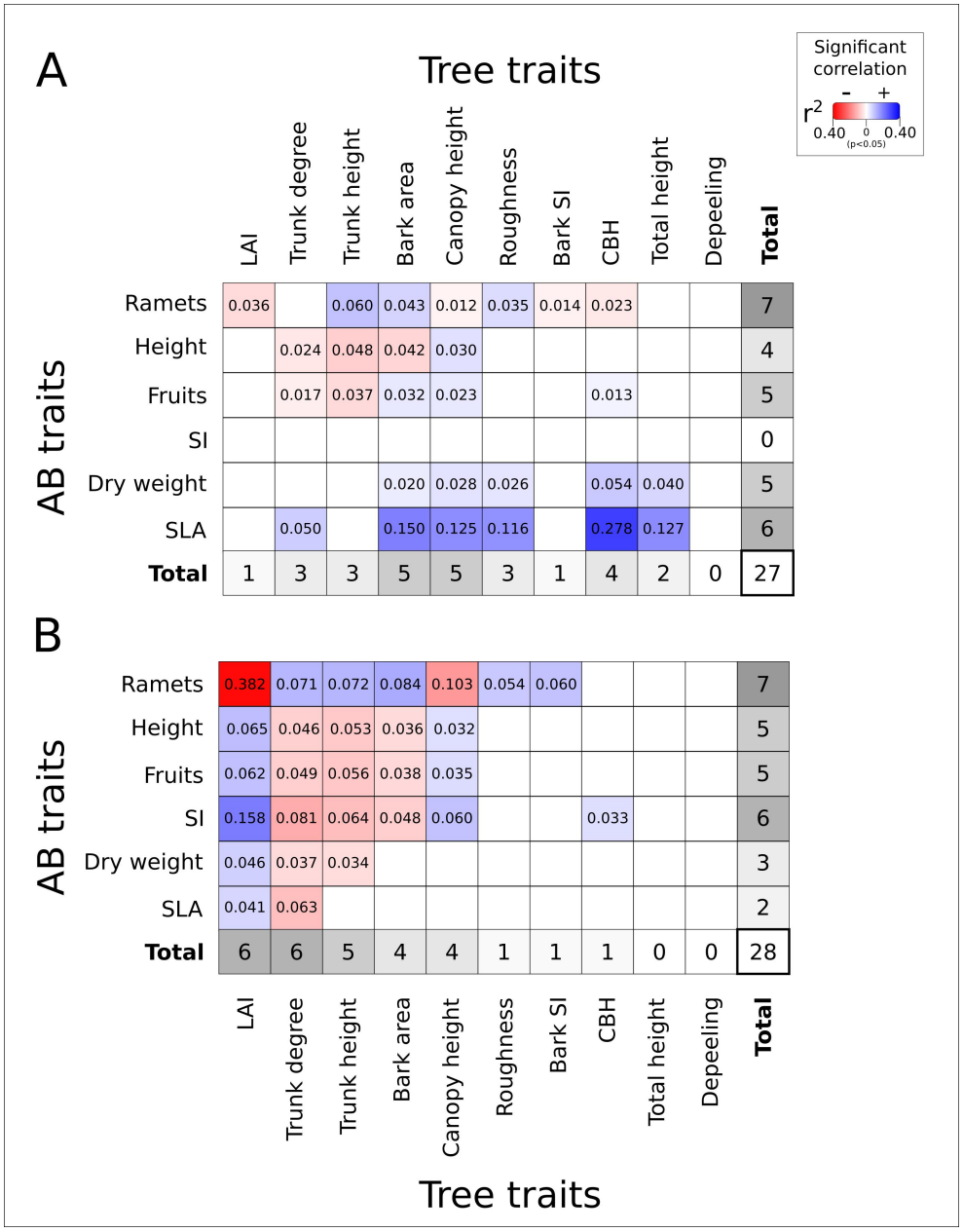

Figure 2. Significant relationships among host trees and atmospheric bromeliads traits in plots under low (A) and high (B) tree density. Blue and red squares indicate positive and negative relationships, respectively. The numbers inside each square indicate the coefficient of determination (r^2).

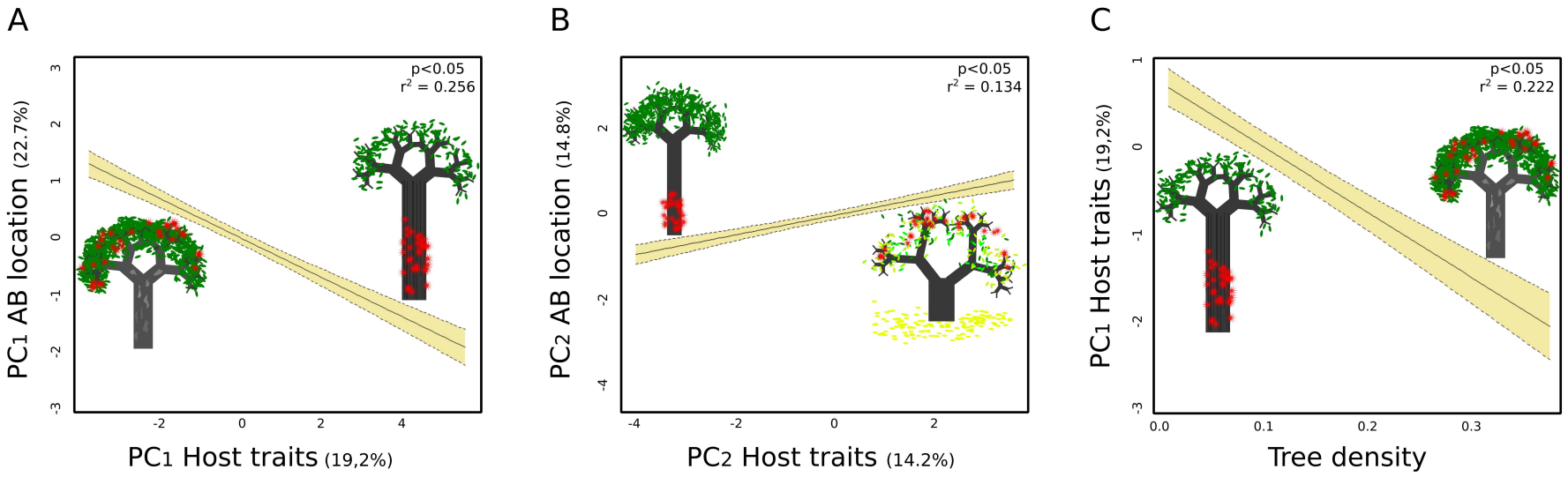

Figure 3. Relationship between the principal components of Host traits (see Table 1) with the atmospheric bromeliads' canopy position (AB location; A-B; see Table 2) and with tree density (C). The figures in each chart illustrate the variance of the main functional types of trees and canopy positions (red stars) according the contribution of each variable grouped by the principal components.

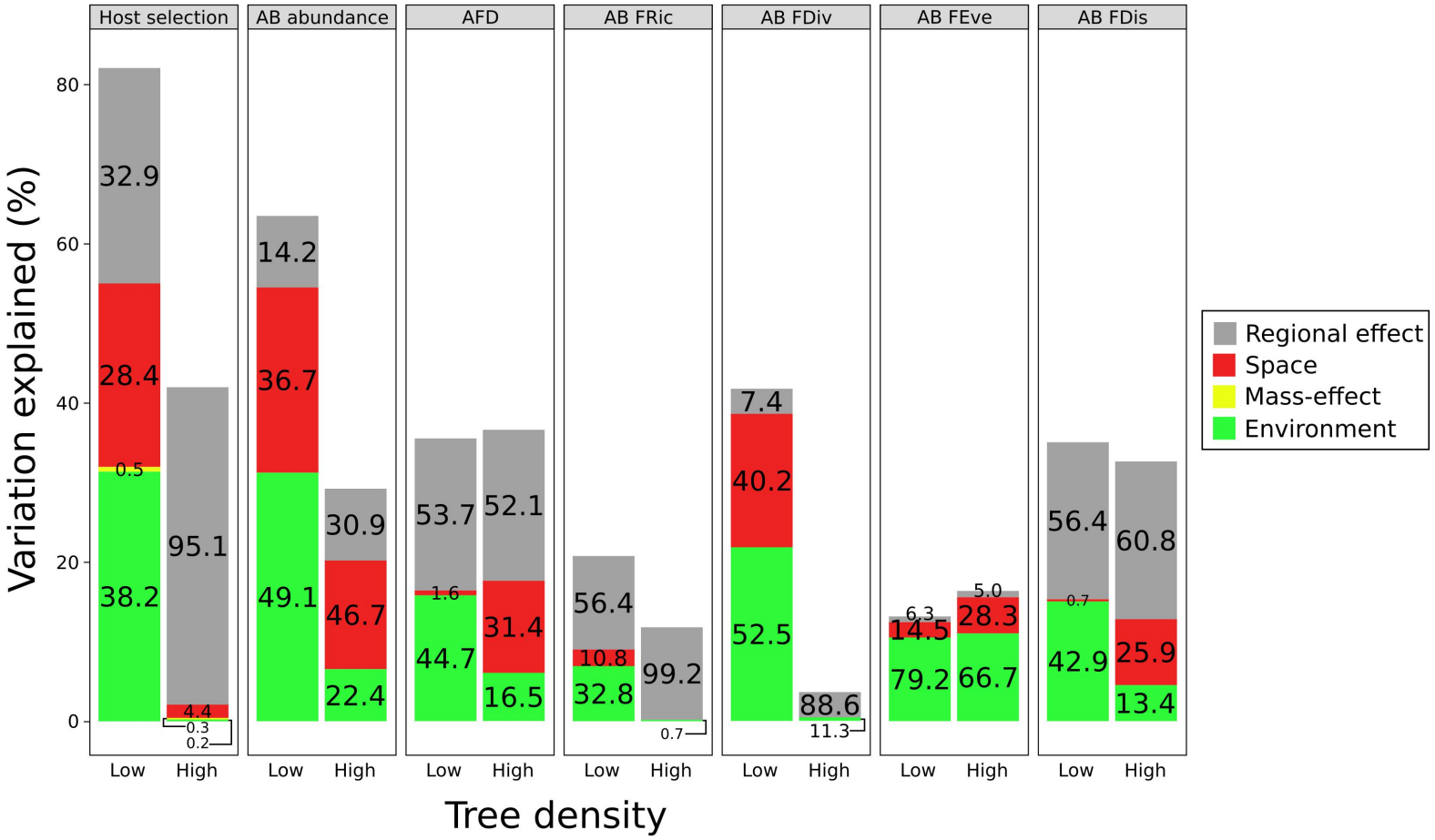

Figure 4. Joint contribution of regional effect, space, mass-effect, and environment on host selection, individual abundance, and functional diversity of epiphytic communities dominated by atmospheric bromeliads under low and high tree density. AFD: Average functional distance among AB individuals; AB FRic: Functional Richness of AB individuals; AB FDiv: Functional Divergence among AB individuals; AB FEve: Functional Evenness among AB individuals; AB FDis: Functional Distribution of AB individuals. The numbers in the bars show the relative contribution (in %) of each factor to the total explained contribution.

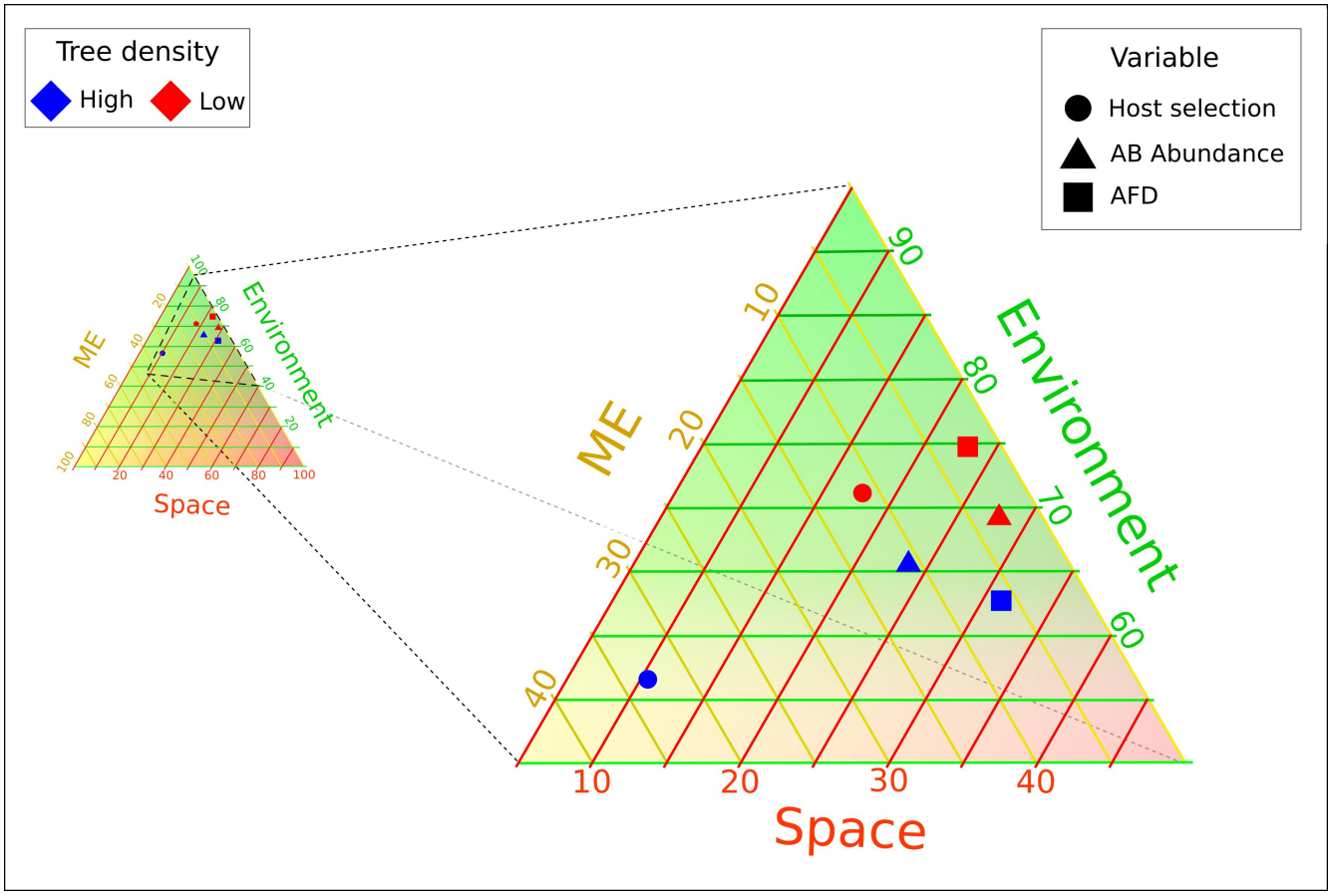

Figure 5. Individual contribution of Environment, Space, and Mass-effect (excluding the regional contribution) for host selection, AB individual abundance, and average functional distances among AB individuals (AFD) of atmospheric bromeliads communities in areas under low and high tree densities.

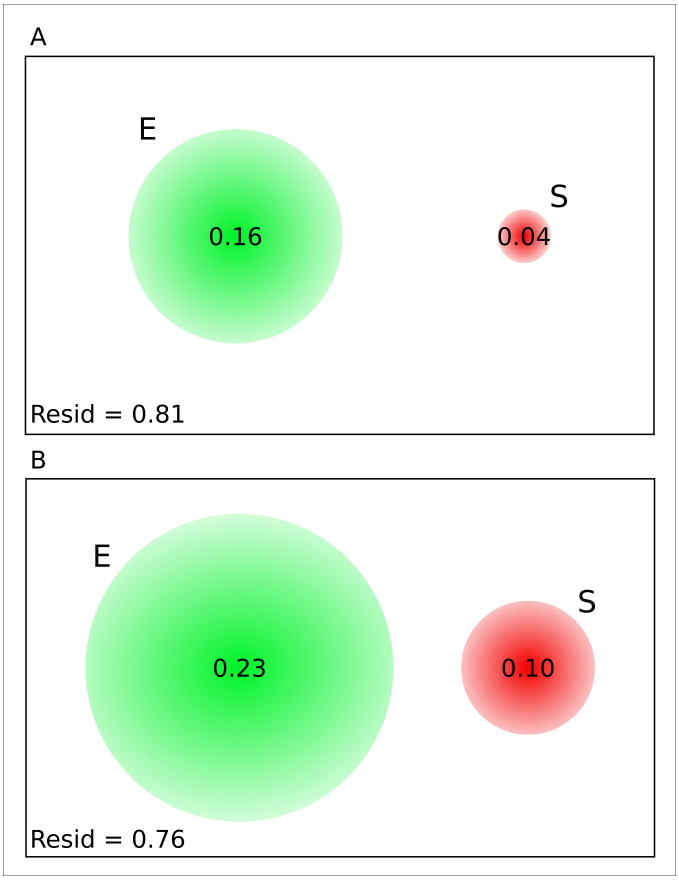

Figure 6. Contribution of Environment (E) and Space (S) for the species composition of epiphytic communities dominated by atmospheric bromeliad in plots under low (A) and high tree density (B).

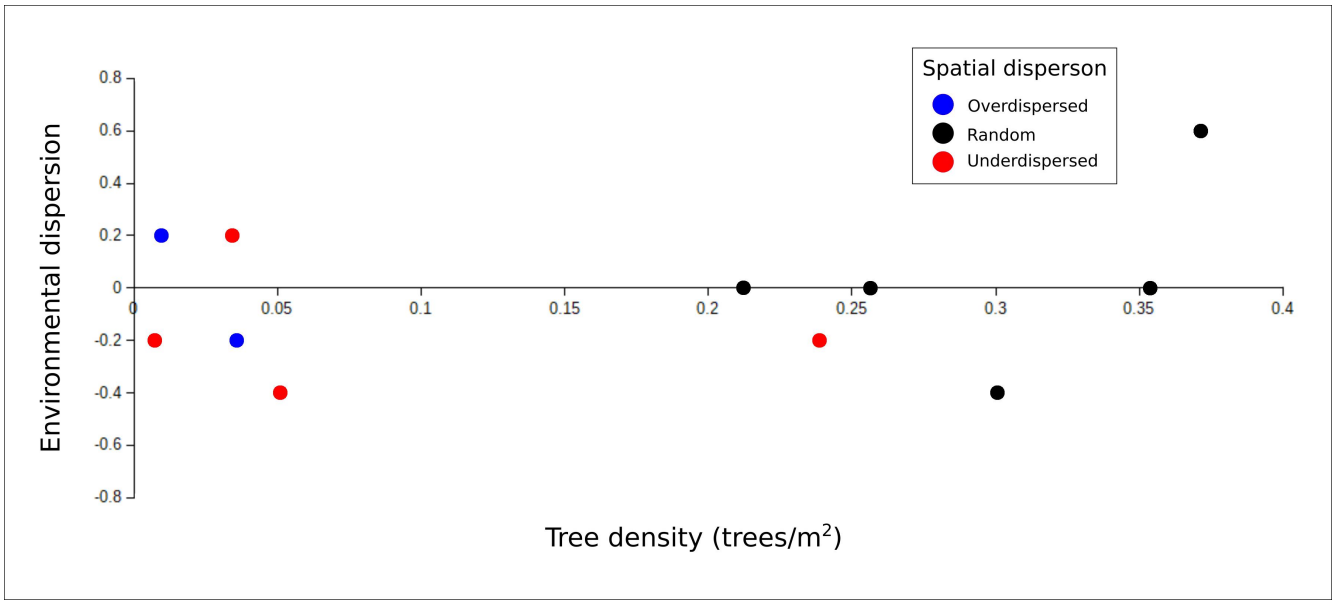

Figure 7. Environmental and spatial dispersion of each epiphytic community dominated by atmospheric bromeliads along a tree density gradient.

CAPÍTULO III

WHO IS AT THE TOP OF THE TREE? UNRAVELING INTRICATE INTERACTIONS AMONG EPIPHYTES WITH HIGHLY OVERLAPPING NICHES

Cleber J. N. Chaves[1]; Davi R. Rossatto[1,2]

[1] Programa de Pós-graduação em Ecologia e Biodiversidade, Universidade Estadual Paulista (Unesp), Instituto de Biociências, 13506-900 Rio Claro, Brazil; [2] Universidade Estadual Paulista (Unesp), Faculdade de Ciências Agrárias e Veterinárias, Departamento de Biologia, 14884-900 Jaboticabal, Brazil

Correspondence

Cleber J. N. Chaves: cleberchaves@gmail.com

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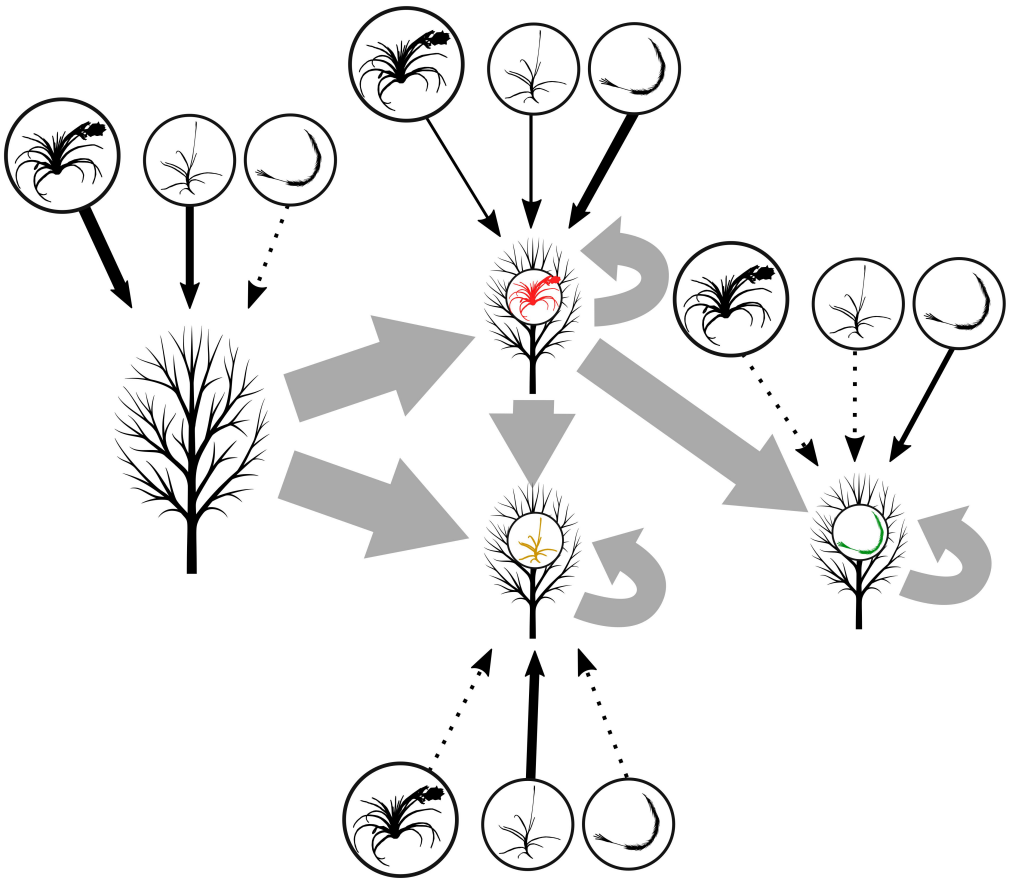

ABSTRACT

Most differences between fundamental and realized niches of species rely on underlying biotic interactions and stochasticity. Epiphytic communities, for instance, are nursed by trees exhibiting combinations of traits that act as environmental filters. Epiphytic communities dominated by atmospheric bromeliads are also strongly affected by stochasticity associated to tree density variations. Here, we studied the interactions among three widespread atmospheric bromeliads with highly overlapping niches (*Tillandsia recurvata*, *T. tricholepis*, and *T. pohliana*), using experimental data of facilitation in seed capturing, interspecific interaction on seed germination, and competition among adult individuals, and verified how these interactions are affected by contrasting dispersal rates in high and low tree densities habitats. We detected a greater colonization ability in *T. pohliana* and distinct strategies of rapid exploitation of environmental patches between *T. recurvata* and *T. tricholepis* in a dynamic typical of opportunistic species. In natural communities, the coexistence among atmospheric bromeliads is hampered by dispersal limitation under high tree density conditions, while competitive patterns observed in the experimental data are overshadowed by mass effect. On the other hand, the facilitation of *T. tricholepis* by *T. pohliana*, detected with experimental data, is still reflected in communities under low tree density, even with the great dispersal level on communities. Our results provide new insights on how atmospheric bromeliads diversified and spread over a large part of the New World, quickly dominating open and human transformed landscapes. Further studies on interactions among atmospheric bromeliads may also elucidate important aspects on the spread of opportunistic plants.

Keywords: atmospheric bromeliads, canopies, competition, dispersal limitation, facilitation, mass effect, species coexistence

INTRODUCTION

Grinnell (1917) and Gause (1934) first coined the concept of 'species niche' as a complex combination of factors that propitiate a species to fulfill its life cycle. According to them, niche differences among species can lead to their coexistence and foster the assembly of a diverse community. Later, Hutchinson (1957) provided a new formalization on the niche concept by defining the 'fundamental niche' as a combination of environmental conditions that would allow a species to exist, and the 'realized niche' as every combination of environmental conditions where a species effectively appears under co-existence with other species. The recognition of which factors lead to differences between fundamental and realized niches has been a major subject in community ecology. Indeed, several factors may underlie differences between fundamental and realized niches, but most of them are related to biotic interactions. A shrinkage or expansion of species niches can be a result of negative (e.g. predation and competition) or positive interactions (e.g. facilitation and mutualism; Hutchinson 1957; Bruno et al. 2003). The balance between such interactions is what gives shape to natural communities (Tilman 1982).

Negative interactions determine that the species maintaining the largest growth rate at the lowest resource level and highest enemy pressure excludes all others (Tilman 1982; Loreau & Mouquet 1999). Positive interactions, otherwise, are more expected to occur via nutrient enrichment or microclimate amelioration in plant communities more limited by physiological strain than by competition (Bertness & Callaway 1994; Wright et al. 2017). The coexistence of competitive species requires a niche differentiation between them, which will promote reduction on the interspecific competition relative to intraspecific competition (Amarasekare 2003). Such niche differentiation usually results from life history trade-offs, in which superior competitors are more dispersal-limited and unable to exploit harsh environments that are, in turn, best exploited by inferior competitors, which have higher fecundity and longer dispersal ranges (Amarasekare 2003).

Beyond negative and positive species interactions, stochasticity has also a major effect on coexistence (Hubbell 2001). Indeed, studies have suggested that species interactions and dispersal limitation can both drive simultaneously the assembling of a community, creating a continuum from niche- to neutral-structured communities (Tilman 2004; Gravel et al. 2006). Stochastic events also affect the community assembly and can be decisive on the dominance of competitively similar species (i.e. preemptive competition; Chase 2003; Amarasekare 2003). Furthermore, stochasticity can even reduce or enlarge the realized niche of species in conditions of dispersal limitation or source-sink

dynamics, respectively (Pulliam 2000). Thus, comprehending how stochasticity affects the interactions among coexisting species may be a key issue on the understanding of community assembly patterns.

Trees play an important facilitative role in ameliorating environmental conditions and also on providing new habitats for the establishment of organisms under and, specially, within canopies (Benzing 2012; Al-Namazi et al. 2017). About 9% of vascular plants are epiphytes and, therefore, mechanically dependent on other plants (Zotz 2013). On the other hand, tree canopies are a stressful environment – spatially disconnected from the ground water and limited to the trunk and branches of trees – that select species tolerant to these conditions (Grams and Lüttge 2011, Benzing 2012) and in which positive interactions arises among epiphytic species (e.g. Scarano 2002). Competition among epiphytes, in turn, is thought as an unimportant process, given the greater mortality due to stressful conditions (Benzing 1990; Mondragón 2015). Still, tree canopies are also a heterogeneous three-dimensional environment defined by a combination of tree traits that likely select epiphytes with distinct tolerance levels (e.g. Pittendrigh 1948; Löbel and Rydin 2010; Chaves et al. 2016). Thus, understanding ecological factors driving the coexistence of epiphytes with similar niches may provide new insights on species coexistence in harsh environments.

Atmospheric bromeliads (*Tillandsia* spp. L., Bromeliaceae) are a dominant epiphytic group of dry and anthropic environments of the New World (Medina 1974; Crayn et al. 2004). Under such conditions, it is common to observe massive communities of atmospheric bromeliads grouped on the branches and trunks of some trees (e.g. Flores-Palacios et al. 2015; Orozco-Ibarrola et al. 2015). Distinct from other epiphytes with scattered individuals across landscapes (see Mondragón et al. 2015), it may be expected that conspecifics and heterospecific individuals of atmospheric bromeliads compete for such ephemeral habitats. Chaves & Rossatto (*in prep.*, second chapter of this thesis) have recently reported that tree traits have an important role as an environmental filter on the assembly of communities dominated by atmospheric bromeliads. However, according to them, tree traits importance varies according to landscape features: mass-effect (i.e. source-sink dynamic; Loureau and Mouquet 1999) has a major role on the assembly of communities under low tree density; but communities under high tree density are mostly driven by dispersal limitation. Here, we aim to investigate the role of species interaction on epiphytic community assembly, integrating experimental and field work data to: (i) measure the niche overlap among three common atmospheric bromeliads coexisting in southeastern Brazil; (ii) describe species interactions from experimental conditions; and (iii) identify how such interactions are reflected in natural communities with contrasting dispersal rates, as recorded by Chaves & Rossatto (*in prep.*). Given their relatedness and great coexistence on the same

trees, we hypothesized that atmospheric bromeliads have an overall large niche overlap. As expected for an epiphytic environment, facilitative interactions may arise among atmospheric bromeliads, but abundant populations of species with similar strategies may also compete for space. These interactions might be better reflected on their coexistence in environments less dispersal limited, due to chance of encounter.

MATERIAL AND METHODS

Studied species

We studied interactions among three of the most common atmospheric bromeliads that coexist massively in natural and human impacted areas of South America: *Tillandsia recurvata* (Gaudich.) Baker, *T. tricholepis* Baker, and *T. pohliana* Mez.. The first two species belong to *Diaphorantema* (Beer) Baker subgenus, produce large amounts of ramets, have an exclusively autogamic sexual reproduction, with cleistogamous flowers (Soltis et al. 1987; Bianchi and Vesprini 2014; Orozco-Ibarrola et al. 2015), and are able to form populations with hundreds of individuals on a single tree (e.g. Chaves et al. 2016). *T. recurvata* probably has the largest distribution of atmospheric bromeliads, extending from Argentina to southern United States (Smith and Downs 1977; GBIF 2017), and produce ca. two fruits by ramet and a few dozen of seeds by fruit (personal observations). *T. tricholepis* is distributed from Bolivia and northern Argentina to Southeast and Northeast of Brazil (GBIF 2017), produce ca. three fruits by ramet and fifty seeds by fruit (personal observations). *T. pohliana*, in turn, belongs to *Anoplophytum* (Beer) Baker subgenus, has a similar distribution to *T. tricholepis* (GBIF 2017), but forms small populations on each host tree (e.g. Chaves et al. 2016). This species often has solitary ramets, but also grow vegetatively (personal observations); can reproduce by selfing and outcrossing (see Siqueira-Filho 2003; Guerta et al. 2015); and produce ca. seven fruits by ramets and hundreds of seeds by fruit (personal observations). A single ramet of *T. pohliana* occupy greater volume (~150 cm^3) than those of *T. recurvata* (~1 cm^3) and *T. tricholepis* (~1 cm^3), but the species take longer times to reproduce (personal observations).

Field data collection

To measure niche overlap and the coexistence among the studied atmospheric bromeliads, we sampled natural epiphytic communities dominated by such species during a wet season (February 2017) in Itirapina Ecological Station, S22.2229 W47.8532 (2,300 ha.), a site in southeastern Brazil with a marked dry season (from April to September), composed by a mosaic of *cerrado* vegetation types, including a forest-like physiognomy (i.e. *cerradão*; Durigan et al. 2004). We sampled two plots with

high tree density (greater than 0.20 trees.m^{-2}) and two plots with low tree density (less than or equal to 0.05 trees.m^{-2}), according to Chaves & Rossatto (*in prep.,* second chapter of this thesis). From each sampled host tree, we measured 11 traits (see Table 1) and randomly collected five individuals per species of atmospheric bromeliads to measure their individual attachment altitude and canopy position (i.e. periphery; according Zotz 1997), and record their location along the canopy (for further details, see Chaves & Rossatto *in prep*., second chapter of this thesis).

Experimental design

To describe distinct stages of conspecific and heterospecific interactions among *Tillandsia recurvata*, *T. tricholepis*, and *T. pohliana*, we conducted the following experiments:

- facilitation on the capturing of wind-dispersed seeds by conspecific and heterospecific adult individuals (Fig. 1.I);
- influence of conspecific and heterospecific adult individuals on seed germination rates (Fig. 1.II);
- competition among conspecific and heterospecific adult individuals (Fig. 1.III).

Following the reproductive season of 2016 (i.e. wet season), we set up the experiments in a sun exposed anthropic environment (except for the facilitation experiment), in which all studied species naturally occur. Bellow, we describe each experiment in details.

Facilitation

We conducted experiments using a horizontal wind tunnel (Fig. 1.I-A) to test the effect of adult individual of each species in the capture of their wind-dispersed seeds. Attaching to one side of the wind tunnel, we alternated different number and width of branches with moderate roughness of multiple trees species, on vertical and horizontal directions (Fig. 1.I-B). These branches were not previously colonized (control), colonized by a single individual (stage 1), or covered by a dense population (i.e. with almost no free space on the bark; stage 2; Fig. 1.I-C) of each studied species (Fig. 1.I-D), totaling 84 distinct 'scenarios' for seed capturing. For each 'scenario', we released 25 seeds of *T. pohliana* at the opposite side of the wind tunnel; 10 cm ahead of a regular desk fan (~950 rpm). We calculated the average number of retained seeds among stages of colonization by each species. We only employed *T. pohliana* seeds in this experiment due to its greater availability, when compared to *T.*

recurvata and *T. tricholepis* seeds, and the high morphological similarity among seeds from these species.

Seed germination

To test the effect of conspecific and heterospecific adult individuals on the seed germination of each studied species, we estimated germination rates in five replicates of ten seeds per species on a branch (control) and below adult individuals of each species attached to the branches (Fig. 1.II). All samples were randomly attached to a same fence during three months of a wet season, in February 2016. We made weekly observations to quantify the amount of germinated seeds.

Competition

To test the intra-specific and inter-specific competition, we attached adult individuals of each atmospheric bromeliad species to squares of 0.25 m^2 of a coarse shading cloth. Individuals were maintained either in a solitary regime (i.e. with no individuals closer than five centimeters) or coexisting with other conspecifics or heterospecifics (Fig. 1.III) for a year (from May 2016 to April 2017). We measured traits related to competitive ability of all individuals (see Table 1) before and after the experiment (Fig. 2).

Data analysis

We performed a mixed Principal Component Analysis (PCA) and Multiple Correspondence Analysis (MCA) combining host tree traits (Table 1) and traits related to atmospheric bromeliads location in tree canopy, using the R package *PCAmixdata* (Chavent et al. 2017, R Core Team 2017),. We then used the first three principal components to calculate a bayesian niche overlap among species with the *nicheRover* R package (Lysy et al. 2014, R Core Team 2017) (Monte Carlo overlap test; Swanson et al. 2015), drawing one thousand samples, and 95% credible intervals.

To better describe interactions among studied species, we compared data from the above experiments using an analysis of variance (ANOVA) with the R package *stats* (R Core Team 2017). Finally, we tested whether the coexistence among atmospheric bromeliad species is greater or lower than expected by chance, under low and high tree density conditions, using data obtained from fieldwork. For this, we created a null model permuting one thousand times the presence/absence of each atmospheric bromeliad species over the sampled host trees using the R package *vegan* (Oksanen et al. 2018; R Core Team 2017). We then measured the correlation between the presence/absence of each pair of species on host trees, excluding trees with the third species, and between each species with both remaining species for the observed and random generated data, using the *netassoc* R package

(Blonder & Morueta-Holme 2017). With this methodology, we expect to reduce the effect of a third species on a pairwise interaction, and also capture the joint effect of both species. We compared the observed values against 95% of confidence interval of null models.

RESULTS

Species niches overlap

We found atmospheric bromeliads occurring on a total of 27 and 48 out of 56 and 107 sampled trees within high and low tree densities plots, respectively. We accounted for 58 and 125 individuals of *T. recurvata* (occurring on 15 and 32 trees, respectively); 93 and 1571 individuals of *T. tricholepis* (on six and 44 trees, respectively); and 22 and 121 individuals of *T. pohliana* (on 15 and 27 trees, respectively) within high and low tree densities plots. These species of atmospheric bromeliads showed a great niche overlap (see Fig. S1). The lowest mean probability of a species individual to be found in another species niche was 52% and the highest probability was 91%, on average (Fig. 2). Individuals of *T. tricholepis* showed the highest probabilities to be found in another species niche, but individuals of *T. recurvata* and *T. pohliana* showed lower probabilities to overlap with *T. tricholepis*' niche (Fig. 2). On the other hand, results showed that the average probability of a *T. recurvata* individual be found in *T. pohliana* niche is similar to the average probability of a *T. pohliana* individual be found *T. recurvata* niche (Fig. 3).

Species interaction

Facilitation

Tillandsia pohliana showed the highest rates of seed capturing (~0.77 and ~0.95; Fig. 4) at both colonization stages. At the first colonization stage (a single individual), *T. recurvata* and *T. tricholepis* captured statistically similar number of seeds when compared to nude branches (Fig. 4). At the second colonization stage (covered branches), in turn, such species captured a similar amount of seeds than *T. pohliana* at the earlier stage (Fig. 4), but the variance on seed capturing by *T. recurvata* at this stage was statistically closer to *T. pohliana*'s rate at the same stage (Fig. 4).

Seed germination

All species showed germination rates lower than 0.5 for all scenarios (i.e. on a nude branch, or with adult individuals of *T. recurvata*, *T. tricholepis*, or *T. pohliana*; Fig. 5). We detected lower germination rates on the nude branches for all species but *T. tricholepis*(Fig. 5). The germination rate of *T. recurvata*'s seeds with conspecifics was as high as on nude branches (Fig. 5); no *T. tricholepis*

seeds germinated either in the presence of *T. recurvata* and vice-versa or in nude branches (Fig. 5); and few seeds of *T. pohliana* germinated under conditions other than on a nude branch (Fig. 5).

Competition

Tillandsia recurvata individuals coexisting with conspecifics showed longer scapes (~74 mm) than solitaries or coexisting with heterospecifics (~50 mm), and greater height increment (~15 mm) than in the presence of heterospecifics (~0.7 mm; Fig. 6). On the other hand, adult individuals of *T. tricholepis* showed greater height increment (~18.9 mm) when coexisting with heterospecifics than solitaries or coexisting with conspecifics (~0 mm; Fig. 6). Unlike the other treatments, T. tricholepis, showed up to three ramets in the presence of conspecifics, (Fig. 6). Finally, *T. pohliana* showed no significant differences in individual measures among these treatments, however, we recorded a death rate of around 40 and 11% when *T. pohliana* individuals were in the presence of heterospecifics and conspecifics, respectively (Fig. 6).

Species coexistence

We observed lower correlation values between *T. recurvata* and *T. pohliana* presence/absence than expected by chance (-0.563; excluding the presences of *T. tricholepis;* Fig. 3) under high tree density; and greater values between *T. tricholepis* and *T. pohliana* (0.371, excluding the presences of *T. recurvata*; Fig. 7) than expected by chance under low tree density. When we tested for correlations between the presence of each species and the presence of any remaining species (Fig. 8), we observed that all species had lower values than expected by chance under high tree density (*T. recurvata* = -0.619, *T. tricholepis* = -0.273, and *T. pohliana* = -0.623; Fig. 8). Under low tree density, on the other hand, only *T. pohliana* showed greater values than expected by chance (0.403; Fig. 8).

DISCUSSION

In this study, we integrated experimental and field work data to measure the niche overlap, describe positive and negative interactions, and verify how these interactions are reflected on the coexistence among three widespread atmospheric bromeliads. *Tillandsia recurvata*, *T. tricolepis*, and *T. pohliana*. As expected, for closely related species that coexist (Valiente-Banuet and Verdú 2007, 2008), we observed that: (i) the studied species share similar environments in tree canopies; (ii) this could be fostered by the interactions among them; and (iii) only positive interactions are reflected in communities under a source-sink dynamic, comparing to dispersal-limited communities. Below, we discuss in detail each of these points.

Species niches overlap

Our results show a great niche overlap among the studied atmospheric bromeliads, indicating that these closely related species have evolutionary conserved niches regarding microclimatic conditions arising from multiple combinations of tree traits (Wiens and Graham 2005; Wiens et al. 2010). Accordingly, it has been suggested that the great diversity in this group may be explained by homoplasic traits that assured several bursts of speciation in distinct parts of the American continent under similar conditions (Benzing 2000; Givnish et al. 2011; Givnish et al. 2014). Indeed, 'extreme' epiphytic adaptations shared by related atmospheric bromeliads fostered their spread, dominance, and coexistence in drier canopies (Benzing 2000, 2012). On the other hand, there are strong evidences of the effect of interspecific interactions on species distributions at smaller scales such as tree canopies (reviewed by Wiens 2011). Therefore, the great niche overlap observed among the studied atmospheric bromeliads can also result from positive and negative interactions among them (see below).

Species interactions

The increasing seed capturing rates detected in our experiments indicates some level of facilitation among the studied atmospheric bromeliads. Indeed, our results showed that *T. pohliana* has a greater effect on increasing seed capture of atmospheric bromeliads, since a single *T. pohliana* individual captures six times more seeds than nude branches and has the same effect of populations of *T. recurvata* or *T. tricholepis*. Given the spatial limitation of epiphytes to trunks and branches, and the wind-dispersal syndrome of atmospheric bromeliad seeds and their overall low seed germination (e.g. Benzing 1978, Bernal et al. 2005; Chilpa-Galván et al. 2018), the increasing on seed capture implies more successful events of dispersal. Positive effects underlying the increase in seed capture of heterospecifics seeds can be relevant in such stressful environment, as canopies (Bertness & Callaway 1994). Smaller species with reduced seed productions, such as *T. recurvata* and *T. tricholepis*, may also benefit from greater capture of conspecific seeds by increasing their chances to reach optimal places and by forming denser populations that might exclude competitors and produce more seeds to colonize farther trees (see Bolker & Pacala 1999). Therefore, higher seed capturing may balance the reduced seed germination of atmospheric bromeliads and boost their spread over new environments (see Mondragón & Calvo-Irabien 2006; Mondragón et al. 2015).

Although we have detected a general increase on seed capturing, our results also show that adult individuals of atmospheric bromeliads could either benefit or harm seed germination and the further development of conspecifics and heterospecifics. For instance, the presence of any adult individual (either heterospecifics or conspecifics) affects *T. pohliana* survival and seed germination. Such species

has a superior colonization ability, given its overall higher seed production and greater seed germination on nude branches, and seems to be the less competitive of the studied atmospheric bromeliads, an expected life history trade-off (see Amarasekare 2003). In fact, our results indicate that *T. pohliana* may nurse *T. tricholepis*, not only by increasing its seed capture, but also fostering its seed germination. Studies have shown that epiphytes can nurse many other plants and, indeed, a great amount of nurse plants within tropical forests are epiphytic tank bromeliads (Scarano 2002). Our results show that *T. pohliana* has a major role on nursing other atmospheric bromeliads within dry habitats, which likely influence the rapid spread of the this group into new environments, specially anthropic transformed landscapes (e.g. McWilliams 1992; Zotz and Hietz 2001; Orozco-Ibarrola et al. 2015).

Our results also indicate distinct strategies for rapid exploitation of environmental patches between *T. recurvata* and *T. tricholepis* (see Bolker and Pakala 1999). While individuals of *T. recurvata* coexisting with heterospecifics seem to recruit sexual offspring by short-dispersal of seeds (shortening scapes), *T. tricholepis* invests on size increment at the same conditions. Coexisting with conspecific, on the other hand, *T. recurvata* invests on longer-dispersal of seeds (enlarging ramets and scapes) and *T. tricholepis* invests on vegetative reproduction, likely producing more fruits and increasing the seed amount by genet. Longer-dispersed seeds in dense conspecific clusters avoid inbreeding, reduce strong intraspecific competition – promoting the coexistence among species with similar dynamics (i.e. heteromyopia; Murrel and Law 2003) – and foster the spreading of these species into new environments (Waser 1985; Holmes and Wilson 1998). Colonization followed by rapid exploitation with increasing local abundance, and further spread into new environments is a commonly reported strategy of opportunistic species (see Counsens and Mortimer 1995). Given the ephemeral characteristics of their substrates, this dynamic may also drive the successful spread of atmospheric bromeliads into new environments.

Species coexistence

Our field results indicate that dispersal is a major topic underlying the coexistence among atmospheric bromeliads in a metacommunity scale. In general, the studied atmospheric bromeliads coexist less than expected by chance under high tree density, and exhibited a random pattern of coexistence under low tree density conditions. According to Chaves & Rossatto (*in prep.*, second chapter of this thesis), higher tree density habitats are characterized by increasing limitations for wind dispersed seeds due to the intense overlap of tree crowns (see Nathan et al. 2002). On the other hand, low tree density conditions are also characterized by a great dispersal level that creates a mass effect

among communities (Chaves & Rossatto *in prep.*). Therefore, whereas the coexistence of atmospheric bromeliads is hampered by the dispersal limitation in high tree density, the massive dispersal of seeds in low tree densities reduces the relative importance of competitive exclusion (Tilman 2004; Gravel et al. 2006).

As observed in our results, experimental data of competitive interactions often differ from the coexistence in natural communities (see Levine et al. 2017). Conversely, our field results reflected the facilitative interaction observed between *T. tricholepis* and *T. pohliana* in experimental data. Under low tree density, the coexistence between these two species was greater than expected by chance. In such condition, besides the mass effect reported by Chaves & Rossatto (*in prep.*), the still high contribution of environmental filter for the metacommunity dynamic (Chaves & Rossatto *in prep.*) and great abundance of *T. recurvata* on trees, may explain the importance of *T. pohliana* facilitation for *T. tricholepis* and its greatest abundance and number of occupied trees under this condition. This result indicates that great dispersal levels can overcome the competition effect of atmospheric bromeliads, but facilitative interactions can still occur in such conditions, increasing even more the abundance and spread of facilitated species.

CONCLUSION

In this study, we showed that interactions among three common species of atmospheric bromeliads with highly overlapping niches are intricate and that these complex interactions influence their coexistence in natural communities under distinct dispersal rates. The joint effect of facilitative interactions and high dispersal levels, that likely overcome local competitive interactions, opens new prospects to understand how this group diversified and spread over a large part of the New World, quickly dominating dry and human transformed landscapes (e.g. Flores-Palacios et al. 2015; Orozco-Ibarrola et al. 2015). Given the great diversification of the group (Benzing 2012), the complex interactions experienced by other species of atmospheric bromeliads may also be a step forward to understand why only some species achieved a wide distribution, as *T. recurvata* and *T. usneoides* (Smith and Downs 1977; GBIF 2017). These results may also elucidate important aspects on the spread of other opportunistic plants.

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AUTHORS' CONTRIBUTIONS

CJNC and DRR designed the field study and coordinated field data acquisition, CJNC developed the conceptual and methodological foundation of this study, conducted the experiments, performed the statistical analyses, and wrote the first draft. All authors read and accepted the final version.

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TABLES AND FIGURES

Table 1. Tree traits measured in this study with their units (or state), specificity level and source of achievement (literature or reference for field measurement).

Trait	Unit	Specificity level	Source
Deciduousness	Deciduous, Semi-deciduous, or Evergreen	species	Lorenzi 2002
Leaf area index (LAI)	units	individual	According Chaves & Rossatto (*in prep.*)
Height	m	individual	From the ground up the tallest point of the crown
Trunk height	m	individual	From the ground up to the first branch
Trunk slope	degrees	individual	Relative to the ground
Crown height	m	individual	Relative to the ground
Circumference at breast height (DBH)	cm	individual	Field measurements
Roughness	cm	individual	Field measurements (see Pérez-Harguindeguy et al. 2016)
Bark area	m^2	individual	Field measurements (see Ruíz-Cordova et al. 2014)
Crown volume	m^3	individual	Field measurements (see Chilpa-Galván et al. 2013)
Bark SI (Succulence Index)	units	individual	Field measurements (see Ogburn and Edwards 2012)

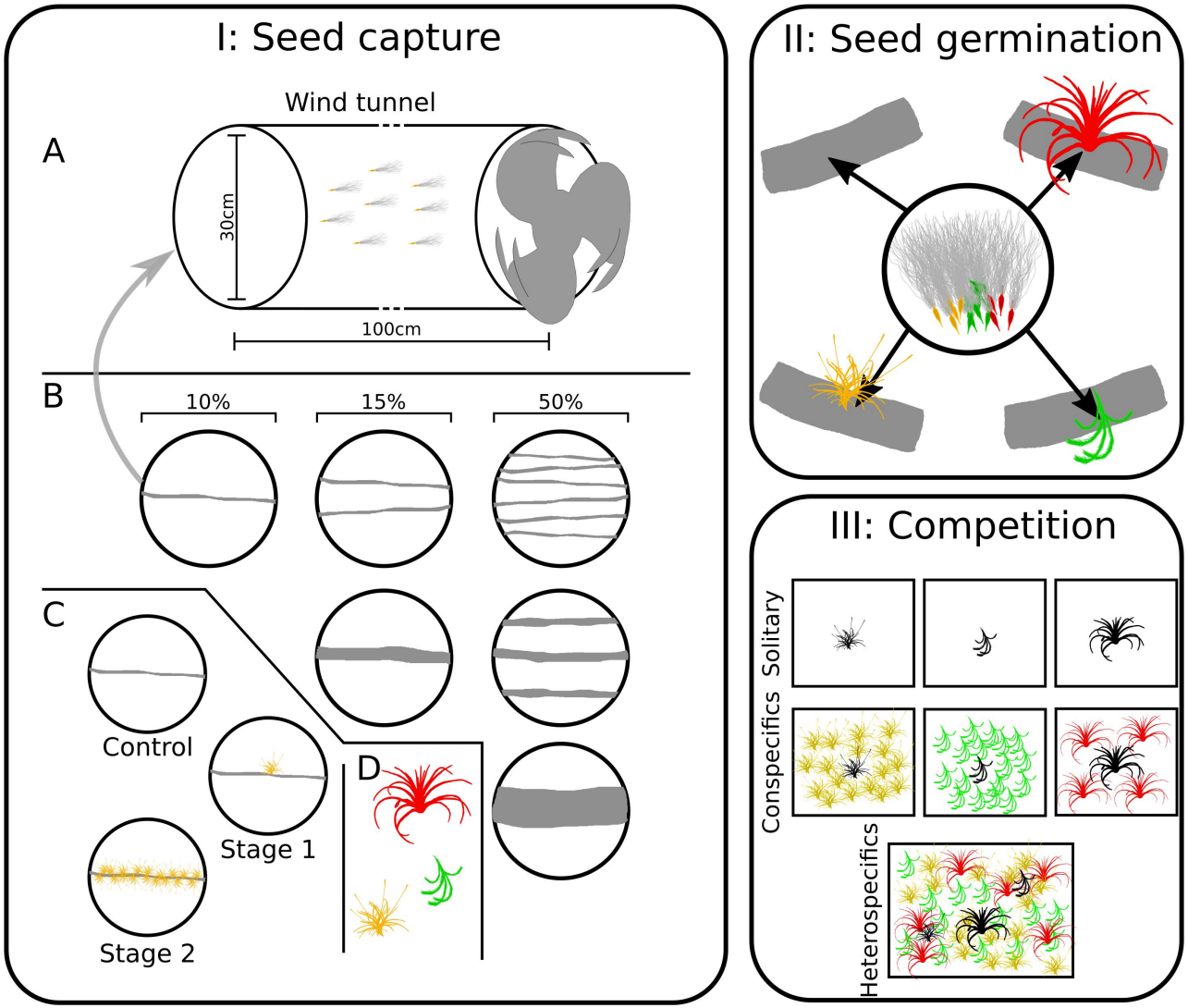

Fig. 1. Overview of the three experiments performed in this study to describe the interactions among *Tillandsia recurvata* (in yellow), *T. tricholepis* (in green), and *T. pohliana* (in red). To test the increase in seed capture of each species (I), we released seeds of *T. pohliana* in a wind tunnel (A) with distinct number and widths of branches (at vertical and horizontal directions), covering distinct percentages of the available area for seed capture (B), in distinct stages of colonization (C) of each studied species (D). We also measured the effect of the presence of adult individuals on seed germination of each species, comparing to germination rates on 'nude branches' (II). Lastly, we measured the effect of conspecific or heterospecific adults on the development of adult individuals of each species (III).

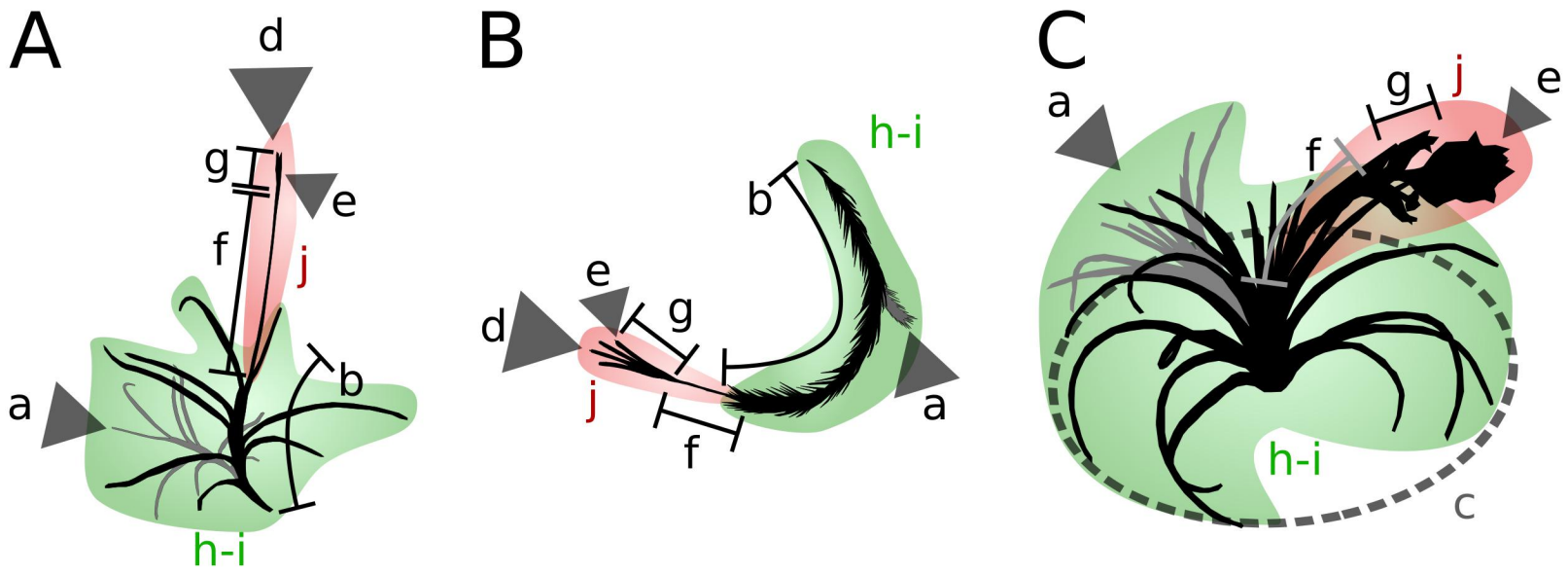

Fig. 2. Traits measured in adult individuals of *T. recurvata* (A), *T. tricholepis* (B), and *T. pohliana* (C) submitted to the competition experiment for one year (Fig. 1.III). a: ramet increment; b: height increment; c: area increment; d: scape number; e: fruit number; f: scape length; g: fruit length; h: vegetative volume (in green); i: vegetative weight (in green); j: reprodutive weight (in red).

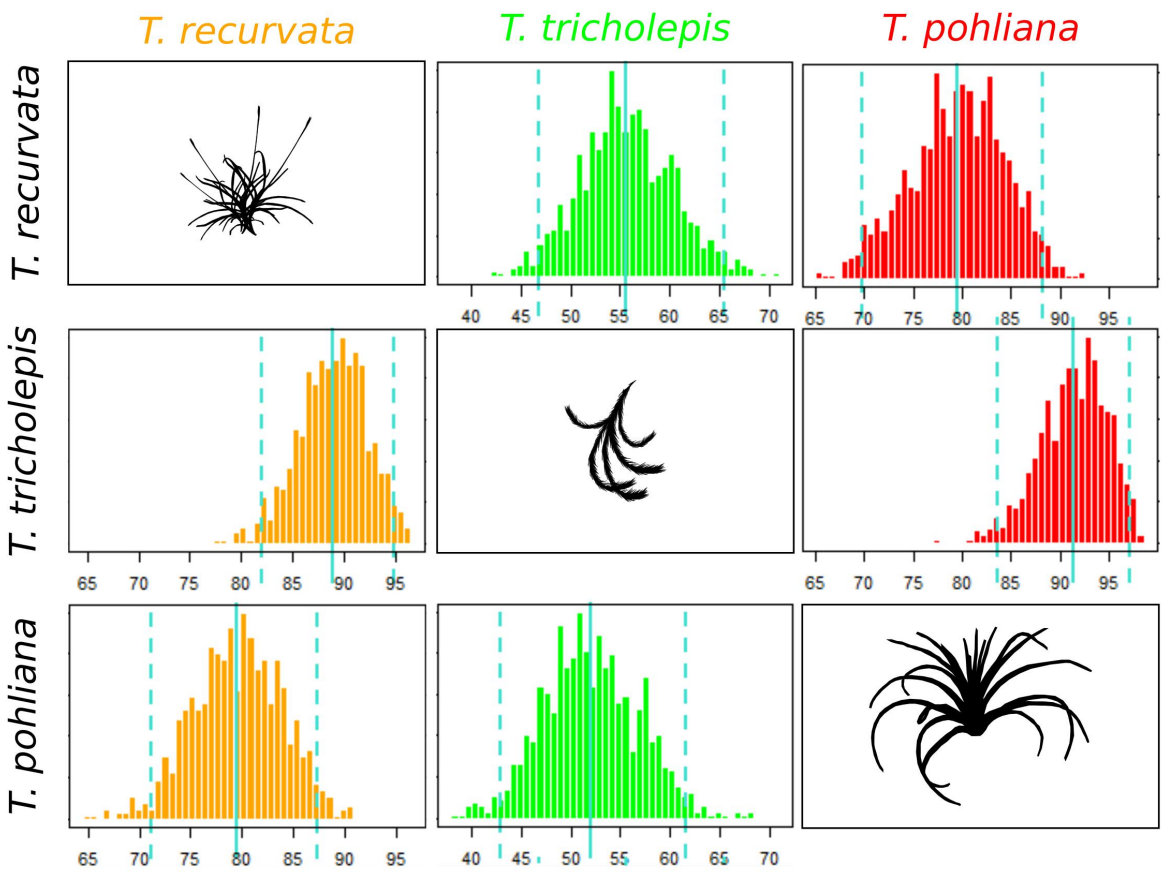

Fig. 3. Posterior distribution of the probabilistic niche overlap (%) of *T. recurvata* (yellow), *T. tricholepis* (green), and *T. pohliana* (red), for the first three principal components grouping the variance of host tree traits. Overlap probability is shown of the species displayed in rows onto those displayed in columns. The posterior means (solid lines) and 95% credible intervals (dashed lines) are displayed in light blue.

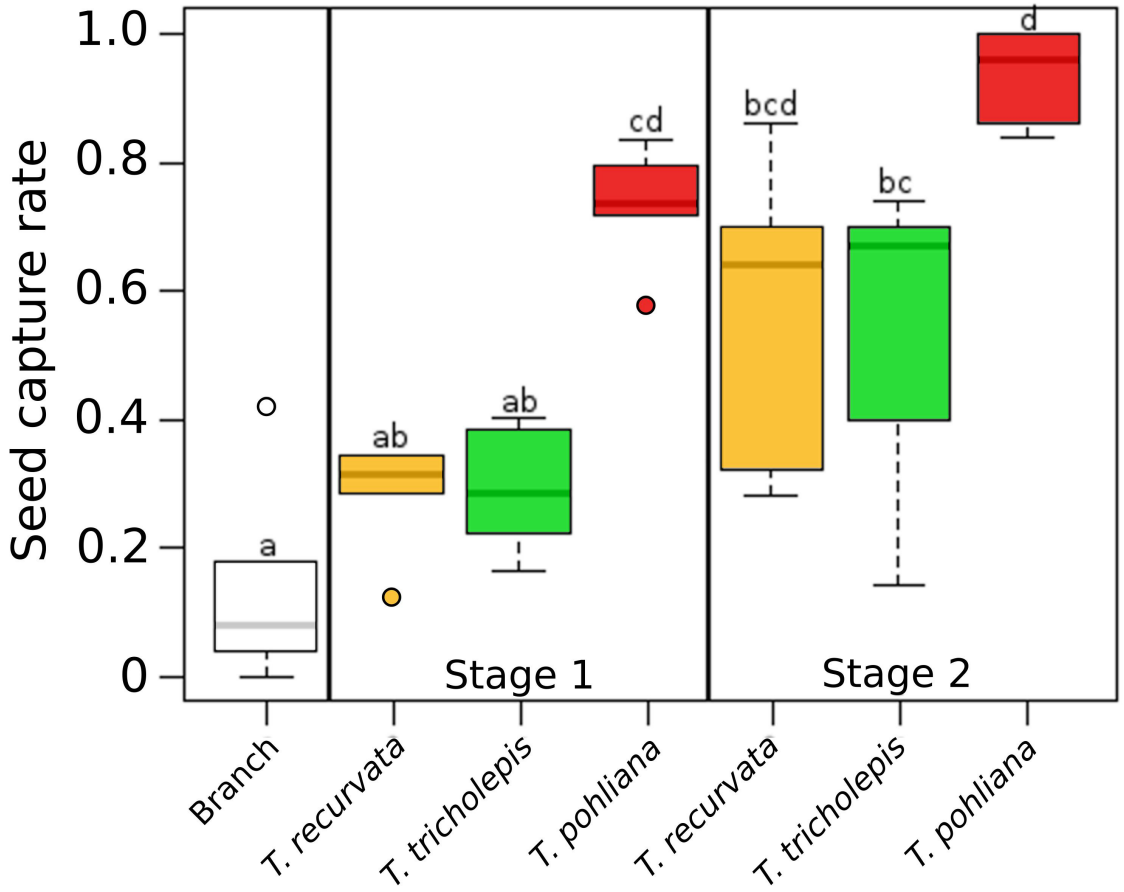

Fig. 4. Average number of seed captured by nude branches and branches in two distinct stages of colonization by *T. recurvata* (yellow), *T. tricholepis* (green), and *T. pohliana* (red) in the wind tunnel, considering distinct 'scenarios' (see Fig. 1 for further details).

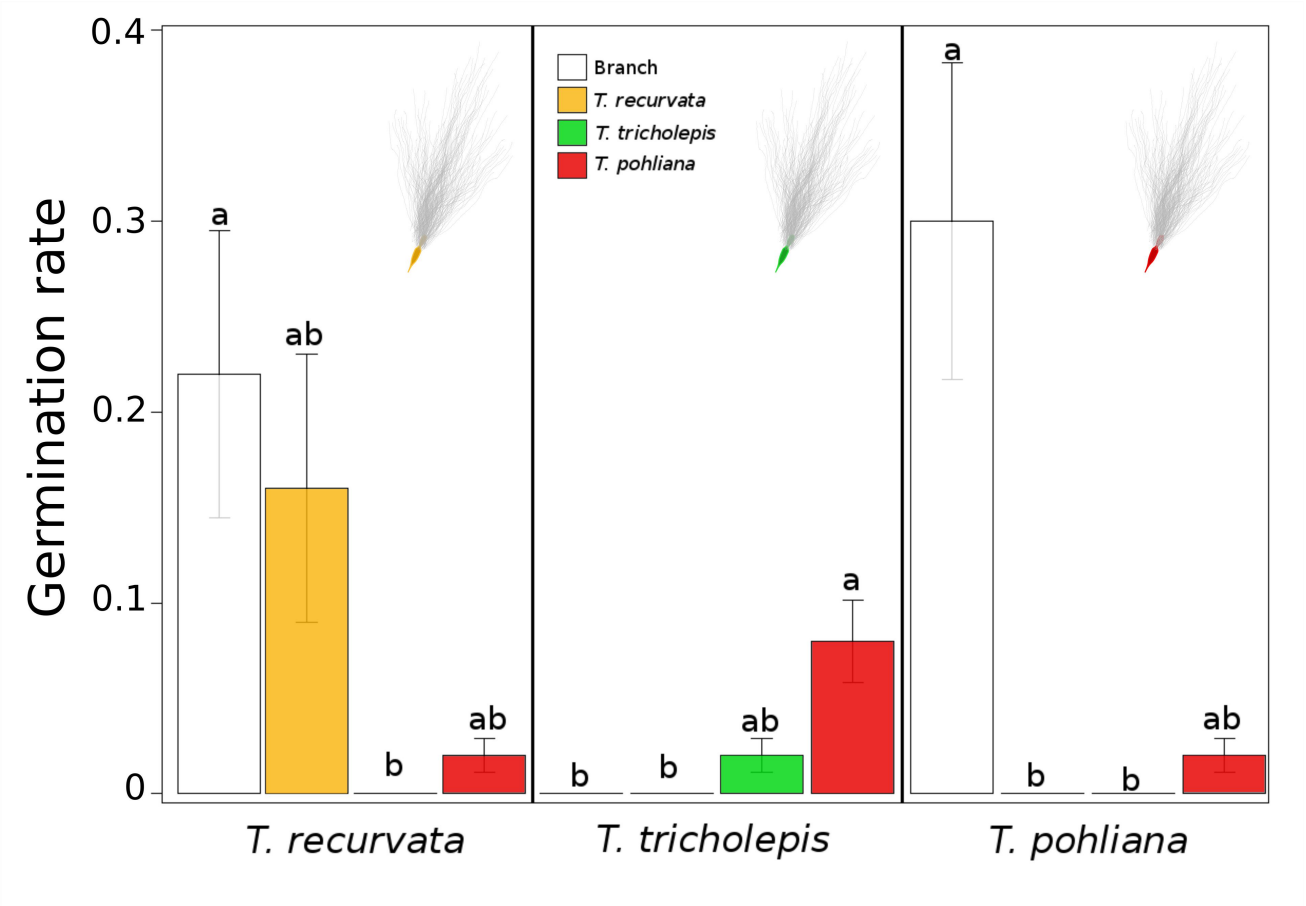

Fig. 5. Average germination rate of seeds of *T. recurvata* (yellow), *T. tricholepis* (green), or *T. pohliana* (red) attached to a 'nude branch' (white columns), or bellow the leaves of adult individuals of *T. recurvata* (yellow columns), *T. tricholepis* (green columns), or *T. pohliana* (red columns). See Fig. 1.II for further information about the experiment.

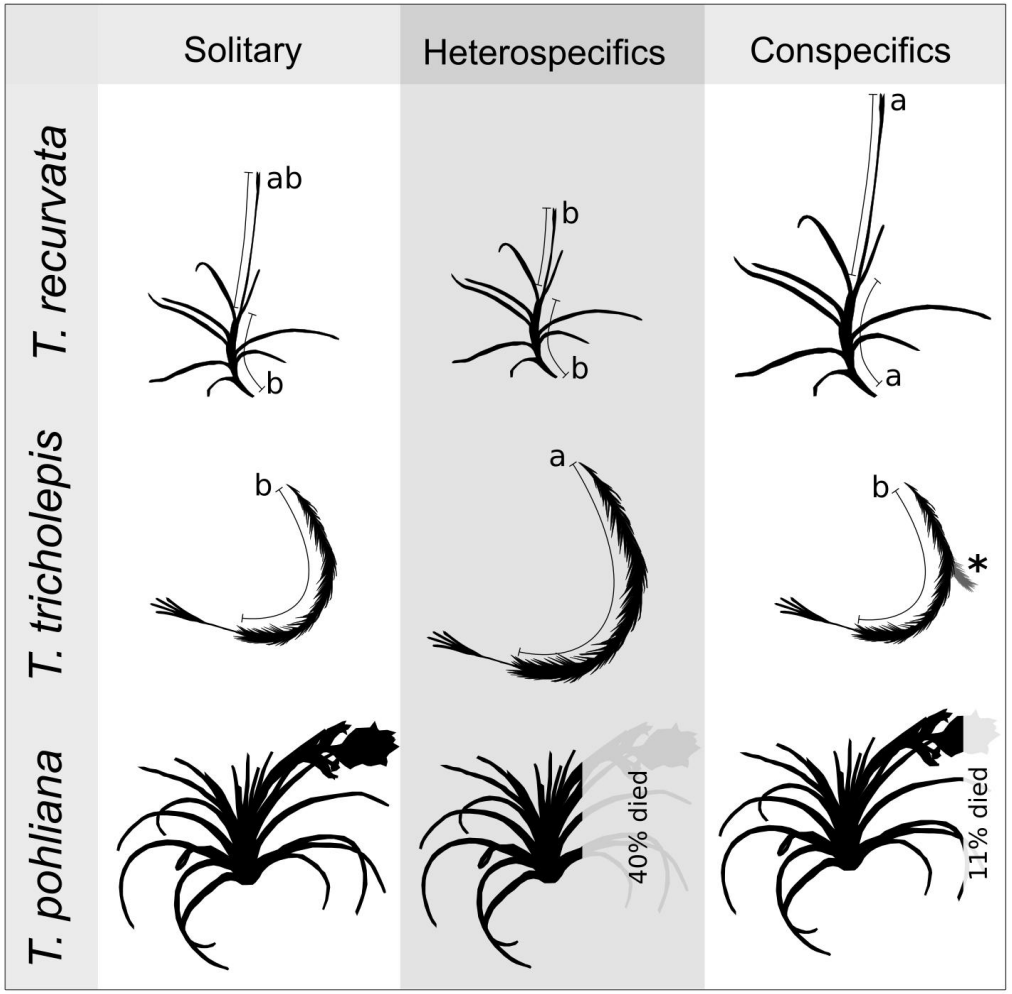

Fig. 6. Summary results of the significant different measures on adult individuals of each studied species in a solitary state or competing with heterospecifics or conspecifics (see Fig. 1.III for further details on the experiment and Fig. 2 for further details on all measures). Same letters represent statistically equal measurements. The asterisk highlight the overall increase on ramet number of *T. tricholepis* individuals coexisting with conspecifics.

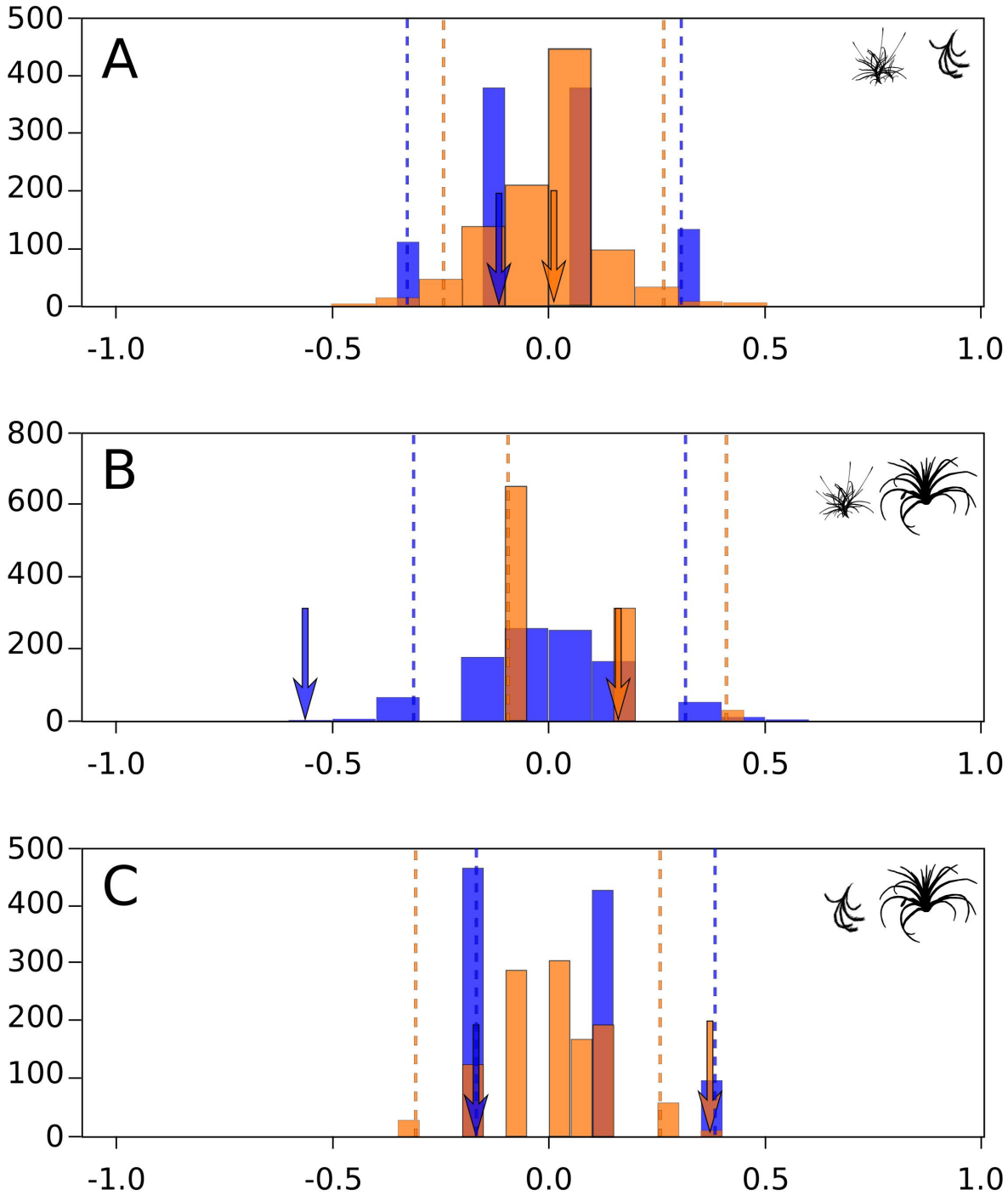

Fig. 7. Observed (arrows) and randomly expected (bars) pairwise correlation between the presence/absence of all studied atmospheric bromeliads on trees under high (blue) and low tree densities (orange) hosting no individuals of the third species. A: *T. recurvata* X *T. tricholepis*; B: *T. recurvata* X *T. pohliana*; and C: *T. tricholepis* X *T. pohliana*. 95% credible intervals are displayed in dashed lines.

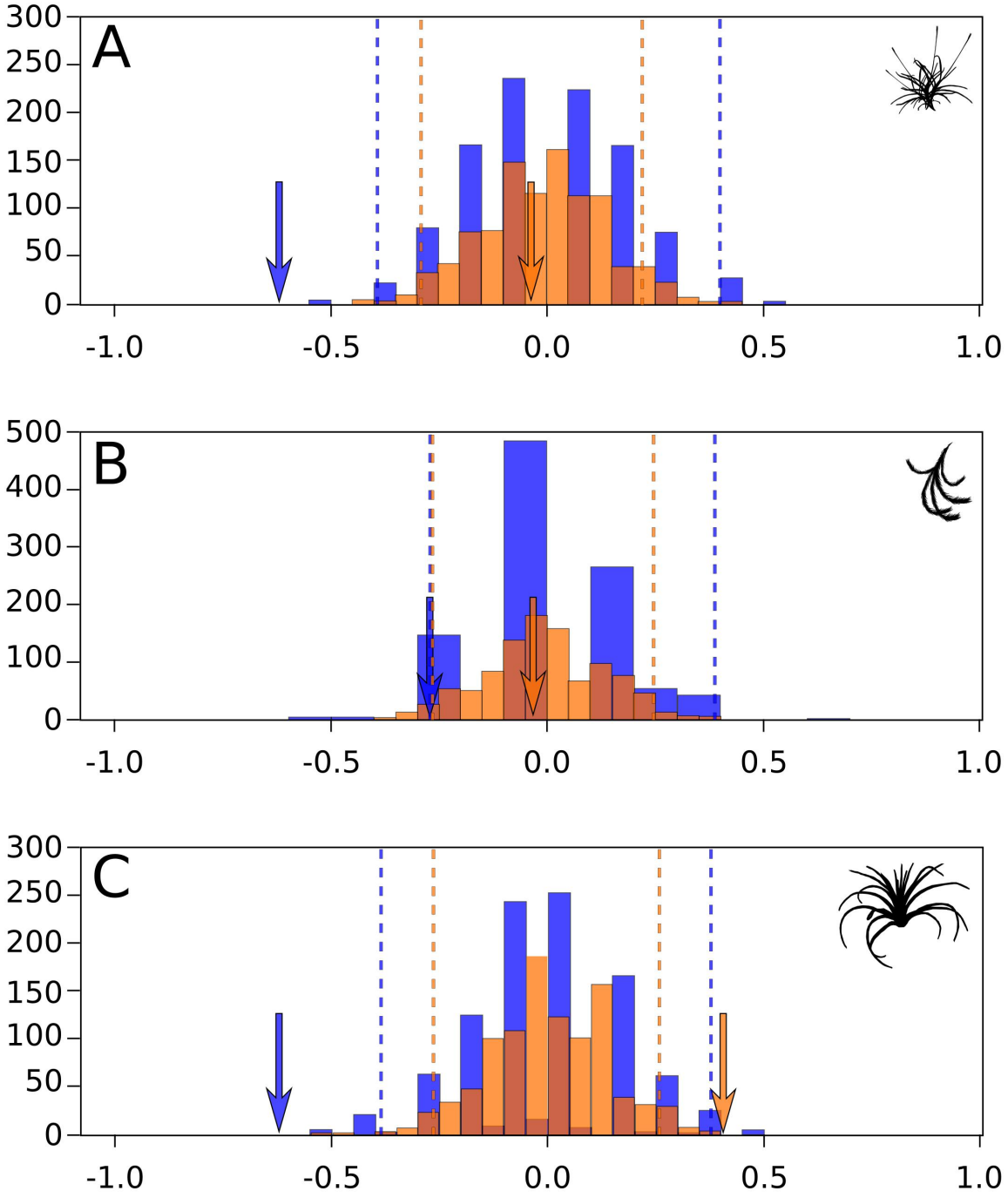

Fig. 8. Observed (arrows) and randomly expected (bars) correlation between the presence/absence of *T. recurvata* (A), *T. tricholepis* (B), and *T. pohliana* (C) with any of the remaining species (both presences summed) on trees under high (blue) and low tree densities (orange). 95% credible intervals are displayed in dashed lines.

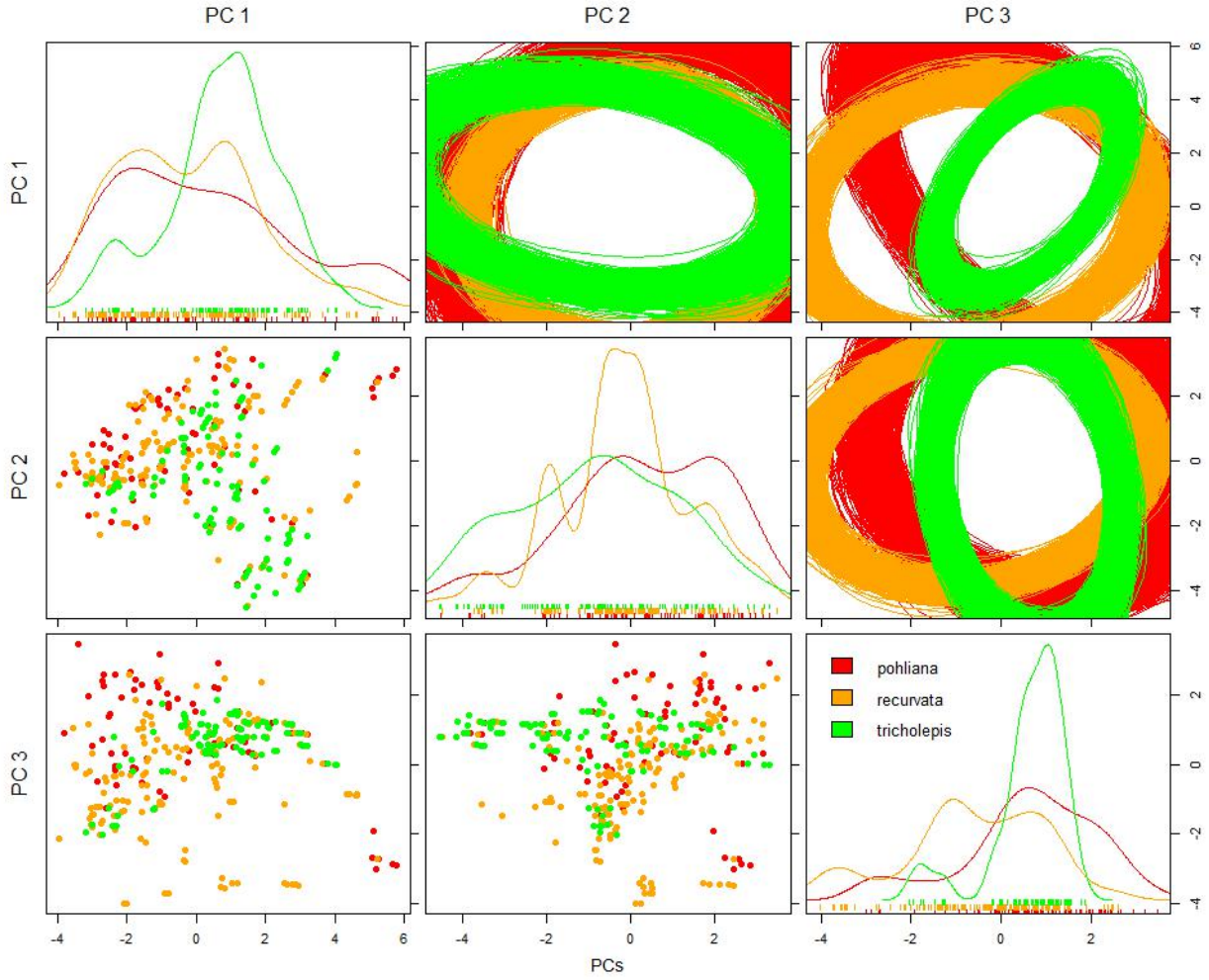

Fig. S1. One thousand elliptical projections of the niche of each studied species and pair of the three principal components grouping the variance of host tree traits. Also displayed are one-dimensional density plots (lines) and two-dimensional scatterplots.

CAPÍTULO IV

SPATIO-TEMPORAL DYNAMICS OF AN OPPORTUNIST PLANT BASED ON GENETIC STRUCTURE VARIATION: COMBINING GENETIC APPROACHES WITH INDIVIDUAL-BASED MODELING TO INVESTIGATE LOCAL SPREAD OF *TILLANDSIA RECURVATA* (BROMELIACEAE)

Cleber Juliano Neves CHAVES[1]*; Bárbara Simões Santos LEAL[1]; Davi Rodrigo ROSSATTO[2]; Uta BERGER[3]; Clarisse PALMA-SILVA[4]

[1] Programa de Pós-graduação em Ecologia e Biodiversidade, Universidade Estadual Paulista, Instituto de Biociências, 13506-900 Rio Claro, Brazil

[2] Departamento de Biologia, Universidade Estadual Paulista, 14884-900 Jaboticabal, Brazil

[3] Institute of Forest Growth and Computer Sciences, Technische Universität Dresden, 01737 Tharandt, Germany

[4] Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, 13083-862 Campinas, Brazil

* cleberchaves@gmail.com

ABSTRACT

1. While many species are migrating or becoming extinct due to the intensive human-induced disturbances on ecosystems, others can thrive in anthropic environments. Opportunistic species often reproduce by cloning and self-fertilization (called 'selfing'), allowing them to establish new populations after long-distance dispersal. However, these breeding systems also increase the spatial genetic structure (SGS) of populations, promoting bottlenecks, reducing local genetic diversity, and increasing inbreeding. Here, we aim to understand how an opportunistic plant with selfing and cloning reproduction successfully spread over new areas, testing whether the time since colonization and the landscape affect its SGS.

2. We performed both population genetic analysis and individual-based modeling (IBM) to study the spreading of *Tillandsia recurvata* (L.) L.. This epiphyte has a wide distribution throughout the American continent and a great adaptability to anthropogenic transformed environments, being often considered an 'epiphytic weed'. We used a set o nuclear microsatellites to access the SGS within a metapopulation of *T. recurvata* established on trees scattered in an anthropogenic fine-scaled landscape in Brazil. We then developed an IBM based on the individual energy budget of *T. recurvata*, to further simulate the effect of time since colonization and tree density on the SGS.

3. The empirical results show a high SGS of *T. recurvata* populations and indicate a phalanx pattern of spreading with a posterior partial isolation driven by selfing and cloning reproduction. Simulated results show that highest levels of SGS appear at the very beginning of colonization, which is then sharply reduced after less than 10 years since colonization. They furthermore indicate that lower tree densities (ca. 0.005 trees/m^2) provide optimal conditions for *T. recurvata* spreading.

4. *Policy implications*. Our results provide an overview of how and how fast an opportunistic plant performing cloning and self-fertilization spread over new areas and how this dynamics is constrained by landscape features. For *T. recurvata,* lower tree densities of anthropic transformed landscapes may have created suitable conditions for the rapid spreading over areas which were previously limiting for its growth and dispersal.

Keywords

atmospheric bromeliads, cloning, epiphytes, fine-scale, landscape genetics, population genetics, selfing, weeds

INTRODUCTION

Intensive disturbances are inherent to human history and have strong effects on natural communities (de Wet and Harlan 1975). Nowadays, ecosystems are subjected to unprecedented rates of human-induced changes that is fostering the sixth mass extinction (Ceballos et al. 2015). Conversely, not all organisms react in the same way to human disturbance (Airoldi and Bulleri 2011). While many species become extinct or migrate, others thrive in anthropogenic environments and can spread into natural environments (Wilcove 1985; Airoldi and Bulleri 2011). Human activities such as those related to changes in soil use, deforestation, fires, construction, gardening, and recreation, have thus allowed the prevalence of many opportunistic species in anthropogenic landscapes (Airoldi and Bulleri 2011). This particular case of opportunistic species is commonly referred as weed and can evolve from introduced or native opportunists that grow under human-disturbances without being cultivated, affecting both environment and economy (Baker 1974; de Wet and Harlan 1975; Richardson et al. 2008).

Between 50 and 80% of all invasive plant species can be classified as weeds, depending on current impacts and human perceptions (Richardson et al. 2008). These species commonly have high dispersal abilities and wide plasticity that enable them to colonize large areas (Baker 1974; Kuester et al. 2014). Indeed, studies have shown that widespread species are more likely to become opportunists as they are usually adapted to wider conditions ranges (Booth et al. 2002). The spreading rate of weeds vary greatly according to the habitat, but continuous invasive fronts across landscapes are uncommon and local and long-distance dispersal often determine their spatial patterns (Pyšek and Hulme 2005). Furthermore, native weeds usually evolve from species that are good colonizers with traits that preadapt them to establish in newly disturbed areas (van Etten et al. 2017).

Uniparental reproduction, such as cloning and self-fertilization (called selfing), is one of the most important adaptations allowing opportunistic plants to establish new populations after long-distance dispersal (Baker 1955; Razanajatovo et al. 2016). Despite their entirely different origins, both cloning and self-fertilization contribute to increase the invasiveness of a species by mitigating the Allee effect on pollen-limitation of small populations, and therefore enhancing the reproductive assurance and genetic transmission (Vallejo-Marín et al. 2010; Rodger et al. 2013; Barrett and Harder 2017). While self-fertilization can increase species' investment in seed production, clonal reproduction speeds up ramet growth and reduces the likelihood of genets` death by sharing stochastic risk over multiple ramets (Klimeš et al. 1997; Barrett 2015). On the other hand, the aggregation of self-fertilized offspring and clones strongly influence the spatial genetic structure of populations, promoting bottlenecks, reducing local genetic diversity, and increasing inbreeding depression (Heywood 1991; Barrett 2013; Barrett et al. 2014; Barrett 2015). These effects lead to a strong population subdivision, that creates a metapopulation dynamic with the frequent extinction in

a site being balanced by the selection of selfing and cloning individuals, due to their higher capacities of recolonization (Pannell and Barrett 1998; Barrett 2013). Thus, the understanding about the local spread dynamics is important to shed light on how selfing and cloning species become opportunists reaching wide distributions, despite their tendency to form highly differentiated populations with low genetic diversity.

Tillandsia recurvata (L.) L. is a widely distributed epiphytic bromeliad, particularly associated to open biomes from Argentina to southern United States (Smith and Downs 1977; GBIF 2017). In these regions, the great abundance and dominance of the species in epiphytic communities constitutes a characteristic feature of the landscape and has long attracted the interest of naturalists (e.g. Birge 1911; McWilliams 1992; Flores-Palacios et al., 2014). Studies have described T. recurvata as the most xerophytic of tropical and subtropical epiphytes (e.g. Benzing 2000; Benzing 2012), with "probably the greatest adaptability of any plant in the Western Hemisphere" (Foster 1945:14). In fact, a number of ecological features such as small size, relatively fast life cycle, absorbent leaf scales, CAM photosynthesis, wind-dispersed seeds, spontaneous self-pollination due to its cleistogamous flowers, and intense cloning allows T. recurvata to quickly generate large populations even on isolated trees (Soltis et al. 1987; Smith et al. 1989; Orozco-Ibarrola et al. 2017; Chilpa-Galván et al. 2018). Both reproductive characteristics, and epiphytic habit likely increase T. recurvata's genetic structure, as each host tree represents an isolated patch of habitat scattered in a harsh matrix (Southwood and Kennedy 1983; Burns 2007) and many dispersed seeds usually fall close to the mother and establish in the same host tree (e.g. Trapnell et al. 2004; Torres et al. 2018).

The great adaptability of T. recurvata fostered its increasing distribution over human-disturbed regions, forming large populations on urban landscapes, actively growing even on fences and electric light wires (e.g. Flores-Palacios et al. 2015; Orozco-Ibarrola et al. 2015). Such great abundance has made some authors to consider T. recurvata as an "epiphytic weed" and some of them even sought to describe herbicides and other techniques to control its spreading (e.g. Claver et al. 1983; Bartoli et al. 1993). Although T. recurvata is not a parasite, studies have listed deleterious effects that its massive populations may have on sympatric epiphytes and even on the growth and reproduction of its host tree, by competing for light with new shoots, modifying barks, and even affecting seedlings growth (e.g. Birge 1911; Flores-Palacios et al. 2014; Aguilar-Rodriguez et al. 2016). Such effects still need further studies, but the reproductive biology, metapopulation pattern, and opportunistic behavior of T. recurvata make this species a good model to study the local spreading dynamics of opportunistic plants.

In this study, we integrate empirical and simulated genetic data to study the local spatio-temporal dynamics of T. recurvata spread. Specifically, we aimed (I) to investigate whether a fine-scaled metapopulation of T. recurvata is genetically structured; (II) to describe the temporal dynamics of its genetic structuring; as well as (III) to investigate whether such genetic structure

varies among landscapes with distinct tree densities. Because obtaining regular data over a significant period of time can be tricky (Epps and Keyghobadi 2015), modeling approaches could be helpful to understand spatio-temporal effects on genetic variation. Here, we employed microsatellite markers to estimate the fine-scale SGS of a T. recurvata metapopulation, and an individual based model (IBM) to simulate the variance of the observed empirical patterns of genetic variation over colonization time and across landscapes with distinct tree densities. These models explicitly incorporate characteristics to individuals (e.g. life stage, size, genotype) and simulate interactions among each other and with the surroundings, exploring how population dynamics over time and space emerge from the variability and behavior of each organism (Grimm and Railsback 2005).

MATERIAL AND METHODS

Empirical population genetics

Study area and sampling

We sampled a total of 224 individuals of *T. recurvata* hosted on 14 trees (16 individuals per tree; hereafter referred as "populations") hosted on distinct neighbor trees scattered in an anthropical transformed landscape of ca. 2,000 m^2 in southwest Brazil (-21.244289S, -48.300486W; Fig. 1). We avoided sampling clones by collecting individuals at distinct branches within each host tree, once new ramets of *T. recurvata* are formed in the axils of the leaves of primary stem, which confers the typical "ball" shape of the species (Birge 1911). The studied landscape is composed by a grove of 20 cultivated trees from *Handroanthus* Mattos genus (Bignoniaceae) with similar ages and growing at a distance from 2.5 to 47.5m from each other (Fig. 1). A recent study estimated a great abundance of *T. recurvata* individuals within this area, accounting for more than 15 thousand individuals (Chaves et al. 2016). The uniform conditions imposed by the low local richness of tree host species allowed us to reduce potential bias caused by tree traits.

DNA extraction and SSR analysis

We extracted the total genomic DNA from fresh leaves of each sampled individual according to Tel-Zur et al. (1999) and characterized them using seven SSR markers designed for other species and cross-amplified by Chaves et al. (2018). We carried out PCR amplifications in a reaction volume of 10 μL containing ~1 ng DNA template, 5 × GoTaq Master Mix (Promega Corporation), 5 pmol forward primer, 10 pmol reverse primer, and 1 pmol universal M13 primer tagged with distinct fluorochromes (FAM, VIC, PET, or NED). Amplifications were performed in a Veriti 96-Well Thermal Cycler (Applied Biosystems), using a touchdown program, as described by Palma-Silva et al. (2007). We, then, genotyped amplified loci for each sample on an ABI 3730

DNA Analyzer Sequencer and sized against a GeneScan LIZ molecular size standard (Applied Biosystems), using GeneMarker software v. DEMO (SoftGenetics).

Genetic analyses

To describe genetic diversity within each *T. recurvata* population, we calculated number of alleles (A), allelic richness (A_R), private number of alleles (A_P), expected (H_E) and observed heterozygosity (H_O), and inbreeding coefficient (F_{IS}), using the R statistical package "diveRsity" (Keenan et al. 2013). Departures from Hardy-Weinberg expectations were also tested with R package "diveRsity". We measured pairwise population differentiation (F_{ST}) and tested hierarchical partition of genetic variance among and within sampled populations by performing an analysis of molecular variance (AMOVA; Excoffier et al. 1992), using the R statistical package "poppr" (Kamvar et al. 2014). Further, we tested the correlation between geographical and genetic distances performing a Mantel test with F_{ST}, Nei's, Edward's, and Reynold's genetic distances, with 1,000 replications, using the R statistical package "ade4" (Dray and Dufour 2007).

We investigated the spatial genetic structure (SGS) by estimating the pairwise kinship coefficient (F_{ij}) (Loiselle et al. 1995) between pairs of individuals and testing their autocorrelation within seven distance classes with the same number of pair units each, using the R package "RClone" (Bailleul et al. 2016). We proceeded a random shuffling (100×) of individual locations to test the statistical significance of mean kinship coefficient values in each distance class in a 95% confidence interval of a random distribution. Finally, we calculated alleles and genotypes replacement (turnover) among populations (Harrison et al. 1992; Jost 2007), using the R statistical package "vegeterian" (Charney and Record 2012).

Individual-based modeling

Model description

The IBM model was implemented in NetLogo 6.0.1 (Wilensky 1999) and was outlined following the ODD (overview, design concepts, details) protocol formulated by Grimm et al. (2006, 2010; see Appendix A). In short, the model simulates the colonization of trees scattered in a new landscape by multiple genetic lineages of *T. recurvata* that annually reach and thrive in the landscape over time (Fig. 2A). Here, each genetic lineage is assumed to group descendants of a single seed from the regional seed rains that reached, grew and thrived the simulated landscape by performing self-fertilization and clonal reproduction. Since the regional seeds may have heterozygous locus, a genetic lineage often groups multiple genotypes. The simulated dynamics are primarily based on the energy budget of each *T. recurvata* individual, which quantifies the amount of energy an individual takes up and expends during its life cycle depending on the shading exerted by host trees (Fig. 2B; see Appendix A, for further explanations).

Parameters estimation

We estimated IBM parameters using an ABC framework ('Approximate Bayesian Computation'; Csilléry et al. 2010). For this, we repeated simulation runs one million times, using a representation of the empirical landscape, and randomly drew parameter values from prior distributions based on literature (Table 1). We run simulations in parallel on NetLogo (Wilensky 1999) through the R environment, with the R package "RNetLogo" (Thiele et al. 2012), using the NCC/GridUNESP cluster. We retained a total of 319,539 simulations that formed populations at least 10 individuals on each of the same sampled trees of the empirical population genetics study above. We recorded the genotypes of up to 15 *T. recurvata* individuals established on these same trees after the 10^{th} simulated year of each retained simulation. We calculated the following summary statistics for retained simulations and empirical data, over loci and populations, using the Arlequin "arlsumstat" console version (Excoffier and Lischer 2010): mean number of alleles (K), mean range of the allele size (R), mean expected heterozygosity (H), mean inbreeding coefficient (F_{IS}), global population differentiation (F_{ST}), and mean modified Garza-Williamson statistic (NGW; Garza and Williamson 2001; Excoffier et al. 2005). These summary statistics were chosen based on their informativeness.

We performed a Global Sensitivity Analysis to test whether summary statistics, as well as *T. recurvata* abundance and total number of genetic lineages, are differently affected by parameters variation. We then tested the accuracy of ABC estimates through a cross-validation procedure (Csilléry et al. 2012), taking a subset of 100 random outputs as "pseudo-data", and employing a 'neural network' algorithm (Blum & François 2010), with thresholds of 0.01, 0.005, and 0.001, using the "abc" R package (Csilléry et al. 2012). We tested the correlation between true values (i.e. 'pseudo-data') and estimated medians, means, and modes. We then compared empirical and simulated summary statistics to estimate parameters posteriors, retrieving 0.005% of simulations (see Fig. S2 in Appendix B), and applying the 'neural network' method. Finally, we tested the correlation among parameters and estimated its significance within retained simulations using the "psych" R package (Revelle 2018).

Colonizing over time and across landscapes

To test the genetic structure dynamic of *T. recurvata* metapopulation over time (hereafter referred as 'time simulation'), we generated 10 thousand simulations of *T. recurvata*'s metapopulation on the empirical landscape during 50 years, using the IBM model described above. We also used the IBM model to test how genetic structure of *T. recurvata* metapopulation varies among landscapes with distinct tree densities (hereafter referred as 'density simulation'), using 100 thousand simulations with five to 150 trees with random heights and the same crown size, scattered randomly across landscapes of ~3,060$m^{2,}$. We set parameter values as estimated by the ABC approach (Table 1) to run both time and density simulations. At each year of time simulations or

after the 10th year of density simulations, we measured total *T. recurvata* abundance and total number of genetic lineages. We also recorded genotypes, genetic lineages, and reproductive origins (from cloning or sexual reproduction) of up to 15 *T. recurvata* individuals established on the same trees as those sampled in the empirical experiment for time simulations, or on up to 15 random trees for density simulations. We then calculated expected heterozygosity (H), inbreeding coefficient (F_{IS}), and global population differentiation (F_{ST}), using the Arlequin 3.1 software. We also calculated the replacement of genotypes and genetic lineages (turnover) among populations (Harrison et al. 1992; Jost 2007), through the R package "vegeterian".

RESULTS

Empirical population genetics

Among the studied populations, number of alleles (A) ranged from 19 to 30, while allelic richness (A_R) ranged from 2.20 to 3.54, and private number of alleles (A_P) was up to 2 per population. Expected (H_E) and observed (H_O) heterozygosity ranged from 0.27 to 0.51, and 0 to 0.2, respectively. As expected, inbreeding coefficient (F_{IS}) were very high in all populations, ranging from 0.520 to 1.0. All populations presented a deficit of heterozigotes in relation to Hardy-Weinberg expectations (Table 2).

Pairwise population differentiation (F_{ST}) ranged from 0.009 to 0.314 (Table 2). AMOVA analysis showed lower genetic variance among populations (17.26%, Φ_{ST} = 0.173) than within populations (82.74%), but it was significantly greater than expected by chance ($p < 0.05$) and expected for an autogamous plant. The greatest kinship values (F_{ij}) were observed at the smallest distance interval (~2.5m), being significantly greater than expected by chance ($p< 0.05$; Fig. 3). The kinship among individuals decayed sharply with increasing distances and becomes significantly lower than expected by chance at the 4th to 6th distance classes (between ~10 to 25m), raising again at the furthest distance class (~30m) and becoming equal to the expected by chance (Fig. 3). Mantel test indicate a significant isolation by distance (IBD), when using Nei's and Edward's genetic distances (0.194 and 0.243, respectively; $p < 0.05$). The allelic and genotypic turnover were 0.031 and 0.537, respectively. Genotypes are evenly spaced among populations, with, in general, one distinct dominant genotype in each of them (Fig. 4).

Individual-based model

Parameter estimation

As expected, *T. recurvata* abundance and total number of genetic lineages were not sensitive to *mutation rate* variation. All the other interactions among summary statistics and parameters variation demonstrate a wide sensitivity (see Fig. S1 in Appendix B). Although parameters estimation through the cross-validation showed a significant correlation between true and estimated

values ($p < 0.001$), *wind speed* and *capture probability* were, respectively, the parameters most and less accurately estimated by the model (Fig. S2 and Table S1 in Appendix B). From the prior 319,539 simulations, this analysis accepted the parameter combination of 1,598. *Wind speed* and *mutation rate* were the parameters that, respectively, most and less narrowed posteriors (Table S2 in Appendix B). We found five significant correlations among parameters in accepted simulations (Table S3 in Appendix B). The two strongest correlations were between *capture probability* and *regional seed rain* ($r = -0.430$), and between *capture probability* and *germination rate* ($r = -0.262$).

Time and density simulations

All measured variables reached a steady state at up to 20 years of time simulations (Fig. 5). While the proportion of clonal individuals, turnover of genetic lineages, as well as the F_{IS} and F_{ST} values, stabilize after 10 years (T1 in Fig. 5), the abundance of individuals and genetic lineages, turnover of genotypes, and expected heterozygosity (H_E), stabilize after 20 years (T2 in Fig. 5). The metapopulation reaches the maximum number of individuals and genetic lineages around, respectively, the 15^{th} and 20^{th} years, (ca. 15,000 individuals and 45 genetic lineages; Fig. 5). Genotypic turnover reaches to a plateau of ca. 0.50, whereas the turnover of genetic lineages stabilized at much lower values, ca. 0.15 (Fig. 5). The values of F_{IS}, F_{ST}, and H_E stabilizes, respectively, in ca. 0.85, 0.15, and 0.65 (Fig. 5).

Density simulations showed greater variance and less stability than time simulations. Figure 6 shows that, under low tree densities (ca. 0.05 tree/m^2; D1), the proportion of clonal individuals, H_E, and F_{IS} reach their maximum (ca. 0.95, 0.40, and 0.90, respectively), while the turnover of genotypes and genetic lineages, as well as the F_{ST} reach their minimum (ca. 0.30, 0.25, and 0.40, respectively). The total abundance reaches its maximum (ca. 3,500) under tree densities close to 0.013 tree/m^2 [D2] In their turn, the number of genetic lineages reach its maximum (ca. 40 lineages) and H_E stabilizes at ca. 0.30, under tree densities close to 0.025 tree/m^2 [D3]. Finally, in tree densities greater than 0.04 tree/m^2 [D4], all measured variables become steady: the proportion of clonal individuals reaches its minimum of ca. 0.65, the turnover of genotypes and genetic lineages equalize themselves, reaching to the maximum of ca. 0.90, and the values of F_{IS} and F_{ST} become equivalent at ca. 0.70.

DISCUSSION

In this study, we integrated empirical and simulated genetic data to provide insights on how *Tillandsia recurvata*, an opportunistic native epiphyte with a naturally widespread distribution and great local abundances, spread into new areas. Our results show a surprisingly high spatial genetic structure (SGS) in populations of *T. recurvata* considering the fine scale in which the metapopulation was sampled. Simulated genetic data by IBM explicitly demonstrate how genetic dynamics of *T. recurvata* populations can be forecast over time and space by modeling the behavior

of individuals in the landscape. Results indicate higher levels of SGS at the very beginning of *T. recurvata* colonization, which is sharply reduced after less than 10 years, and that landscapes with lower tree densities represent the optimal condition for *T. recurvata* spreading. Below, we discuss our findings based on ecological features of this model species, highlighting the importance of understanding spatio-temporal dynamics of genetic structure in opportunistic species.

Fine-scale genetic structure

Patterns of SGS of populations at fine scales often result from limited gene flow (Vekemans and Hardy 2004; Ward 2006). In this study, we found high SGS in populations of *T. recurvata* at a fine scale (ca. 2,000m^2), as suggested by the high and significant values of population differentiation (F_{ST} and Φ_{ST}), autocorrelation between individuals at the nearest distance class, and genotypic turnover among populations. Moreover, the pattern of isolation by distance and the existence of up to two private alleles in six of the 14 studied populations also indicate a limited gene dispersal among studied populations of *T. recurvata*. This SGS likely arisen as an outcome of the breeding system and life form of *T. recurvata* (Vekemans and Hardy 2004; Ward 2006), since other studies have reported similar patterns for selfing (e.g. Pettengill et al. 2016; Atwater et al. 2018), cloning (e.g. Li and Dong 2009; Atwater et al. 2018), epiphytic (e.g. Trapnell et al. 2004; Ren et al. 2017; Torres et al. 2018), and fast-growing plants (e.g. Barluenga et al. 2011; Charbonneau et al. 2018). Beyond breeding system and life form effects, the high fine-scale SGS in *T. recurvata* populations could also result from consecutive founder events (Hewitt 1996; Ward 2006). The low allelic turnover among populations indicates, specifically, that *T. recurvata* expansion across the landscape was gradually conducted by several source populations in a phalanx pattern, rather than just by one leading population (Hewitt 1996). In its turn, the selfing and clonal reproduction of *T. recuvata* may be responsible for the evolution of subpopulations in partial isolation, creating the strong genotypic turnover observed among the studied populations (Ward 2006). Conversely, genetic drift resulting from founder events, as well as the increasing amount of seeds released from large populations, likely intensify the metapopulation dynamics of repeated extinction and recolonization events, contributing to decrease population differentiation over time in this species (Baker 1955, Pannell and Barrett 1998; Razanajatovo et al. 2016).

SGS over time

Our results from time simulations resemble diffusion models of spread (e.g. Counsens and Mortimer 1995), showing three distinct phases of *T. recurvata* spreading: the lag, log, and stationary phases. During the lag or establishment phase (up to the 5th year), the lower number of individuals and genetic lineages increases the genetic differentiation, leading to a reduction of heterozygosity due to self-fertilization (Barrett et al. 2014). At the same time, the lower proportion of clonal individuals increases the local heterogeneity of each population, leading to a reduction on

F_{IS}. During the log or rapid-spread phase (between the 5th and 15th year), in its turn, abundance jumps from a few up to nearly 15,000 individuals and the genetic differentiation among populations reaches its minimum. The continuous input of new genetic lineages leads to an increase of heterozygosity, despite the opposite effect resulting from self-fertilization (Barrett et al. 2014). At the same time, the increasing proportion of clonal individuals homogenizes local populations (Ward 2006) and boosts the seed production of some genetic lineages, increasing F_{IS} and reducing the turnover of genotypes and genetic lineages, and of F_{ST} afterward. Relationships between the turnover of genetic lineages and genotypes for simulated data agree to what was discussed for the allelic and genotypic turnover of empirical data, reinforcing the phalanx pattern of *T. recurvata* described above.

The time simulations of our IBM model also indicate that all parameters reach the stationary phase after up to 20 years of *T. recurvata*'s colonization. However, the time to reach equilibrium varies for each parameter analyzed, as has been observed in other theoretical studies (see Epps and Keyghobadi 2015 for a revision). Measures of genetic differentiation (i.e. F_{ST}, and genotypic and genetic lineages turnover), as well as F_{IS} and proportion of clonal individuals, were the first parameters to approach the stationary phase (around the 10th year), followed then by the heterozygosity and total abundance (around the 20th year). Such differences could be explained either by the great exchange of migrants per generations among populations (Varvio et al. 1986; Epps and Keyghobadi 2015) and by the high mutation-rate of the microsatellites of *T. recurvata*, which increases the divergence of populations descending from the same genetic lineage (Epps and Keyghobadi 2015). The quick reduction and stabilization of SGS in *T. recurvata* indicate that, after ca. 10 years of spreading into new areas, the metapopulation could already behave as a large source population that supports the spreading over other areas. Although it requires further investigations, this pattern shall be common to other opportunistic plants.

SGS across landscapes with distinct tree densities

Results from density simulations show that the greatest abundance of *T. recurvata* individuals occurs at low tree densities, ca. 0.005 trees/m^2. Above and below this value, the tree density increasing has opposite effects on the SGS of *T. recurvata* populations. At lower values (<0.005 trees/m^2), increasing tree densities reduce the SGS among *T. recurvata* populations, due to the increasing in habitat amount for this species, since each host tree account as a habitat patch (e.g. Snäll et al. 2005; Belinchón et al. 2017). At higher values (>0.005 trees/m^2), in the other hand, increasing tree densities maximizes the SGS, due to the enhancement of seed dispersal resistance among *T. recurvata* populations, as winds are typically stronger and produce greater wind-dispersal distances in opener areas (Nathan et al. 2002). Indeed, a number of studies has also implemented IBM approaches for distinct systems and showed that habitat amount and resistance to gene flow across landscapes strongly influence the SGS among populations (e.g. Cushman et al. 2012;

Jackson and Fahrig 2016). For *T. recurvata*, however, increasing number of trees may either increase the habitat amount, at lower tree densities, or promote a reduction of seed dispersal distances, at higher tree densities.

Besides the importance of wind speed for seed dispersal, the variation of SGS in *T. recurvata* populations according the tree density can also be explained by its preference for drought environments (e.g. Smith et al. 1989; Orozco-Ibarrola et al. 2017; Chilpa-Galván et al. 2018). This ecological feature often reduces the populations to a few individuals constrained to drier and upper layers of dense forests (e.g. Vergara-Torres et al., 2010; Flores-Palacios et al. 2015). Indeed, denser forests curtail seed dispersal distances and drop both genetic diversity and proportion of clonal individuals, creating ephemeral, isolated and smaller populations that boosts SGS by genetic drift (Barrett & Kohn 1991). This explains the massive abundance of *T. recurvata* individuals at lower tree densities and the fleeting attachment of only a few individuals to trees at the border of landscapes with the highest tree densities, simulated by the IBM. The proliferation of *T. recurvata* at low tree densities suggests an important role of human-induced deforestation on driving the rapid spread of opportunistic plants on landscapes that could otherwise limit population abundance and gene dispersal.

Further considerations

Sensitivity tests performed for the IBM model provide important insights into the influence of parameters on the genetic structuring of *T. recurvata* populations over time and across distinct landscapes. Results showed that high mutation rates of microsatellites can significantly decrease F_{IS} and F_{ST}, and increase the heterozygosity (H_E), as have been observed in other studies (e.g. Kronholm et al. 2010). The sensitivity tests also suggest that strong winds, massive regional seed rains, and high rates of germination and seed capturing have a homogenizing effect on *T. recurvata* metapopulations (see Fig. S1 in Appendix B). The combined effect of these parameters explains why *T. recurvata* is able to successfully spread over human-transformed landscapes, despite its transitory high genetic structure (e.g. Caldiz & Fernández, 1995; Flores-Palacios et al., 2014).

Opportunistic species provide excellent opportunities to examine the process of successful colonization of novel environments (van Etten at al. 2017). Our results show that the effects of high spatial genetic structure, reduced genetic diversity, and inbreeding, associated to self-fertilizing and cloning systems of opportunist plants (e.g. Heywood 1991; Barrett 2015; Razanajatovo et al. 2016), can be overwhelmed by a rapid spread across optimal landscapes. We demonstrate here that the reduced tree densities commonly found in anthropic transformed landscapes may have created suitable conditions for the rapid spreading of *T. recurvata* over areas which were previously limiting for its survival and seed dispersal. Therefore, afforestation of landscapes dominated by this kind of opportunist species might be an effective strategy to control its spreading. For the sake of simplification, we constructed the IBM model using static landscapes. A next important step would

be, thus, to test how the species' spread changes in dynamic landscapes, according to the occurrence of growing or falling trees, or under deforestation, afforestation, or urbanization conditions.

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TABLES AND FIGURES

Table 1. IBM model parameters. Prior ranges are based on literature or previous simulations tests. Posterior ranges are based on results of ABC, while estimated values are based on the accuracy of each parameter value obtained by the ABC cross-validation tests.

Parameter	Definition	Prior range (min-max)	Prior distribution	Posterior range (CI 95%)	Estimated value (measure)	Reference
Regional seed rain	Number of seeds that arrive on the landscape at each reproductive season	100-500	uniform	102-415	170 (median)	Previous simulations tests
Wind speed	Magnitude of seed dispersal (non-dimensional values)	1-20	uniform	11.84-20.89	14.832 (mode)	Previous simulations tests
Mutation rate	Average SSR mutation-rate	10^{-6}-10^{-2} (mean=10^{-4}; sd=$10^{-3.5}$)	normal	$10^{-5.69}$-$10^{-2.02}$	$10^{-2.42}$ (median)	Anmarkrud et al. 2008; Udupa and Baum 2001; Marriage et al. 2009
Germination rate	Seed germination rate	0.0083-0.30	uniform	0.133-0.307	0.242 (mean)	Bernal et al. (2005); Chilpa-Galván et al. (2018)
Capture probability	Probability of a seed be captured in the canopy	0.01-0.30	uniform	0.109-0.300	0.208 (mean)	Unpublished data

Table 2. Sample number (N), number of alleles (A), allelic richness (A_R), private alleles (A_P), expected heterozygosity (H_E), observed heterozygosity (H_O), and inbreeding coefficient (F_{IS}) for each sampled population.

Population	N	A	A_R	A_P	H_E	H_O	F_{IS}
1	16	19	2.50	0	0.400	0.120	0.710 *
2	16	21	2.46	1	0.360	0.070	0.814 *
3	16	29	3.50	2	0.480	0.200	0.595 *
4	16	25	2.98	0	0.450	0.000	1.000 *
7	16	19	2.41	0	0.360	0.170	0.520 *
8	15	24	2.95	0	0.460	0.000	1.000 *
9	16	21	2.68	0	0.420	0.120	0.700 *
10	15	19	2.20	2	0.270	0.000	1.000 *
11	16	23	2.63	1	0.340	0.040	0.895 *
15	15	25	2.96	0	0.430	0.000	1.000 *
17	16	21	2.61	0	0.380	0.070	0.811 *
18	16	30	3.54	1	0.510	0.000	1.000 *
19	16	23	2.61	1	0.380	0.150	0.594 *
20	16	24	2.93	0	0.440	0.010	0.980 *
Mean	15.8	23.1	2.78	0.6	0.406	0.068	0.830 *

* Deviations from Hardy-Weinberg Equilibrium ($P<0.05$).

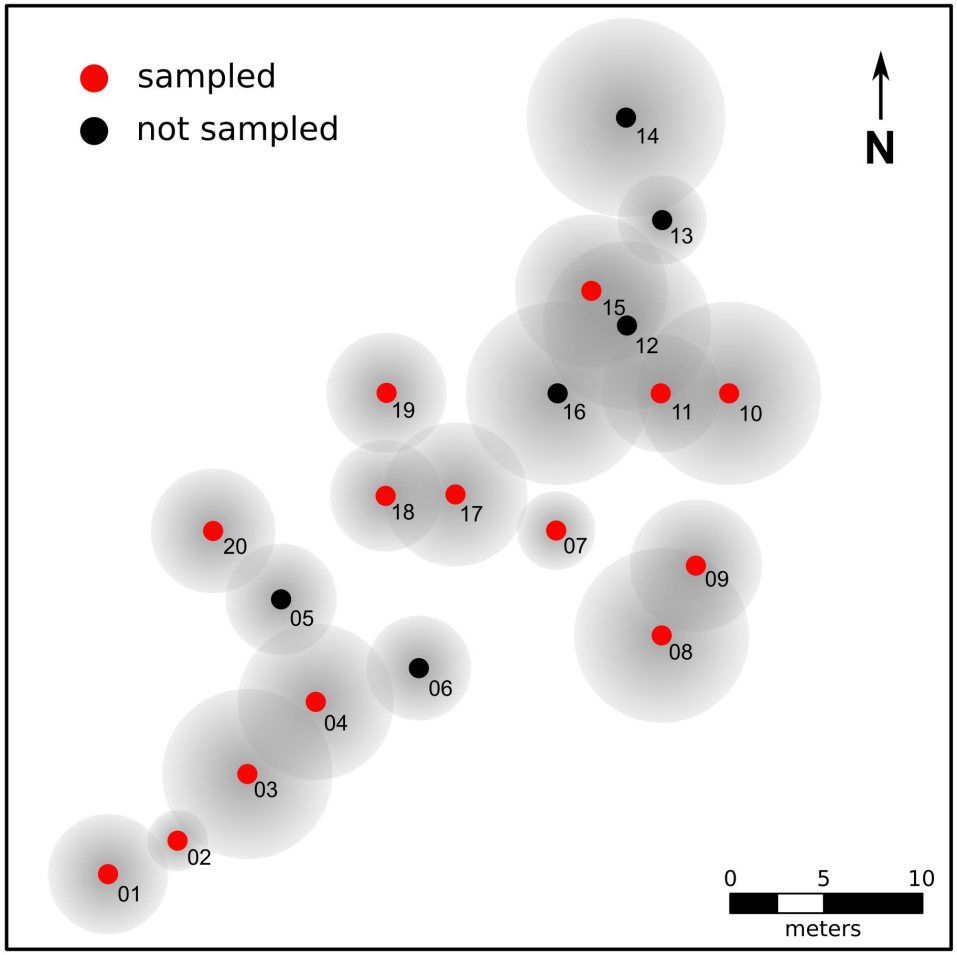

Figure 1. Spatial distribution of trees within the studied landscape. Numbers refers to the ID of trees hosting the analyzed *T. recurvata* populations. Gray circles around each dot are representation of the crown area of each tree.

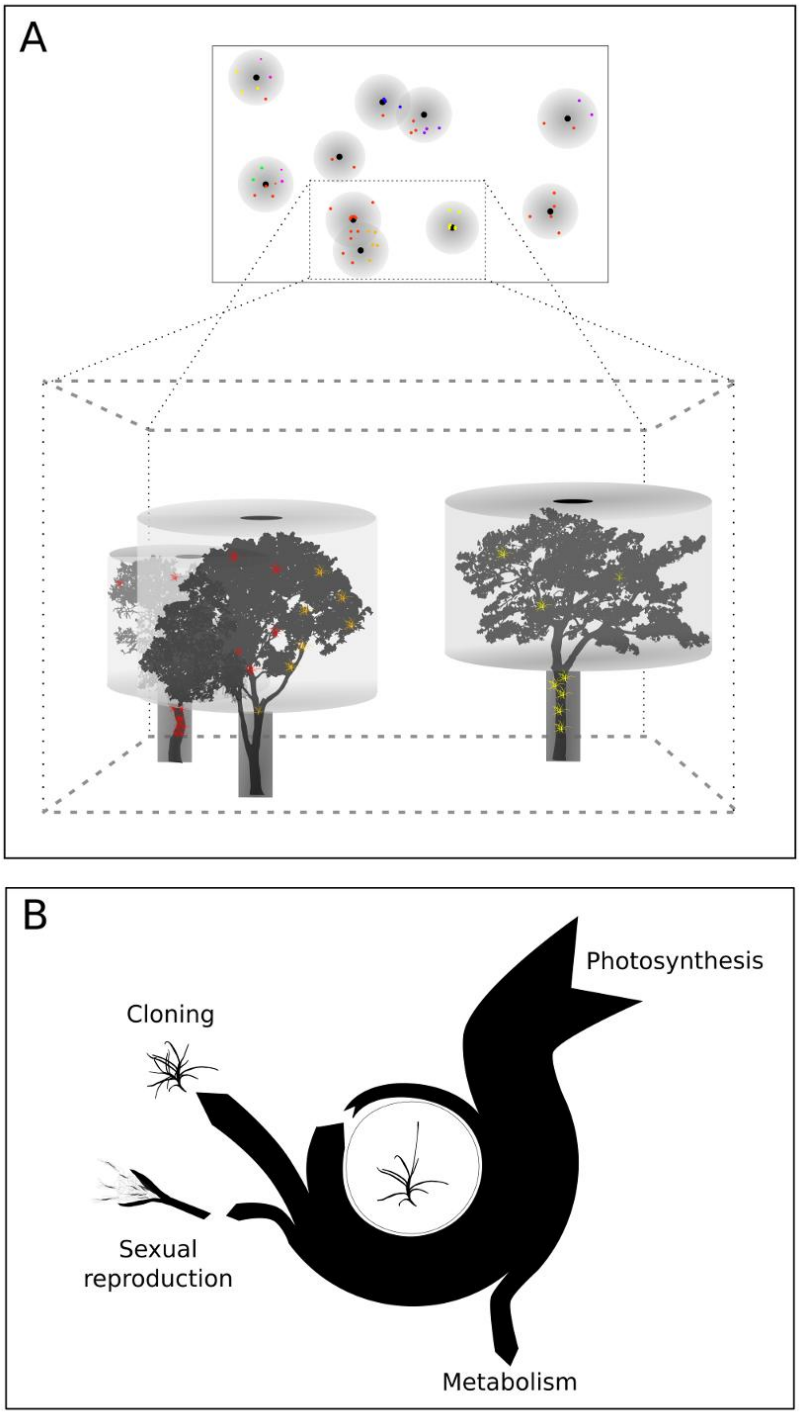

Figure 2. Schematic representations of the individual based model. (A) 2D representation of a 3D simulated landscape. Points with distinct colors represent T. recurvata individuals of distinct genetic lineages. (B) Energy budget of a single individual of T. recurvata. The arrow nocks and arrowheads represent, respectively, energy inputs and outputs during a cycle. The width of the arrow indicates the amount of energy being earned, lost, or accumulated and varies according the local shading rate.

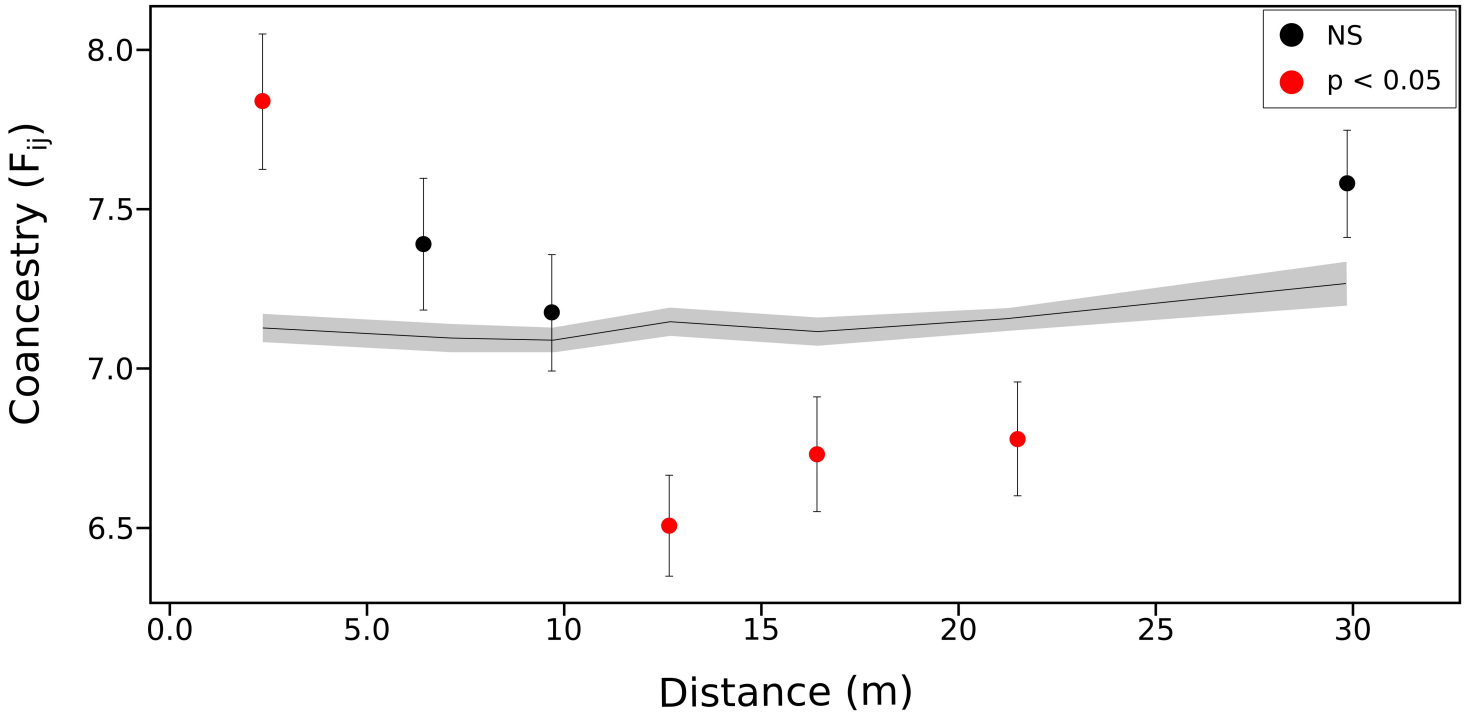

Figure 3. Correlogram from spatial autocorrelation analysis using the correlation coefficient F_{ij} (Loiselle et al. 1995) and seven distance classes. The grey area represents the 95% confidence intervals around the null hypothesis of absence of spatial genetic structuring (horizontal line), and black lines around mean F_{ij} values represent their 95% confidence intervals generated by jackknifing loci.

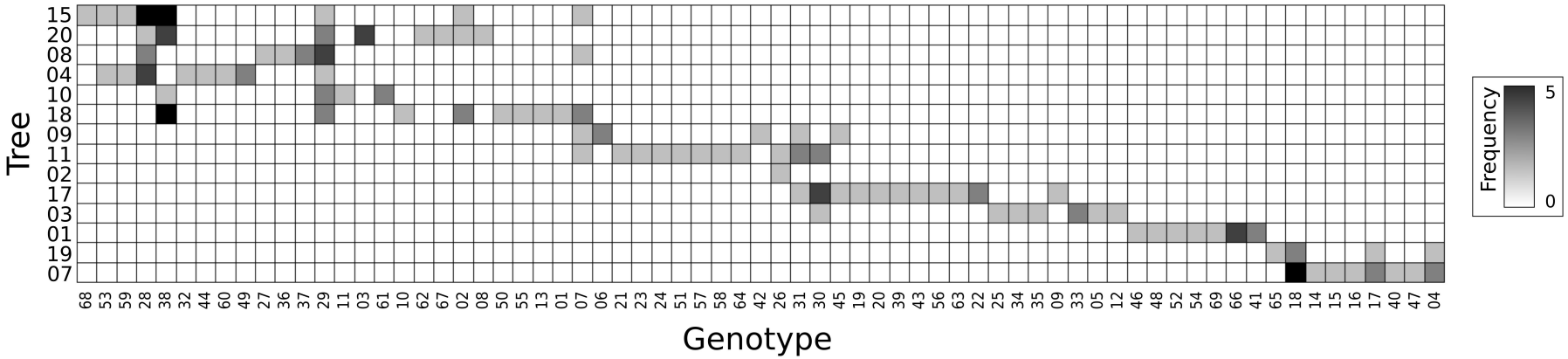

Figure 4. Adjacency matrix showing the occurrence of each genotype of T. recurvata (columns) on each sampled tree (rows). Grey gradient colors represent the frequency of each genotype per tree.

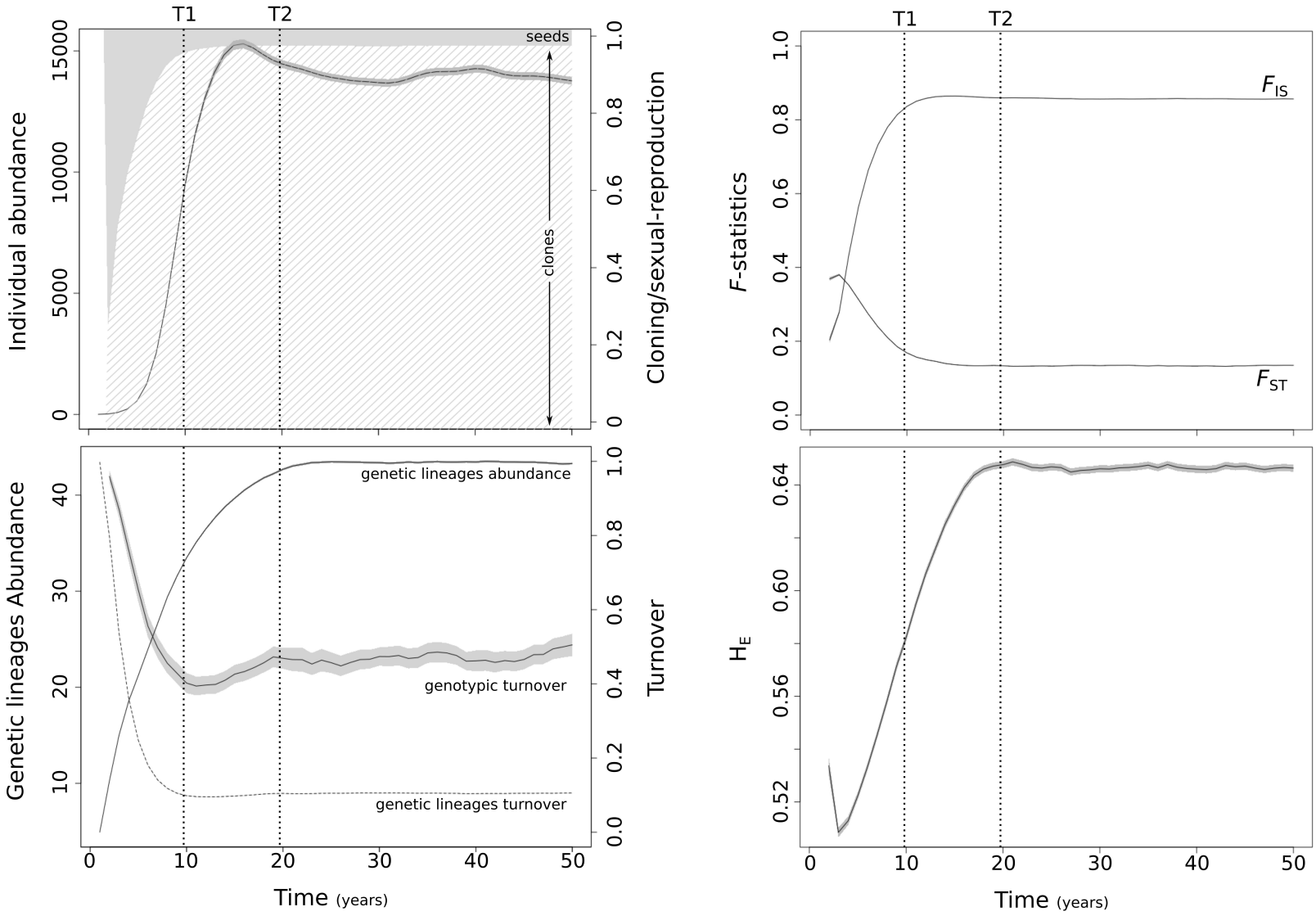

Figure 5. Temporal dynamic of T. recurvata metapopulation. The lines and grey areas around them represent average and 95 % confidence intervals of 10 thousand simulations. Periods of parameters stabilization are highlighted as T1 and T2. H_E = expected heterozygosity.

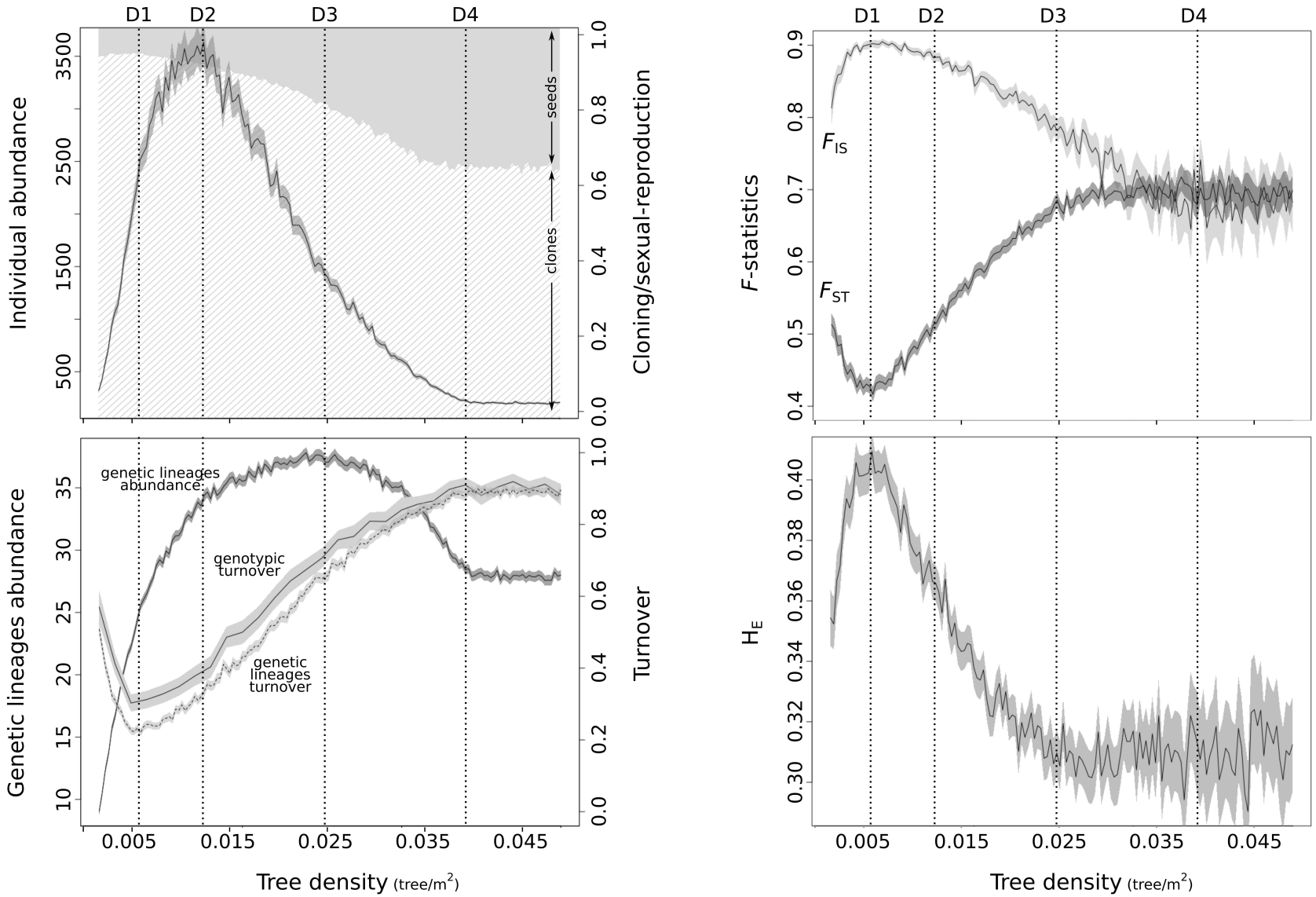

Figure 6. Tree density effect on T. recurvata metapopulation. The lines and grey area around them represent average and 95 % confidence intervals of 100 thousand simulations. Critical tree densities for parameters variation are highlighted as D1, D2, D3, and D4. H_E = expected heterozygosity.

APPENDIX A – ODD (overview, design concepts, details) of the IBM model of the establishment of a *Tillandsia recurvata* (L.) L. metapopulation

Purpose

This model simulates the colonization of a group of trees by distinct genetic lineages of one of the most common atmospheric bromeliads species, *Tillandsia recurvata* (L.) L.. This epiphytic bromeliad occurs in the American continent, from Argentina to the south of U.S.A. (Smith and Downs 1977; GBIF 2017), and is able to form populations of hundreds of individuals in trees and shrubs of native and anthropological transformed environments (e.g. Birge 1911; McWilliams 1992; Flores-Palacios et al., 2015). Despite its huge distribution, individuals of *T. recurvata* could produce just a few dozens of seeds in each reproductive season and many of them are sterile. In the other hand, the species has a rapid life cycle, cleistogamous flowers (i.e. doesn't need a partner to produce fertile seeds), wind dispersal seeds, and its genets are able to group dozens of ramets that stay linked together producing their own seeds at each reproductive season (Soltis et al. 1987; Smith et al. 1989; Orozco-Ibarrola et al. 2017; Chilpa-Galván et al. 2018).

With this model, we propose to reproduce the empirical results obtained with our empirical study, and transcend it forecasting the past and future of the *T. recurvata* metapopulation and the changes of this results in simulated landscapes with distinct tree densities. For us, the observed spatial genetic structure (SGS) in the real landscape is due to the higher probability of seeds be attached on the same tree where they were produced, forming populations with low genetic diversity. However, these results could have distinct outcomes in distinct colonization times and in landscapes with distinct tree densities (Fig. 1). At the very beginning of the *T. recurvata* spreading over a new landscape the SGS should be the strongest, but it reduces according the genetic lineages spread over the trees and become a single large population (Fig. 1A). The SGS could also changes under distinct tree densities. The overlap of tree crowns in areas with intermediate tree densities, for instance, could acts as a bridge for the seed capturing, but the massive overlap among these crowns, under high tree densities, could acts inversely, reducing the local wind speed and shading, which hamper the seed dispersal, increase the boundary layer and reduce the photosynthesis rate (Fig. 1B). Since *T. recurvata* is a drought adapted species (e.g. Benzing 2000; Benzing 2012), this environmental conditions could led to a reduction in its population and increase its mortality. Conversely, the seed capturing in areas with very low tree densities could also be hampered, since there are less obstacles for attachment of seeds, also increasing SGS (Fig. 1B). At the same time, all this SGS dynamic will also depend on: (i) the wind speed that carry the seeds of *T. recurvata*; (ii) the amount of seeds from the regional seed rain that reach the landscape at each year; (iii) the

germination rate of *T. recurvata* seeds; (iv) the probability of a tree capture dispersal seeds; (v) the mutation rate of *T. recurvata* microsatellites.

Entities, state variables, and scales

This model follows monthly the growth and spreading of a *T. recurvata* metapopulation on trees scattered in a two-dimensional landscape. The landscape area is comprised by multiples 0.01 m^2 patches of soil, and can be a representation of an empirical or simulated landscape. The empirical has trees with predefined sizes and positions (Table 1) scattered in the ~2,400 m^2 area where we performed the empirical study with *T. recurvata* populations. The simulated landscape has a squared area of ~3,500 m^2 with randomly distributed trees with previously specified sizes. Each tree in the landscape has its own size (in meters), which is divided in trunk height, crown height, and crown area. Individuals of *T. recurvata* are characterized by their age (in months), lifespan (in months), height of attaching on the host tree (in meters), origin ("seed" or "cloning"), location on the host tree ("canopy" or "trunk"), genotype (comprising two alleles of each of the seven SSR markers used in the empirical study), and energy (in units). Here, energy is based on a hypothetical energy budget which reflects the energy gains, by photosynthesis, and expenses, by metabolism and sexual and vegetative reproduction (Fig. 2).

Process overview and scheduling

Based on the scientific literature and personal observations on the life cycle of *T. recurvata*, the following list of processes is executed once per time step (i.e. monthly):

- **Update:** The model updates the age in months of all *T. recurvata* individuals and calculates their energy budget (Fig. 2). The energy budget includes algorithms that simulate the gains and expenses by photosynthesis and metabolism and take into account the shading rate, local space sharing, and individual age.
- **Reproductive season:** Every year (i.e. 12 time steps) the model adds new bromeliad seeds to the system. These seeds came from outside of the system (hereafter referred as 'regional seed rain') or from reproducing individuals already attached to trees of the system (hereafter referred as 'local seed rain'). The regional seed rain are, initially, the main source of genetic diversity for local populations, as each new introduced seed has a random distinct genotype where the heterozigozity of each locus follows the observed by Chaves et al. (2018). The genotypes of seeds from local seed rain, in their turn, are a combination of the mother gametes genotypes, which contributes to increase the abundance of local genetic lineages. Here, genetic lineages are referred as a group of individuals in which the common ancestor is the first individual that arrived from the regional seed rain. Nevertheless, locally produced seeds can also increase the genetic diversity of population, since they are subject to

mutations. Moreover, adult individuals could also reproduce vegetatively, producing new ramets that stay attached to them and have the same genotypes. To reproduce, vegetatively or through seed dispersal, bromeliads have to have enough energy at the reproductive season. This energy is achieved along the year and is balanced with the energy spent on metabolism. For this reason, it is reduced in locals under heavy competitions or strong tree crown overlapping (i.e. shading rate).

- **Seed movement:** Dispersal seeds move straightforward in a random direction, gradually reducing their height. They can be captured if they are on the same height and location of a tree trunk or crown. If, by chance, the seed be not captured by the canopy, its velocity reduces drastically, due to the weaker wind speed inside the canopy (Nathan et al. 2002). Seeds that reach to the ground or to the margins of the simulated landscape are excluded from the model.
- **Seed germination:** The model calculates the germination probability of seeds in the month after been captured by a tree trunk or crown. If not germinate, they are excluded from the model.
- **Mortality:** If a bromeliad reach their lifespan age or if their accumulated energy reaches to zero, it is also excluded from the model.

Design Concepts

- *Basic principles*

We assume that *Tillandsia recurvata* is a drought tolerant epiphytic species with a cleistogamous reproductive system, which have closed flowers that self-germinate to produce new seeds. Under this view, *T. recurvata* has 'closed lineages', where the genetic diversity in a population increases only by the arrival of new lineage seeds or by the mutation of local produced offspring.

- *Emergence*

The genetic structure of the simulated *T. recurvata* metapopulation emerges from the reproductive and seed dispersal processes, and from the parameters set on the setup procedure (i.e. wind speed, regional seed rain, seed capture probability, mutation rate, and tree density). It is measured with *a posteriori* analysis that use the genotypes of random sampled bromeliads composing the populations assembled during the simulations.

- *Sensing and interactions*

Since *T. recurvata* is not a parasite, trees are not able to sense them. However, to setup the landscape, new trees are established only on areas with no other tree trunks. In their turn, seeds and

adult individuals of *T. recurvata* are able to sense the presence of tree trunks and crowns, and how many crowns are shading them (i.e. shading rate). To be captured by a tree crown or trunk, dispersal seeds are able to sense them when they reach to the same patch as they. If seeds are not captured, their dispersal speed is largely reduced, due to the wind speed reduction inside the canopy. Adults sense how many tree crowns are shading them and where they are located in canopy (i.e. periphery), reducing the energy units they acquire each month. Their energy is also reduced according the number of neighboring bromeliads (due to a space competition).

- *Stochasticity*

If the landscape is set as simulated, the position of trees is chosen randomly from the unoccupied patches. Random is also from where the regional seeds came from, or to which direction each seed will disperse. If activated, disturbance events occur randomly once each five months, harming all bromeliads and reducing drastically their stored energy and, according its magnitude, causing their death.

- *Observation*

A 2D-display produced on NetLogo software allows for the monitoring of the *T. recurvata* metapopulation assembling on the simulated landscape. It shows a top view looking down on a landscape formed by trees, represented by green circular crowns with a trunk shown as a brown and smaller concentric circle. Each *T. recurvata* individual is represented by colorful points that move, when are dispersed seeds, or stay stagnant, when they are trapped by a tree trunk or crown and develop as an adult. Distinct colors for each individual indicate distinct genetic lineages. Despite displayed as a 2D-reproduction, all simulations have a '3D behavior', once it is assigned distinct heights of each tree trunk and crown. Therefore, each tree could be think as a disk shaped crown with a cylindrical trunk attached to its core. Moreover, despite the representation shows a 2D-movement, each dispersal seed also changes its altitude at each movement step.

Initialization and input data

The simulation can starts with (1) a representation of the empirical landscape; or with (2) a simulated landscape. In the first choice, 20 trees with specific heights of trunks and crowns are distributed over the area in specific positions (Table 1). In the second choice, the set number of trees are distributed randomly over the available area with a previously set average crown area and hosting no *T. recuvata* individuals. All simulations are run in a homogeneous environment, where, despite the chosen wind speed, only the number of trees and their crown overlaping affect the dispersal speed of seed dispersal.

Submodels

In the following, details of the main processes are presented.

1. **Update**

Every time step (i.e. simulated month), the age and energy of all bromeliads are updated. The age is updated adding a unit (i.e. a month), and the energy is updated according their energy budget that reduces the energy spent for metabolism from the energy produced through photosynthesis:

- Energy expense: the metabolism processes take a 0.3 or 0.5 unit of the accumulated energy of, respectively, adults (age > 12 months) and seedlings (age < 12 months). This difference is due to the greater energy spent by seedlings for their growth;
- Energy gain: the photosynthesis add a variable amount of energy, according the following function:

$$energy\ gain = (((2 - (1 - periphery)) / shading)\ compet) \quad (1)$$

where *periphery* is where in the tree crown the *T. recurcata* individual is located ($bromeliad_{altitude} / tree_{height}$), *shading* is the number of tree crowns that covers it, and *compet* is the number of other adult individuals in a radius of 15 cm.

2. **Reproductive season**

The reproductive season takes place every year (i.e. each 12 time steps), where new individuals of *T. recurvata* are added to the system from outside of the system (regional seed rain) of from other reproducing individuals in the system. All individuals with at least 10 units of energy reproduce up to twice during its lifespan, producing new seeds and new ramets. Therefore, both submodels always run together. After that, each reproducing individual loses two thirds of their original energy.

Regional seed rain

A previous set number of regional dispersed seeds are included in the simulation. Their alleles in each of the defined locus, are randomly chosen between the shortest and longest alleles found in the empiric study, in accordance with their motifs (dinucleotide or trinucleotide) and with the heterozygosity observed in the empirical study. The dispersal origin of these seeds could be previously defined as north, south, east, west, or random. Their starting height are randomly chosen from 1 meters to up to five meters more than the average height of trees in the simulated landscape. The color which can be observed in the 2D-display for each seed is chosen randomly and can be seen as a new genetic lineage entering in the simulated landscape. If they reproduce during the simulation, this color is inherited by their offspring.

The regional seed rain can also be increased every year along the simulation. The increment can be linear:

$$regionalseedrain = seeds + (seeds * year) \quad (2)$$

or exponential:

$$regionalseedrain = seeds + seeds^{\sqrt{year}} \quad (3)$$

where *seeds* is the previously set number of seeds in the seed rain. These increments tries to mimic an increase of external populations outside of the simulated landscape along the simulated period. The square root of year is used in equation 2 to reduce the computational time consumption required when the seed number is raised to the power of the year.

Seed production

The number of seeds that a reproducing individual produce is ten times their amount of energy. Each new produced seed starts to move from the same location where it was produced in a random direction. As *T. recurvata* is an cleistogamous species, each produced seed has a genotype that is a random recombination of the alleles of its mother. However, if the mutation option in the model is 'on', each allele of the new seeds genotypes can gain or lose repeat units by chance, simulating the process known as "DNA replication slippage" of microssatelites, in a rate that is also previously set in a range between 10^{-2} and 10^{-6}. Therefore, in this model, mutation is the single source of variation within genetic lineages. To track back their genetic lineages, each new seed has a flag indicating the ID of the first individual of its lineage that appeared in the simulation.

Cloning

During the reproductive seasons, the same bromeliads that produced seeds also reproduce vegetatively, producing as more ramets (hereafter referred as 'clones') as they have energy ($ramets_N = energy/5$). Half of the initial energy of the reproducing bromeliad is shared equally among all new ramet. The clones stay attached close to their mother and have the same genotype and genetic lineage as them.

3. **Dispersal seed movement**

move

T. recurvata seeds are only dispersed by the wind during the reproductive season (here delimited by a month at a year). Their movement is randomly divided into five 'steps', representing the distinct conditions they can face throughout the landscape. The wind speed is previously set by the user and is measured by a hypothetical metric that is related to the seed dispersal speed during

the reproductive season. This metric represents how many model patches (0.01 m^2) the seed moves at each step.

During a reproductive season, a dispersal seed moves straightforward, in a random chosen direction, loosing altitude by chance. The distance they can move at each movement step depends on their position, above or below the average height of tree crowns in the surrounding ~3 meters. If they are above this threshold, their horizontal movement is five times the set wind speed, and their altitude is reduced in 0.1 m at each step. However, if the seeds are below this threshold, the wind speed effect on their movement is decreased as the following function:

$$stepdistance = windspeed - (2 * shading - (0.1 * altitude)) \quad (4)$$

where, *shading* is the number of canopies that covers its model patch and *altitude* is where the dispersal seed is in the air, measuring from the ground. According to it, the number of trees crowns covering a space reduce the speed of seed dispersal, but this effect is cushioned by the seed's height inside the canopy. In other words, as high a seed is in the canopy, and less trees are in the landscape, greater is the effect of wind in its dispersal. Seeds below the canopy threshold, also decrease in altitude 0.5 m at each movement step.

If a seed reaches to a tree trunk, it will be captured by it, but, if it reaches a tree crown, the model calculates its capture probability. This probability is previously set in the model by the user (ranging from 0-100%) and it is multiplied to the number of tree crowns that cover the space. All seeds that reach the ground or the landscape margins, or that are not captured during the reproductive season, die before the next month.

4. **Seed germination and seedling survival**

From all seeds that enter in the simulated landscape or are produced in it, the model calculates the germination rate that is previously set by the user (from 0 to 100) and a 0.65 of seedling survival.

5. ***Mortality***

A bromeliad dies when its age reaches its lifespan limit of three years (i.e. 36 months) or when its energy is lower than zero. To reach to this energy value the energy gain of a bromeliad has to be lower than its expense. The energy of a bromeliad can be also reduced in a stochastic event, if it is activated in the model. If so, it can occur in a random month of each half time of the simulated period of 10 years. During these events all bromeliads are affected loosing 5-25 energy units, according its severity, which is also randomly set.

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TABLES AND FIGURES

Table 1. Coordinates and features measured on the trees of empirical landscape.

ID	Lat	Lon	Tree height	Trunk height	Longest spread	Longest perpendicular spread	DBH
1	-20.75595	-47.69973	9.79	1.0	5.5	5.0	21.0
2	-20.75593	-47.69970	5.34	1.8	4.0	3.5	7.5
3	-20.75590	-47.69967	8.01	1.8	6.5	6.0	15.2
4	-20.75587	-47.69963	10.68	1.6	6.5	5.5	18.5
5	-20.75582	-47.69965	8.90	1.6	5.1	5.0	17.7
6	-20.75585	-47.69958	8.90	2.8	6.0	4.0	13.1
7	-20.75578	-47.69952	5.34	1.7	4.5	4.0	15.2
8	-20.75583	-47.69947	9.79	2.0	8.0	5.0	25.5
9	-20.75580	-47.69945	9.79	1.6	5.5	5.5	19.0
10	-20.75572	-47.69943	10.68	1.8	7.0	6.0	18.5
11	-20.75572	-47.69947	9.26	1.6	6.0	4.5	21.0
12	-20.75568	-47.69948	9.79	1.7	7.0	5.5	19.6
13	-20.75563	-47.69947	9.79	1.0	5.1	4.0	23.9
14	-20.75558	-47.69948	10.68	3.0	7.0	6.5	20.2
15	-20.75567	-47.69950	10.68	1.6	7.0	5.0	25.8
16	-20.75572	-47.69952	9.79	2.4	7.0	6.0	16.7
17	-20.75577	-47.69957	10.68	3.4	6.0	5.5	19.9
18	-20.75577	-47.69960	8.90	1.8	5.1	5.0	19.5
19	-20.75572	-47.69960	7.12	3.6	5.5	5.0	18.0
20	-20.75578	-47.69968	10.68	4.5	5.6	5.1	18.0

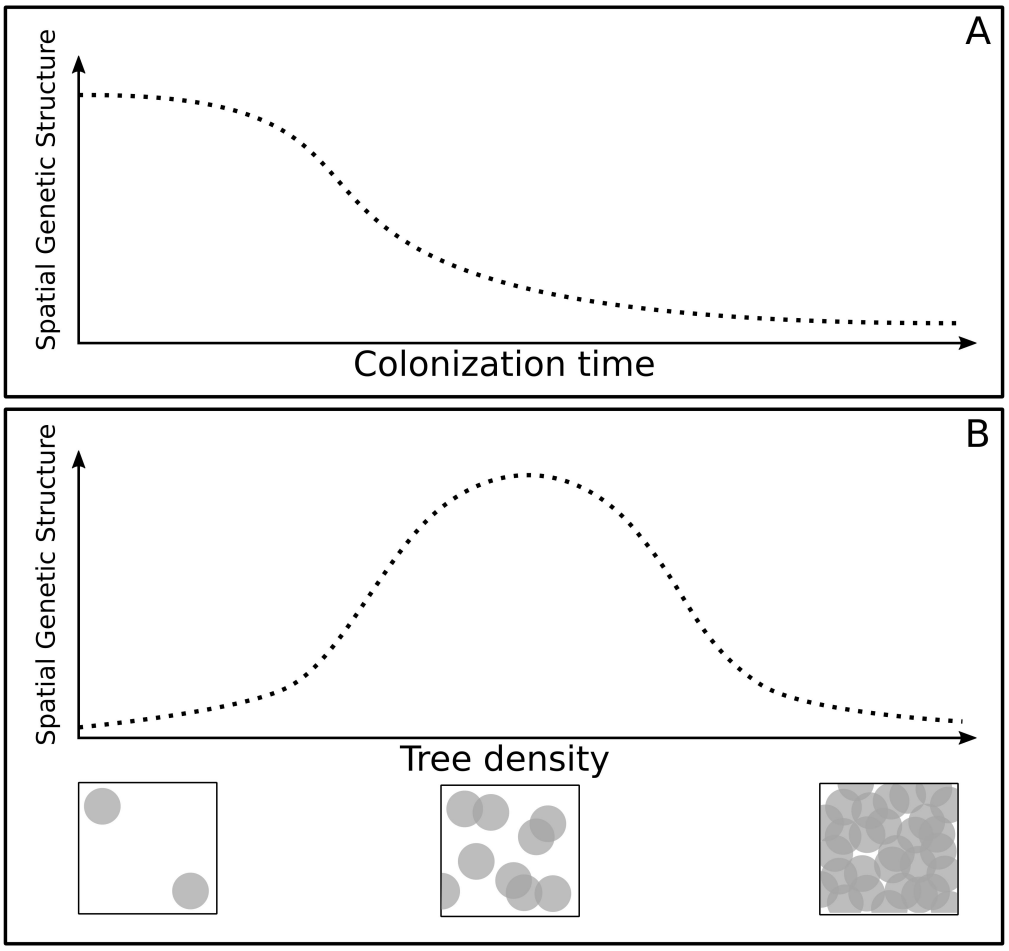

Figure 1. Schematic representation of the relationship of the spatial genetic structure of *Tillandsia recurvata* metapopulation with the colonization time of a landscape (A), and with the tree density o a landscape. The squares in B represent landscapes with distinct numbers of trees (gray circles) at a top view looking down.

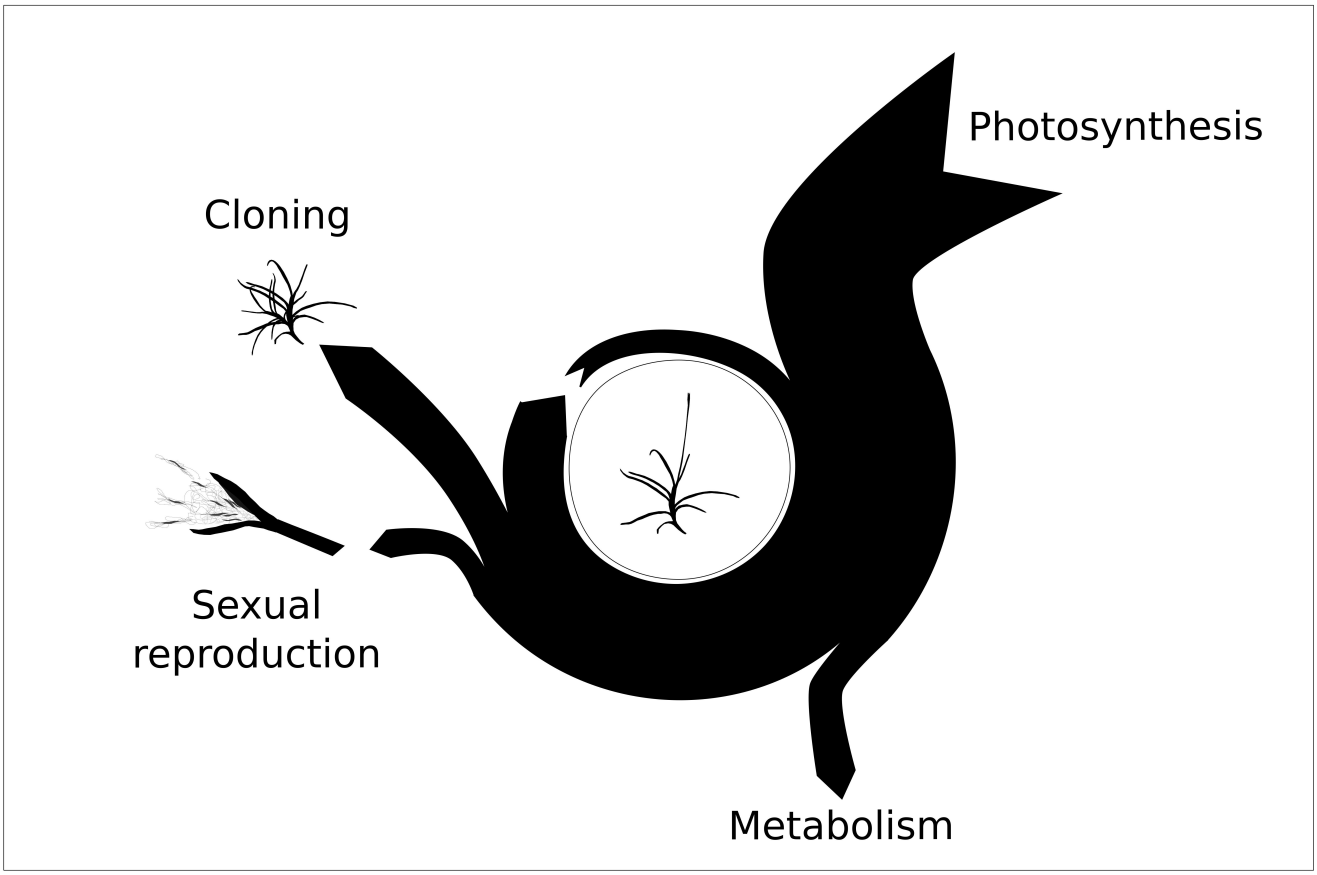

Figure 2. Representation of the energy budget of an individual of *T. recurvata*, in which all model is based. The arrow nocks and arrowheads represent, respectively, energy inputs and outputs during a cycle. The width of the arrow indicate the amount of energy being earned, lost, or accumulated and is variable according the local shading rate.

APPENDIX B – Supplementary material of "Spatio-temporal dynamics of an opportunist plant based on genetic structure variation: combining genetic approaches with individual-based modeling to investigate local spread of *Tillandsia recurvata* (Bromeliaceae)"

Table S1. Correlation coefficients between estimated and true parameter values of pseudo-data in the cross-validation. In bold are the greatest correlation coefficients for each parameter used in time and density simulations of the IBM model (Table 1).

value	regional seed rain	wind speed	mutation rate	germination rate	capture probability
median	**0.495**	0.670	**0.370**	0.221	0.124
mean	0.359	0.692	0.266	**0.356**	**0.160**
mode	0.430	**0.723**	0.319	0.289	0.143

Table S2. Range and differences between prior and posterior distributions of parameters' values. The values of each parameter were scaled according to their final accepted values (see Table 1).

Parameter	prior	posterior	difference
Regional seed rain	2.353	1.841	0.512
Wind speed	1.281	0.610	0.671
Mutation rate	1.653	1.599	0.054
Germination rate	1.205	0.719	0.486
Capture probability	1.394	0.918	0.476

Table S3. Correlation among IBM parameters for the retained simulations. Correlation coefficients are shown in the upper triangle and their p-value are shown in the lower triangle of the matrix.

	Regional seed rain	Wind speed	Mutation rate	Germination rate	Capture probability
Regional seed rain	1.000	0.162	0.025	0.099	-0.430
Wind speed	0.000	1.000	-0.018	-0.069	0.034
Mutation rate	0.316	0.480	1.000	0.020	0.053
Germination rate	0.000	0.006	0.948	1.000	-0.262
Capture probability	0.000	0.172	0.172	0.000	1.000

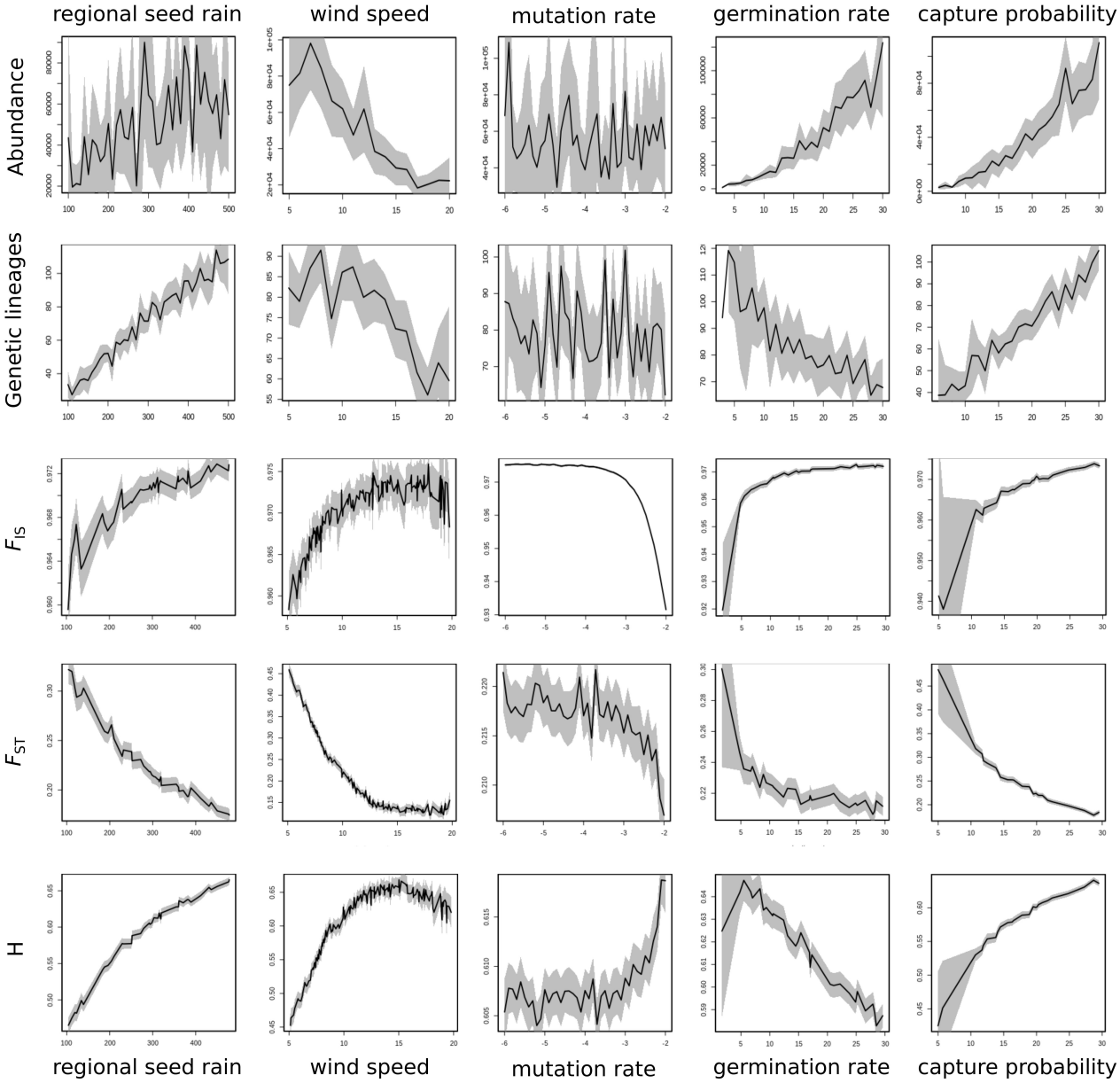

Figure S1. Sensitivity analysis of the IBM model. X-axes represent the parameters' variation; Y-axes represent the summary statistics, as well as *T. recurvata* abundance and total number of genetic lineages. F_{IS}: mean inbreeding coefficient; F_{ST}: mean population differentiation; H: mean expected heterozygosity.

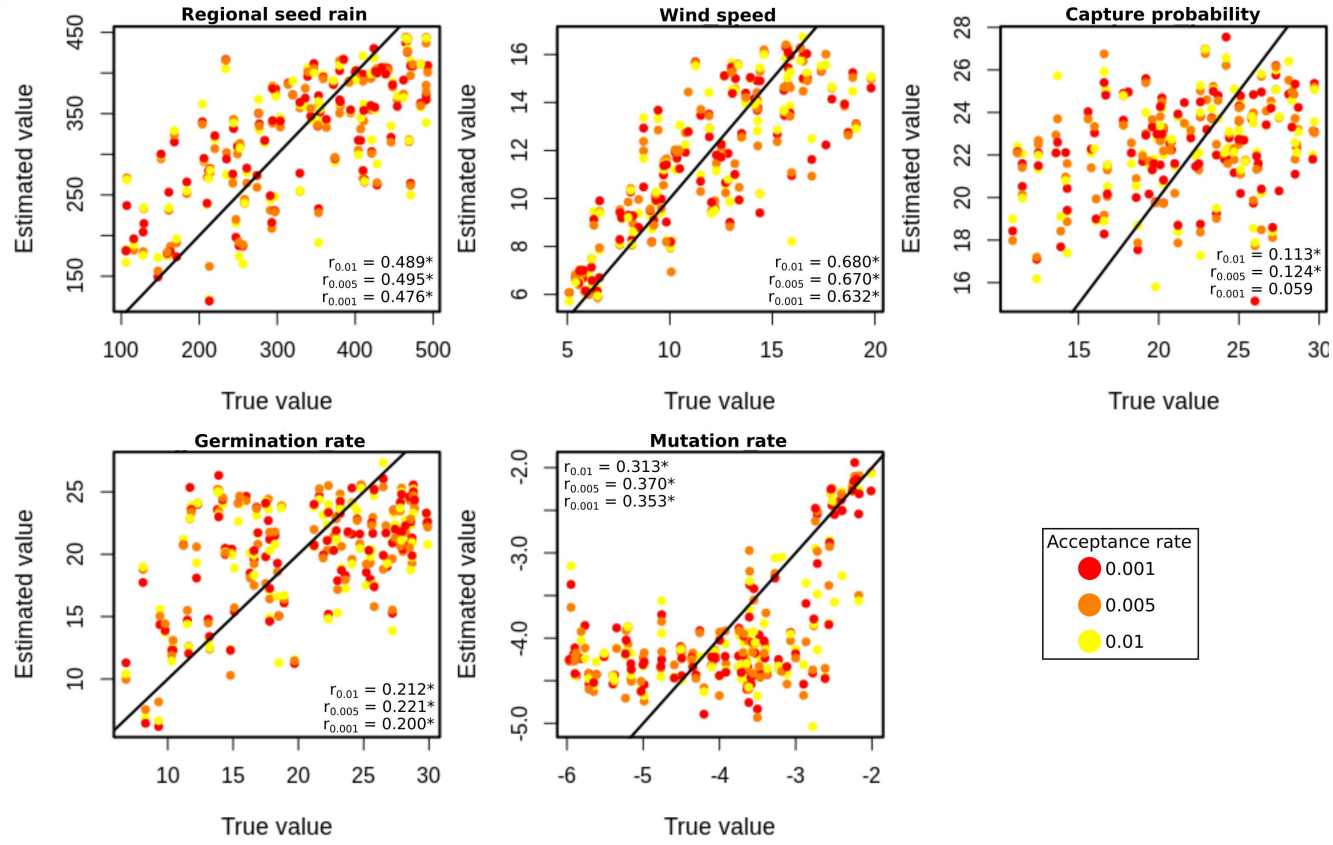

Figure S2. Cross-validation for parameter estimation. Parameter values estimated by ABC in relation to true values for each of the five IBM parameters. Correlation coefficients r are shown at each panel for each acceptance rate.

CONSIDERAÇÕES FINAIS

Concluímos, ao longo dos quatro capítulos que compõem essa tese, que a estruturação de metacomunidades epífitas dominadas por bromélias atmosféricas depende do grau de heterogeneidade e conectividade entre suas comunidades locais. Especificamente, a formação desses sistemas está relacionada à combinação dos diferentes atributos arbóreos locais que compõem o dossel e à densidade arbórea regional. Observamos que:

(I) a interação de múltiplos atributos arbóreos pode gerar diferentes microclimas no interior dos dosséis e atuar como um importante fator ambiental na montagem de comunidades locais. Mas diferentes combinações de atributos arbóreos podem resultar em diferentes abundâncias e distribuições de bromélias atmosféricas nas árvores hospedeiras;

(II) diferentes combinações de atributos arbóreos afetam diferentemente a morfofisiologia (e o fitness) de bromélias atmosféricas, influenciando sua distribuição no dossel, sua seleção de hospedeiro, sua abundância e sua composição funcional e de espécies na metacomunidade. Mas, a limitação ou incremento da dispersão de suas sementes pelo vento (efeito de massa), resultante de diferentes densidades arbóreas regionais, pode reduzir a contribuição relativa dos atributos arbóreos na formação das metacomunidades;

(III) espécies de bromélias atmosféricas com grande sobreposições de nichos apresentam interações locais complexas entre si, mas a coexistência entre elas também dependerá do grau de conectividade entre as comunidades locais. Em ambientes com dispersão limitada, a interação local será reduzida e não refletirá na coexistência global entre as espécies. Em ambientes com uma dispersão maciça, enquanto o efeito de interações positivas é refletido na coexistência global entre elas, o efeito de interações negativas é sobrepujado pelo efeito de massa entre as comunidades locais;

(IV) a auto fecundação espontânea e crescimento clonal de muitas bromélias atmosféricas, como *Tillandsia recurvata*, podem acelerar a colonização de novos ambientes e que um rápido e eficiente ciclo de vida contribui para reduzir o efeito da endogamia, alta estruturação e baixa diversidade genética oriundos desses tipos de reprodução. Além disso, baixas densidades arbóreas podem reduzir a estruturação de populações de bromélias atmosféricas e contribuir para o seu rápido espalhamento em novas paisagens.

Os resultados gerados nesta tese demonstram que comunidades de bromélias atmosféricas possuem um grande potencial para o estudo de metacomunidades devido ao fácil acesso a múltiplas comunidades locais (próximos ou dentro de centros urbanos). A grande abundância de indivíduos em cada comunidade, apesar da baixa diversidade de espécies, também é um facilitador, pois reduz o efeito de muitas espécies raras que são de difícil localização e triagem. Além disso, a biologia reprodutiva e a rápida colonização de novos ambientes por muitas bromélias atmosféricas

demonstra que esses sistemas podem ser utilizados como modelo para o estudo da dinâmica de espalhamento de espécies oportunistas. De fato, observamos ao longo dos quatro capítulos dessa tese que o rápido espalhamento de bromélias atmosféricas pode ser estimulado por interações positivas entre elas e, principalmente, pela redução da densidade arbórea (i.e. deflorestamento), que (i) seleciona árvores com maiores capacidades hospedeiras; (ii) aumenta a velocidade do vento entre as árvores, aumentando o fluxo e as distâncias de dispersão entre comunidades locais e reduzindo a estruturação genética entre populações; e (iii) reduz o efeito de interações locais negativas. Ressalta-se que o espalhamento de bromélias atmosféricas, ao contrário de muitas outras epífitas vasculares, é de fato beneficiada por ações antrópicas indiretas, como o deflorestamento, e ações diretas como transplantes entre árvores, construção de componentes abióticos que possivelmente atuam como conectores entre comunidades (e.g. postes e fios de eletricidade), ou até mesmo pelo uso como objetos decorativos. Novos estudos poderiam, portanto, explicar as diferenças ecológicas existentes entre diferentes grupos de epífitas e elucidar as diferenças de distribuição e abundância existentes entre espécies de bromélias atmosféricas.