UNIVERSIDADE FEDERAL DE ALFENAS
UNIFAL- MG

JOÃO PEDRO COSTA ELIAS

INFLUÊNCIA DAS VARIÁVEIS DO FORÓFITO E FONTE DE SEMENTE NA OCORRÊNCIA DE EPÍFITAS EM MATRIZ DE PASTAGEM

ALFENAS/MG
2018

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Dissertação apresentada como parte dos requisitos para obtenção do título de Mestre em Ciências Ambientais pela Universidade Federal de Alfenas. Área de concentração: Diversidade Biológica e Conservação

Orientador: Dr. Flavio Nunes Ramos
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ALFENAS/MG

2018

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JOÃO PEDRO COSTA ELIAS

“Influência das variáveis morfométricas do forófito no estabelecimento de epífitas em matriz de pasto”

A Banca julgadora, abaixo assinada, aprova a Dissertação apresentada como parte dos requisitos para a obtenção do título de Mestre em Ciências Ambientais pela Universidade Federal de Alfenas. Área de Concentração: Ciências Ambientais.

Aprovado em: 15 de fevereiro de 2018.

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Dedico aos meus familiares e à Melissa, meus principais alicerces e portos seguros.

AGRADECIMENTOS

Agradeço aos amigos Renan, Mona e Natália pelo grande apoio em coletas de campo, discussões, e principalmente pelos momentos fora da “selva acadêmica”.

Aos amigos Valdeci, Hugo, Magda e Anézio pelas conversar nos corredores, pelas horas de lazer extra-faculdade e pela amizade para a vida toda.

Ao pessoal da graduação pelas ajudas nos campos (desculpa, eu juro que ainda pagarei o açaí!), e ao pessoal da química Welton, Patrícia, Letícia, Tati, Professoras Marisi e Dani pelas contribuições e amizade.

Ao Prof. Flavio, que ao longo de seis anos me ensinou o que é ciência, o que é ser uma pessoa ética e consciente, e com certeza será uma memória associada à saudade. Que a Força esteja com você!

Ao Dr. Maurício, Prof. Dr. Eduardo van den Berg e Prof. Dr. André Felippe Nunes de Freitas pelas contribuições no artigo e pela disponibilidade.

Ao Ecofrag/Ecoveg pelas discussões e oportunidades de amadurecimento intelectual.

Aos profissionais que nos ajudaram com as identificações de nossas queridas epífitas.

Às colegas Carol e Tamires pela ajuda nos primeiros passos desta caminhada.

À secretaria Denise por toda sua disponibilidade e boa vontade em ajudar os mestrandos perdidos.

Aos meus pais João e Rita, e à minha mãe Celi, por possibilitarem minha existência e crescimento. Sem vocês, não seria possível nem aqui estar.

Aos meus irmãos Nino, Valéria, Marina, Graciele, Helena e Kemily por estarem presente em toda minha vida, e meus cunhados Clayton, Fernando e Fernanda por fazerem da minha família uma família ainda mais incrível!

À Melissa, minha companheira de ontem, hoje e sempre, por toda paciência com meus devaneios, por todo suporte, por estar do meu lado nos momentos felizes, e principalmente nos difíceis. Eu te amo!

A todas as outras pessoas que de alguma forma cruzaram meu caminho, e ajudaram a moldar quem sou hoje.

À Universidade Federal de Alfenas, pelo ensino público, gratuito e de qualidade, e à CAPES pelo financiamento da pesquisa.

Sinto-me grato a cada um de vocês!

Faça. Ou não faça. Não existe a tentativa.

(Mestre Yoda)

RESUMO

A diversidade de plantas é conhecida pela ampla variedade de estratégias e formas de vida. Entre estas formas, o epifitismo, representado pelas epífitas, refere-se às plantas que utilizam como suporte e substrato outras árvores e arbustos, estes denominados forófitos. A presença de epífitas não exerce nenhum prejuízo fisiológico ou morfológico ao forófito, sendo esta relação descrita como comensalismo, porém em casos esporádicos a ocupação desenfreada de epífitas pode tornar a relação desvantajosa aos forófitos. As epífitas podem ser divididas em grupos: holoepífitas, ou "epífitas verdadeiras", que nunca fixam raízes no solo; hemiepífitas que em algum estágio de desenvolvimento fixará suas raízes no solo; facultativas, que podem ocorrer em outros substratos, como rochas e solo; e acidentais ou casuais, as quais apresentam hábito epifítico em casos isolados. Por depender de fatores internos e externos em conjunto, a ocorrência destas plantas é limitada (i) às suas características e necessidades, (ii) às características dos forófitos, e (iii) ao local de ocorrência. As espécies de epífitas podem apresentar um conjunto de características que permitam ampla ou restrita ocorrência em diversos *habitats*. Estratégias fisiológicas (fotossíntese CAM, tecido de armazenamento de água), reprodutivas (autocompatibilidade, reprodução clonal), e ecológicas (interações generalistas com polinizadores e dispersores) podem garantir maior diversidade de *habitats* ocupáveis, e eventualmente status de dominância em ambientes perturbados, enquanto determinadas características e demandas podem restringem possíveis ocupações de *habitats*. Em conjunto às características das epífitas, a morfologia e fisiologia dos forófitos também são importantes fatores de influência. Uma mesma característica, como rugosidade da casca, é descrita em relações positivas, negativas e neutras, variando em função da composição e características das epífitas, e também em função do ambiente. O ambiente, por sua vez, pode exercer limitações a partir dos filtros ambientais, selecionando espécies segundo um conjunto de fatores ambientais, como também pode atuar na limitação à dispersão de propágulos. Desta forma, o ambiente de ocorrência pode facilitar a chegada de novos propágulos, e estabelecimento de plântulas, como também pode atuar limitando a chegada e colonização de determinadas espécies de epífitas.

Palavras-chave: diversidade biológica, ecologia de comunidades, facilitação, interações ecológicas.

ABSTRACT

The plant diversity is known for the wide variety of life strategies and lifeforms. Among these lifeforms, the epiphytism, represented for epiphytes, refers to plants that use other trees and shrubs as support and substrate, these called phorophytes. The epiphyte presence does not cause anyone physiological or morphological prejudice, being that relationship a commensalism relation, but in sporadic cases, the unlimited epiphyte ocupation could be disadvantageous to phorophyte. The epiphytes species could be separated into groupings: holoepiphytes, or "true epiphytes", what never set roots in soil; hemiepiphytes, what in some development stage will set root in soil; accidental or casual, which have epiphyte habit in isolated cases; and facultative, what could occur in another substrate. For together internal e external factors dependence, the epiphyte occurrence is limited by (i) epiphytes characteristics and dependencies, (ii) phorophytes traits, and (iii) local of occurrence. The epiphytes species could have a characteristic set what allow or restrict occurrence in wide habitat variety. Physiological strategies (CAM photosynthesis, water storage tissues), reproductive (self-compatibility, clonal reproduction) and ecological (generalist interaction with pollination and dispersers) could enable greater occupiable habitats diversity, and eventually dominant status in perturbated habitats, while some characteristics and demands could restrict possible habitats occupation. Together with the epiphyte characteristics, the phorophytes morphology, and physiology, are important factors of influence. The same characteristic, as the bark rugosity, is described in positive, negative and neutral relationships, varying in function of species composition and epiphyte characteristics, and environmental influence too. The environment can exercise limitation by the environmental filters, selecting species according to epiphytes characteristics, and can limit the propagule dispersion. In this way, the occurrence environment can facilitate the propagule arrive, and seedling establishment, and may also represent in others cases colonization limitations of specifics epiphytes species.

Key-words: biological diversity, community ecology, ecological interactions, facilitation.

SUMÁRIO

REVISÃO BIBLIOGRÁFICA

A relação de comensalismo entre epífitas e forófitos tem sido abordada em estudos recentes com o objetivo de evidenciar quais fatores a influenciam. As plantas epifíticas recebem diferentes classificações, segundo sua forma de vida, e cada forma de vida pode apresentar um conjunto específico de fatores de influência na sua relação com os forófitos. Assim, as epífitas podem ser denominadas holoepífitas ou "epífitas verdadeiras", quando não apresentam contato com o solo em nenhum momento de seu desenvolvimento e crescimento. Já as hemiepífitas são epífitas que em algum estágio de crescimento possuem raízes fixas ao solo. Outro grupo pode ser considerado como epífitas acidentais, pois são espécies que não possuem o hábito epifítico, mas podem acidentalmente ocorrer sobre outra planta; epífitas casuais ou facultativas, que além de crescer em outros substratos, como solo e/ou rochas, podem ocorrer sobre outras plantas. Os grupos mais abundantes de epífitas são as holoepífitas e hemiepífitas, distribuídos em ampla diversidade de biomas e *habitats*, e sendo os mais frequentemente abordados em pesquisas da relação epífita/forófito (ZOTZ, GERHARD; HIETZ, 2001).

A ocorrência de epífitas é diretamente influenciada por uma ampla gama de fatores. Apesar dos fatores intrínsecos às epífitas (p.ex., exigências fisiológicas), as características dos forófitos também podem facilitar ou dificultar a ocorrência de epífitas, além da ampla influência do ambiente de ocorrência. Podemos dividir esse conjunto de fatores em três grandes grupos de características de influência, sendo: (a) características do forófito, ou seja, da planta utilizada como hospedeira; (b) características intrínsecas das epífitas; e (c) e dependência da fonte de propágulo. Nesta revisão serão abordados aspectos das três abordagens pertinentes ao presente trabalho, visando entender como ocorre a manutenção das comunidades de epífitas em ambientes abertos, como a pastagem aqui utilizada como área de estudo.

1.1 Características intrínsecas das epífitas

Assim como para o restante dos organismos, epífitas possuem características específicas, apresentando um amplo repertório de histórias de vida e nichos, amplamente diversificados entre famílias, subfamílias e gêneros (WOLF; GRADSTEIN; NADKARNI, 2009). Essas características também exercem influência na ocorrência de epífitas nos forófitos, podendo ser determinantes, ou até mesmo o único fator de interferência na ocorrência. Dominância e síndromes de dispersão podem ser destacadas como características das epífitas determinantes para sua ocorrência ou não em determinado local (IZUDDIN; WEBB, 2015).

A dominância de uma espécie se dá principalmente pelo favorecimento de sua ocorrência por determinada(s) característica(s) do ambiente, pela sua alta capacidade reprodutiva e/ou pela sua alta capacidade de dispersão (HOLL, 1999; TOLEDO; NASCIMENTO; ZARTMAN, 2016). Como exemplo do favorecimento por características do ambiente, temos os ambientes abertos, como pastagem. Nestes ambientes a incidência de ventos e radiação solar é maior, enquanto a disponibilidade de água se torna restrita, o que altera o microclima e consequentemente os fatores bióticos (HOLL, 1999). Sendo assim, serão favorecidas as espécies que conseguem aumentar seu crescimento e desenvolvimento sob maior disponibilidade de luz, dispersas pelo vento, e com baixa demanda por água (HOLL, 1999; MARCANO-VEGA *et al.*, 2014; VICTORIANO-ROMERO *et al.*, 2017). Sob maior incidência solar, algumas espécies, predominantemente generalistas, conseguem estabelecer e realizar reprodução assexuada através de clonagem, provavelmente alcançarão o estágio reprodutivo mais rapidamente, aumentando sua taxa reprodutiva, e conseguindo maior abundância em relação às demais espécies (OROZCO-IBARROLA *et al.*, 2015; SRITONGCHUAY *et al.*, 2014). Dentre estas espécies favorecidas reprodutivamente, aquelas com maiores chances de se tornarem dominantes são as que têm maiores capacidades de dispersão e colonização, sendo que no caso de ambiente aberto serão aquelas espécies dispersas pelo vento (PINA-RODRIGUES; AOKI, 2014). Sendo assim, os filtros ambientais se tornam importantes modeladores da ocorrência das espécies, influenciando na relação de dominância dentro da comunidade (WAGNER; MENDIETA-LEIVA; ZOTZ, 2015).

Os mecanismos e vetores utilizados para dispersão estão entre as principais variáveis limitantes à ocorrência de plantas. Estes mecanismos são amplamente diversos em epífitas, o que causa uma ampla variação nos fatores de influência (SILVA; RODAL, 2009). As principais fontes de dispersão de epífitas são o vento e animais, anemocoria e zoocoria, respectivamente. Cada uma destas síndromes de dispersão depende de fatores completamente distintos. Para dispersão anemocórica, a presença de correntes de vento, mais abundantes em ambientes abertos, favorece a dispersão nestes ambientes até distâncias maiores (HOLL, 1999; RUIZ-CORDOVA; TOLEDO-HERNÁNDEZ; FLORES-PALACIOS, 2014). Neste caso, espera-se que epífitas anemocóricas possuam ampla distribuição em ambientes abertos, como pastagens, e dispersão em distâncias mais restritas em ambientes fechados, como florestas (PINA-RODRIGUES; AOKI, 2014; VICTORIANO-ROMERO *et al.*, 2017). Por outro lado, a dispersão zoocórica é moldada principalmente por fatores associados ao animal dispersor, variando fortemente em função das especificidades dos vetores (GRAHAM, 2001). Epífitas e vetores especialistas tendem a apresentar ocorrência restrita a *habitats* específicos, normalmente conservados e com baixo grau de perturbação (DONDINA *et al.*, 2017). Por sua vez, epífitas generalistas podem ocorrer em uma diversidade de *habitats*, e possuir maior variedade de vetores, independente das características abióticas ou grau de perturbação (EINZMANN; ZOTZ, 2016).

1.2 Influência das características do forófito

A presença das epífitas não causa prejuízo fisiológico ao forófito, o que torna esta relação um comensalismo (SÁYAGO *et al.*, 2013), embora casos raros tenham encontrado diminuição na taxa fotossintética dos forófitos quando epífitas saturam a área disponível em suas copas (BENZING, 1979; MONTAÑA; DIRZO; FLORES, 1997). As epífitas, como qualquer outra forma de vida, demanda um conjunto de variáveis para seu estabelecimento, sobrevivência e desenvolvimento. Como seu crescimento ocorre sobre outra planta, sua ocorrência está diretamente ligada às características da planta hospedeira: o forófito (ZOTZ, GERHARD; HIETZ, 2001). De acordo com características morfofisiológicas do forófito, ou seja, sua morfologia e características fisiológicas, a epífita pode alcançar um desenvolvimento ótimo, ou ter dificuldades para desenvolver, podendo até mesmo não conseguir sobreviver (e.g. WOLF, 2005).

As características morfológicas dos forófitos podem facilitar ou dificultar a ocorrência de determinadas espécies de epífitas. Uma mesma variável do forófito, como diâmetro do tronco, pode favorecer uma determinada espécie (FREIBERG, 2015), dificultar a ocorrência de outra (KIEBACHER *et al.*, 2017), ou não apresentar nenhuma interferência sobre uma terceira (DISLICH; MANTOVANI, 2016). Esta variação ocorre principalmente em função da ampla gama de estratégias de vida epifíticas, variando intra e inter famílias e subfamílias

(WOLF; GRADSTEIN; NADKARNI, 2009). Pela alta complexidade das relações entre forófitos e epífitas, acrescidas às diversas influências do ambiente, tornam-se necessários os estudos de assembléias em diferentes *habitats* (IZUDDIN; WEBB, 2015). Desta forma, podemos encontrar as mesmas características da árvore em relações positivas, neutras ou negativas com a ocorrência de epífitas, variando entre *habitats* e/ou diferentes espécies (SÁNCHEZ; ARMENTERAS; RETANA, 2016). Por exemplo, a influência da densidade de folhagem da copa varia entre ambientes. Em ambientes florestais, altas densidades de folha na copa podem aumentar a complexidade da estrutura de redes de interação epífita/forófito, uma vez que as espécies florestais, sensíveis às altas radiações solares, ficariam protegidas, e com melhores condições para desenvolvimento (SÁYAGO *et al.*, 2013). Por outro lado, nas pastagens, ambiente com grande incidência solar e espécies adaptadas a essa condição, altas densidades de folhagem na copa podem representar um efeito negativo na riqueza de epífitas (POLTZ, 2011).

A influência da altura total da árvore hospedeira tem sido amplamente descrita na ocorrência de epífitas, tendo casos principalmente com influência positiva ou neutra. Em alguns casos a altura da árvore apresenta relação positiva, indicando que riqueza e abundância aumentam com o tamanho da árvore (FLORES-PALACIOS; GARCÍA-FRANCO, 2006; SÁYAGO *et al.*, 2013). Esta relação positiva pode ser resultado principalmente da tendência de árvores maiores oferecerem maior variação de características ambientais, como temperatura e luminosidade, o que poderia disponibilizar maior variedade de *habitats*, e possíveis maiores diversidades de epífitas (DISLICH; MANTOVANI, 2016). A complexidade dos habitats pode ser decorrente do fato de que luminosidade e umidade relativa do ar, fatores limitantes do crescimento de epífitas, variam verticalmente no dossel (ROSA-MANZANO *et al.*, 2014). Assim sendo, uma árvore maior pode conter gradiente vertical de tais fatores, formando ampla gama de pequenos microclimas e *microhabitats* (RUIZ-CORDOVA; TOLEDO-HERNÁNDEZ; FLORES-PALACIOS, 2014). Porém, para algumas espécies de epífitas e/ou presentes em diferentes ambientes, a altura da árvore pode apresentar relação neutra. Algumas espécies de epífitas podem estar associadas a outras características das árvores, como deciduidade do forófito (ROSA-MANZANO *et al.*, 2014), ou distância da fonte de propágulo (DISLICH; MANTOVANI, 2016), e não serem influenciadas pela altura da árvore. Outra possibilidade é que árvores maiores poderiam oferecer maior diversidade de *habitats* para as epífitas, o que favoreceria maiores diversidades de epífitas, porém a variação vertical das características abióticas não resulta em diferenciação de *microhabitat*, o que tornaria a altura um fator neutro (ROSA-MANZANO *et al.*, 2014).

A complexidade de *microhabitat* em função da variação das características ambientais, favoráveis a maiores diversidades, pode ser resultado de outras características, além da altura da árvore. A altura do fuste também pode ser responsável por aumentar a complexidade de *habitats*, e, possivelmente, a ocorrência de epífitas (IZUDDIN; WEBB, 2015). Fustes baixos podem tornar a copa maior e mais aberta, o que na maioria das vezes resulta em maior disponibilidade de *microhabitat* (WOODS; CARDELÚS; DEWALT, 2015). A ramificação principal pode disponibilizar bases propícias à deposição de diásporos e agentes dispersores, favorecendo a dispersão e o estabelecimento de plântulas, independente de sua altura (IZUDDIN; WEBB, 2015; RUIZ-CORDOVA; TOLEDO-HERNÁNDEZ; FLORES-PALACIOS, 2014). Fustes mais complexos são favoráveis ao acúmulo de água, nutrientes lixiviados do tronco, e matéria orgânica em decomposição (IZUDDIN; WEBB, 2015). Como diversas espécies de epífitas não estabelecem contato com o solo (OSTER *et al.*, 2009), as principais fontes de água e nutrientes para estas são oriundas do forófito, como folhas caducas e lixiviação do tronco, e da atmosfera, como partículas dispersas no ar (IZUDDIN; WEBB, 2015). Ambas as fontes de nutrientes podem ser acumuladas nos vértices das ramificações, o que contribui para o crescimento e desenvolvimento das epífitas nestas áreas (ZOTZ; HIETZ; SCHMIDT, 2001). Assim como na altura, o fuste baixo pode não exercer relação com ocorrência de epífitas, ou até desempenhar uma relação negativa. Fustes baixos podem impedir a ocorrência de epífitas que demandam alta radiação solar em locais com formação de dossel, uma vez que a luz tende a ser pouco abundante em regiões inferiores dos dosséis (RUIZ-CORDOVA; TOLEDO-HERNÁNDEZ; FLORES-PALACIOS, 2014).

O diâmetro do tronco pode influenciar na ocorrência de epífitas por disponibilizar maior diversidade e quantidade de *habitat* disponíveis (FLORES-PALACIOS; GARCÍA-FRANCO, 2006). Também relacionado às características do tronco têm-se os tipos de casca e rugosidade, que influenciam a capacidade de colonização e estabelecimento das epífitas. Algumas árvores apresentam descamação do ritidoma (esfoliação), o que dificulta o estabelecimento de epífitas, uma vez que a casca perdida poderia estar fornecendo suporte para alguma epífita, e sua queda também representar a queda da epífita (BOELTER *et al.*, 2014a). Além do tipo de casca, a rugosidade desta pode influenciar a diversidade de epífitas (POLTZ, 2011; VERGARA-TORRES; PACHECO-ÁLVAREZ; FLORES-PALACIOS, 2010). Quanto mais rugosa a casca, maior o fornecimento de suporte mecânico para deposição e germinação de propágulos, fixação de raízes e consequente estabelecimento de plântulas, aumentando as chances de ocorrência e crescimento das epífitas (CHAVES; DYONISIO; ROSSATTO, 2016; SÁYAGO *et al.*, 2013). A casca mais rugosa também pode ser maior fonte de nutrientes para as epífitas, a partir da lixiviação, e um maior reservatório de água e umidade, pois possui maior capacidade de absorção e retenção de água (BOELTER *et al.*, 2014b; MEHLTRETER; FLORES-PALACIOS; GARCÍA-FRANCO, 2005). Por outro lado, a lixiviação de substâncias químicas da casca pode ser um fator negativo para epífitas, caso sejam liberadas substâncias inibitórias de germinação e/ou de desenvolvimento (BOELTER *et al.*, 2014b).

A complexidade de *habitats* de uma árvore, e sua eventual diferenciação em regiões (tronco e copa), pode possibilitar a ocorrência de maior diversidade de epífitas, principalmente pela demandas fisiológicas de diferentes epífitas (RUIZ-CORDOVA; TOLEDO-HERNÁNDEZ; FLORES-PALACIOS, 2014). Por exemplo, na copa interna, mais próxima ao fuste, a luminosidade pode não ser tão abundante quanto na copa externa o que cria condições para o estabelecimento de espécies que se desenvolvem melhor em meia sombra ou sombra completa (CHAVES; DYONISIO; ROSSATTO, 2016; RUIZ-CORDOVA; TOLEDO-HERNÁNDEZ; FLORES-PALACIOS, 2014). O fator luminosidade recebe também influência de outras características das copas. A densidade de folhagem de uma copa pode interferir no quanto de radiação solar penetra até seus galhos e tronco, e o quanto é contido pelas folhas (MASSARO *et al.*, 2012). Copas com folhagem rala permitem maior penetração de luz, enquanto mais densas possuem grande incidência solar apenas na área externa (POLTZ, 2011; SÁYAGO *et al.*, 2013). Desta forma, a densidade da copa pode ser um importante fator de interferência na ocorrência de epífitas. Além da densidade de folhagem, a deciduidade da árvore influencia no regime de luz. Uma árvore decídua perde parte ou toda a folhagem em determinada época do ano, e nas demais tem a copa cheia (WULF; KOLK, 2014). Desta forma, em determinada época do ano o ambiente fica favorável às espécies de sombra e meia sombra, enquanto em outra são favorecidas espécies de plena luz (CHAVES; DYONISIO; ROSSATTO, 2016; WOLF, 2005). Nesta situação, espera-se riqueza maior de espécies, uma vez que todas as preferências fisiológicas estão contempladas (CHAVES; DYONISIO; ROSSATTO, 2016; EINZMANN *et al.*, 2014). Porém os períodos desfavoráveis às necessidades fisiológicas podem resultar em maior menor abundância de indivíduos, e menor tamanho destes, uma vez que seu desenvolvimento possa ser prejudicado (WOLF, 2005).

O formato da copa também pode influenciar na ocorrência de epífitas por alterar a disponibilidade de variáveis ambientais (KERSTEN; SILVA, 2001). Existem os mais diversos formatos de copa: colunar, globosa, elíptica horiontal, vertical, etc. Pela alta diversidade de formas, são altas as variações de características abióticas como luminosidade, vento e umidade (IZUDDIN; WEBB, 2015; WOODS; CARDELÚS; DEWALT, 2015). Uma copa elíptica vertical, por exemplo, tende a apresentar uma estratificação vertical maior do que uma elíptica horizontal, podendo ter uma diferenciação maior de *microhabitats*, favorecendo maior número de espécies. Desta forma, a elíptica horizontal poderia apresentar uma mesma disponibilidade de radiação em toda sua extensão, favorecendo menor número de espécies, mas maior abundância de espécies de pleno sol (CARDELÚS; CHAZDON, 2005; ZHANG; HU; ZHANG, 2016).

1.3 Dependência da fonte de propágulo

Como a zoocoria e anemocoria possuem maior chance de dispersão nas árvores mais próximas, a distância entre forófitos pode ser uma variável de influência (DISLICH; MANTOVANI, 2016; IZUDDIN; WEBB, 2015). A dispersão possui maior chance de acontecer na árvore mais próxima, pois esta árvore seria a primeira barreira e parada de propágulos (RUIZ-CORDOVA; TOLEDO-HERNÁNDEZ; FLORES-PALACIOS, 2014). As zoocóricas, que dependem da movimentação do dispersor, também tendem a ocorrer na árvore mais próxima, principalmente para vetores com movimentação reduzida (EINZMANN; ZOTZ, 2016; MANNING; GIBBONS; LINDENMAYER, 2009). Neste caso, as árvores próximas funcionariam como “stepping stones”, estruturas imersas dentro da matriz que facilitam o deslocamento dos indivíduos entre fragmentos a partir do fornecimento de poleiro e recursos, aumentando a capacidade de movimentação (MANNING; GIBBONS; LINDENMAYER, 2009). Mesmo sendo uma abordagem pouco frequente no estudo de epífitas, a distância da árvore em relação ao forófito mais próximo, com este atuando como fonte de propágulos, influenciaria negativamente a ocorrência de epífitas (DISLICH; MANTOVANI, 2016; IZUDDIN; WEBB, 2015). Como consequência do fluxo restrito de propágulos, podemos encontrar decréscimos na abundância e riqueza de epífitas em árvores tanto para ambientes fechados, como fragmentos florestais (DISLICH; MANTOVANI, 2016; SÁYAGO *et al.*, 2013), quanto em ambientes abertos, como pastagens (IZUDDIN; WEBB, 2015).

Além do forófito mais próximo, a distância em relação à borda do fragmento também pode representar um fator de limitação de fluxo de propágulos em matrizes adjacentes aos fragmentos florestais, como as pastagens (GUEVARA; LABORDE, 1993). Em uma paisagem fragmentada, os remanescentes florestais funcionam como fonte de propágulos para as matrizes adjacentes, na sua maioria de epífitas florestais (IZUDDIN; WEBB, 2015). Neste caso, a proximidade das árvores em relação à borda do fragmento aumenta a chance destas árvores serem colonizadas por epífitas (BARRANTES; PEREIRA, 2002; POLTZ, 2011). A saída de propágulos de epífitas do fragmento, e posterior deposição nas árvores isoladas, podem ocorrer tanto do fragmento via corrente de ar, no caso das anemocóricas (VICTORIANO-ROMERO *et al*., 2017), quanto por vetores animais, os quais podem utilizar as árvores isoladas como ponto de parada, e possível deposição de propágulos (PIZO; DOS SANTOS, 2011). Neste caso, a relação negativa da borda de fragmento com a assembleia de epífitas ocorre tanto em relação à riqueza (HIETZ-SEIFERT; HIETZ; GUEVARA, 1996; IZUDDIN; WEBB, 2015), quanto à abundância (IZUDDIN; WEBB, 2015), principalmente por árvores distantes não apresentarem ampla ocorrência de espécies florestais, ficando restritas aquelas comuns da matriz (HIETZ-SEIFERT; HIETZ; GUEVARA, 1996).

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2. ARTICLE: SEED SOURCE AND HOST TREE TRAITS DIFFERENTLY INFLUENCE FOREST AND GENERALIST EPIPHYTE SPECIES IN PASTURE

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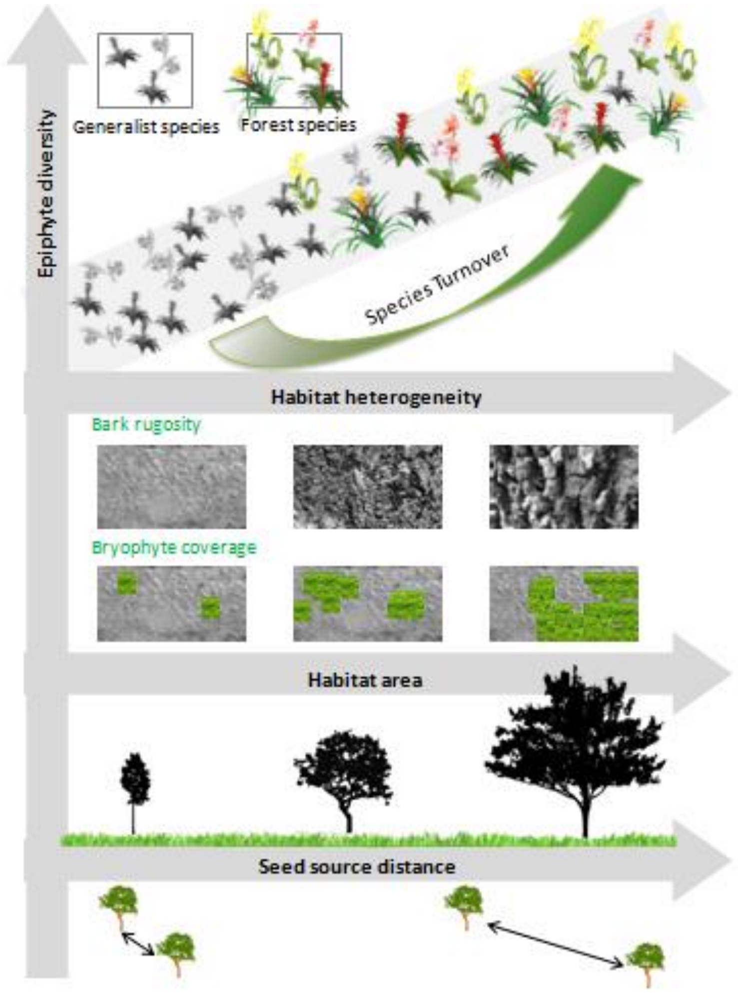
Abstract: Phorophyte traits and seed source dependence can act together in epiphyte assembly. However, there is little information about the ecology of this plant group in disturbed habitats such as pastures. Thus, our primary objective was to identify whether epiphyte occurrence in pastures is affected by tree traits or distance from a seed source, and test whether this effect varies according to epiphyte functional groups. Most epiphyte studies only investigate the influence of tree traits. We hypothesize that (i) the occurrence of epiphyte generalist species is associated with tree trait predictors of habitat availability, and these species have neighboring remnant phorophytes as their seed source; while (ii) the occurrence of forest species is associated with tree trait predictors of habitat heterogeneity, and these species have forest fragments as their seed source. To test these hypotheses, we quantified 9567 holoepiphyte individuals of 16 species belonging to four Angiosperm families, in 759 isolated remnant trees, distributed in 15 pastures adjacent to forest fragments. We measured

12 tree traits, as well as the distance from isolated remnant trees to (i) the forest edge and (ii) the neighboring phorophytes. We divided epiphyte species into two functional groups, namely (i) generalist species and (ii) forest species. We found that both seed source dependence and phorophyte traits affect epiphyte community assembly, but differently for generalist and forest epiphytes, confirming our hypothesis. Thus, in order to promote the conservation of most forest epiphyte species in agricultural landscapes, farmers should maintain large isolated remnant trees in pastures with rugose bark, which provide microclimate buffering in harsh pastures and with moisture indicators (i.e. bryophyte coverage).

Keywords: Anthropic landscape, commensalism, holoepiphytes, scattered trees.

Graphical Abstract



Graphical abstract: Greater tree traits of habitat heterogeneity (bark rugosity and bryophyte coverage) and area (tree height, crown area, and diameter), as well as seed source distance (distance between phorophytes) promote both higher epiphyte diversity (richness, abundance and coverage) and species turnover from generalist to forest epiphyte species.

2.1 Introduction

Epiphytes are a vital plant group for fauna (Duarte & Gandolfi, 2017; Fernandez Barrancos, Reid, & Aronson 2017) and represent about 9% of vascular flora worldwide (Zotz 2013). They show high diversity and endemism in tropical forests (Forzza et al., 2012; Freitas et al., 2016), however, they are being decimated due to habitat loss (Armenta-Montero, Carvajal-Hernández, Ellis, & Krömer 2015; Del Castillo, Trujillo-Argueta, Rivera-García, Gómez-Ocampo, & Mondragón-Chaparro 2013; Haq, Ahmad, Alam, Ahmad, & Rahatullah 2010), mainly due to the conversion of forest to pastures, which represents about 70% of the land use in the tropics (Holl, 1999; Woods, Cardelús, & Dewalt 2015).

Original forest structure has been drastically changed to pastures, thereby affecting its microclimate and microhabitat (Holl, 1999). The maintenance of some scattered trees in pastures is a valuable conservation strategy (Harvey et al., 2011; Karvatte et al., 2016; Manning, Gibbons, & Lindenmayer 2009; Siqueira, Calasans, Furtado, Carneiro, & van den Berg 2017), wherein those trees could act as "stepping stones" for dispersing forest species through the matrix (Athayde & Morellato, 2014; Manning et al., 2009). The presence of scattered host trees could provide protection to epiphytes from harsh pasture microclimates (i.e. larger crown), and be a propagule source, helping to maintain their populations (Flores-Palacios & García-Franco, 2006; Hietz-Seifert, Hietz, & Guevara 1996; Poltz, 2011).

Certain phorophyte characteristics may affect the structure and composition of epiphyte assemblage (Wagner, Mendieta-Leiva, & Zotz 2015), such as diameter (e.g., Sáyago et al., 2013), height (e.g., Fayle, Chung, Dumbrell, Eggleton, & Foster 2009), bark roughness (e.g., Ceballos, Chacoff, & Malizia 2016), crown size (e.g., Poltz, 2011) and crown complexity (e.g., Ventre-Lespiaucq et al., 2017). According to studies in pastures, tree traits related to habitat area and habitat heterogeneity have (A) a positive relationship with epiphyte richness and abundance, for instance: (i) crown size and complexity (Flores-Palacios &

García-Franco, 2006; Izuddin & Webb, 2015; Poltz, 2011); (ii) tree size (Flores-Palacios & García-Franco, 2006; Poltz, 2011); and (iii) bark rugosity (Poltz, 2011). However, some studies have also shown (B) a negative relationship with epiphyte richness and abundance, for example: (iv) crown size (Poltz, 2011); and in relation to seed source, (v) the distance from forest edge (Hietz-Seifert et al., 1996). These results could be biased due to the occurrence of generalist species, once they are dominant in disturbed habitats (e.g., pasture). The recuperation of forest species in disturbed sites is more relevant because of the ecological roles they provide and for gaining back functional diversity (Gotsch et al., 2016), thus focusing their conservation on disturbed sites is imperative. Understanding which factors are important to increase diversity of forest and sensitive epiphyte species on host trees could aid in their conservation and in developing management strategies (Duarte & Gandolfi, 2017).

In anthropogenic matrices, such as pastures, generalist species commonly dominate the community (Estavillo, Pardini, & Da Rocha 2013; Holl, 1999; Izuddin & Webb, 2015; Poltz, 2011), because they are mostly xeromorphic (Rundel & Dillon, 1998), atmospheric (Chaves, Dyonisio, & Rossatto 2016), anemochorous (Victoriano-Romero, Valencia-Díaz, Toledo-Hernández, & Flores-Palacios 2017), and reproductively self-compatible (Orozco-Ibarrola, Flores-Hernández, Victoriano-Romero, Corona-López, & Flores-Palacios 2015).

There are many studies linking tree traits with epiphyte occurrence, however few of them investigate the effect of tree traits and seed source on community assembly of epiphyte at the same time (Dislich & Mantovani, 2016; Paggi et al., 2010; Victoriano-Romero, Valencia-Díaz, Toledo-Hernández, & Flores-Palacios 2017). Additionally, the number of studies becomes even smaller if we consider only those on anthropogenic matrices and degraded sites (Guevara & Laborde, 1993; Hietz-Seifert et al., 1996; Izuddin & Webb, 2015; Kiebacher, Keller, Scheidegger, & Bergamini 2017). Thus, there is a significant knowledge gap in epiphyte ecology on non-natural ecosystems.

We wish to know whether tree traits and distance to seed source differently influence the diversity of generalist and forest species on pastures. We hypothesized that the richness and abundance of: (i) generalist epiphyte species are positively associated with tree trait predictors of habitat area, such as tree height and crown area; and (ii) forest epiphyte species are positively associated with tree trait predictors of both habitat heterogeneity (i.e. rugose barks) and buffering of harsh microclimate, such as humidity availability (i.e. bryophyte coverage) and shading indicators (e.g., crown leaf density and deciduousness). We also hypothesized about the seed source, that: (i) generalist epiphyte species occur more often in neighboring remnant trees, while (ii) forest epiphytes occur more often in remnant trees closer to forest fragments.

2.2 Materials and Methods

2.2.1 Study site

Our study was carried out in 15 pastures located in Alfenas, south of Minas Gerais State, Brazil (45º56'W and 21º25'S) (Fig. 1, Table 1). The landscape is highly fragmented from being mostly human-disturbed, containing only 9% of the original seasonal semi-deciduous forest cover. The most common land use types are pastures (51%), coffee plantations (17%) and annual crops (mainly sugar cane and corn, 7%) (Olivetti, Mincato, Bernardes Ayer, Naves Silva, & Curi 2015). Mean annual rainfall is 1500 mm, with annual temperatures ranging between 17 °C and 24 °C, with two well defined seasons (warm and wet/cold and dry). The elevation varies between 790m and 1000m a.s.l. (Alvares, Stape, Sentelhas, De Moraes Gonçalves, & Sparovek 2013).

2.2.2 Tree survey

We selected 15 pastures adjacent to forest fragments, within non-overlapping buffers (centralized on each pasture) of one kilometer radius and with 20 to 40% forest cover. The forest cover of 20 to 40% on each buffer area was summarized to eliminate the effect of habitat loss in our epiphyte community assembly, based on the assumption that the epiphyte community from each pasture were the most similar possible. We delimited a single plot of 1.96 ha (196 m × 100 m) in each studied pasture, deliberately arranged to contain the largest possible density of scattered trees, starting at 3 meters from the fragment edge. We sampled all trees in the plots with a minimum diameter at breast height (DBH) of five cm (N = 759 trees, belonging to 96 species and 32 families, Appendix 1). We recorded 14 variables from each sampled tree, two seed source limitation indicators, and 12 tree traits (Table 3). We used the distance between sampled phorophytes and: (i) the closest fragment edge, and (ii) the nearest scattered host distance, both measured using QGIS, version 2.14.2, as indicators of distance from host tree to seed source. Tree traits obtained for habitat availability were: DBH; crown area, by the multiplication of the largest and smallest diameter; crown volume, by ellipsoid volume formula (crown volume = 4/3 * PI * half vertical diameter * half height); estimated total tree height. For tree predictors of habitat heterogeneity we evaluated: bark shedding (presence/absence); bark rugosity (0 = rugosity absent, 1 = small grooves, 2 = superficial cracks, 3 = deep cracks, Fig. 2); deciduousness, categorized as deciduous/evergreen from the literature; crown shape (1 = columnar, 2 = flabelliform, 3 = globe-head, 4 = horizontal elliptical, sensu Andrade et al., 2012) (Fig. 3); crown leaf density (1 = very sparse foliage, 2 = sparse foliage, 3 = dense foliage, 4 = very dense foliage, Fig. 4); tree bryophyte coverage (0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%); bark capacity for water absorption after being dried and immersed in water for 24 hours (Fig. 5a); bark capacity for water retention after 24 hours immersed in water, and four hours of heating (Fig. 5b).

2.2.3 Epiphyte survey

We surveyed all Angiosperm holoepiphytes in each sampled tree using binoculars. We registered epiphyte richness (number of species), abundance (number of epiphyte stands) and cover. To quantify epiphyte cover, we used a method adapted from Kersten, Kuniyoshi, and Roderjan (2009), which consists in estimating the cover through a semi-quantitative scale of scores representing a joint estimate of dominance and cover, where a score of 1 was attributed to epiphyte species with only one small individual in the phorophyte; score 3, for some small individuals, or medium-sized individuals; score 5, for several small, or some medium-sized individuals; score 7, for many medium-sized, or some large individuals; and score 10, for many large, or some extra-large individuals (Fig. 6). We calculated the total abundance and cover of each species as the sum of their values in all s in each landscape. We classified the epiphyte species into two groups, generalist (thereafter a generalist species) and forest specialist species (thereafter a forest species) associated with their preference and capacity to occur on the scattered host trees in pastures and/or the trees on the forest fragments (Table 2). Our criteria for the division were: (i) the frequency of studied scattered host trees (generalist); and (ii) the frequency of forest fragments adjacent to the pastures (forest species) (Almeida, Ávila, Sampaio & Ramos, unpublished data).

2.2.3 Data analysis

We used path analysis from the “plspm” R package (Sanchez, Trincheira & Russolillo 2017) to assess the relationship between tree characteristics, seed source, and epiphyte groups. For this, we correlated each tree feature with epiphyte data from generalist species and forest species using the phorophyte as sample unit. Numeric traits were scaled to standardized values (mean=0 and variance=1). Pearson’s correlation test was used to inspect the correlation and multicollinearity among all tree trait variables. Based on this we removed crown volume from all posterior analysis because of its high correlation with crown area and tree height ($r \geq 0.70$).

Next, we calculated beta diversity partition using the Jaccard Index from the "betapart" R package (Baselga et al., 2018) to understand which component of beta diversity, turnover or nestedness drives epiphyte assembly in pastures among large and small trees. We used the tree height, diameter and crown area as tree trait predictor of space availability, divided into two size groups (by their median value) and four size groups (by their quartile values). The turnover result suggests a successional process in epiphyte assemblage by species replacement between tree size groups. Moreover, the nestedness result suggests that one tree size group is a subset of the other tree group. The tree traits were divided as follows: (a) two groups - height: <7.5m and >7.5m; diameter <16cm and >16cm; crow area <22.5 m^2 and area >22.5m^2; and (b) four groups – height (<6, 7.5, 8.5, >11m), diameter (<8.8, 16, 33, >33cm) and crown area (<9.5, 22.5, 57.5, 67>m^2).

All statistical analyses were carried out in R software, version 3.4.1 (R Core Team, 2013).

2.3 Results

We recorded 9567 holoepiphyte individuals distributed in 16 species and four families (Table 2). The three most abundant and dominant epiphyte species were *Tillandsia recurvata* (6731 individuals), *T. pohliana* (1530) and *T. tricholepsis* (562) (Bromeliaceae). The three species with higher frequency in pastures were *T. recurvata* (100%), *T. pohliana* (87%) (Bromeliaceae) and *Epiphyllum phyllanthus* (67%) (Cactaceae). The abundance found for each family was: Bromeliaceae (8934 individuals), Orchidaceae (510), Cactaceae (62) and Piperaceae (61). However, we only found a single species for Cactaceae and Piperaceae.

The generalist group was formed by 7 species and 8974 individuals. We found that tree traits associated with richness, abundance and coverage of generalist species, as well as abundance and coverage showed significant relationships with distance to seed source (Fig. 7). Generalist species richness was positively correlated with DBH (r=0.16), bark rugosity (r=0.26), and bark shedding (r=0.14). Generalist species abundance had a positive relation with edge distance (r=0.35), and a negative relation with crown area (r=-0.11), tree height (r=-0.09) and bark rugosity (r=-0.12). Generalist species coverage had a positive relation with crown area (r=0.36), tree height (r=0.25), DBH (r=0.32) and edge distance (r=0.39), and a negative relation with the distance of the nearest host tree (r=-0.27).

The forest species group was formed by 9 species and 593 individuals. We found that tree traits associated with richness and coverage of forest species showed a relation with tree traits. We also found that forest species abundance was related to the distance of the seed source (Fig. 7). Forest species richness was positively correlated to crown area (r=0.19), tree height (r=0.13), DBH (r=0.19), and bark rugosity (r=0.24). Forest species abundance had a positive relation with distance of the nearest phorophyte (r=0.17). Coverage had a positive relationship with bryophyte coverage (r=0.23).

Beta diversity among small and large trees, regardless of size criteria (height, diameter and crown area), was consistent among tree trait predictors of space availability, and the two and four size groups (Table 4). The representation of regional diversity (γ) vary between 56 to 43% (two size groups) or 70 to 68% (four size groups). About 92 to 65% (two groups) or 59 to 53% (four groups) of the beta diversity was generated by the species turnover, while the species nestedness consisted of 35 to 8% (two groups) or 47 to 41% (four groups).

2.4 Discussion

Our hypothesis of tree traits was confirmed by the associations we found (i) between generalist epiphyte species and tree trait predictors of habitat area, and (ii) between forest epiphyte species and tree trait predictors of habitat heterogeneity. In the seed source distance approach, we confirmed our hypothesis that (i) scattered host trees closer to one another harbored more generalist epiphytes, but our data did not support our hypothesis that (ii) scattered host trees closer to forest fragments would have more forest epiphytes.

Tree traits and seed source differently affected the two epiphyte groups (generalist species and forest species) on the scattered host trees. To the best of our knowledge, our study is the first to find that (i) bark rugosity in scattered host trees positively influenced the richness of forest and generalist epiphyte species, but negatively influenced the abundance of generalist ones; and that (ii) the distance from the forest fragment positively influenced the quantity (both abundance and coverage) of generalist epiphytes. However, the distance to seed source did not influence epiphyte richness.

2.4.1 Tree traits

We found tree size (height, crown area, and diameter) to be an essential predictor of epiphyte occurrence. Flores-Palacios and García-Franco (2006) found that young trees have more available area for colonization, while mature ones could be already saturated. Generalist epiphyte species could be favored in the initial stage of tree development because of their greater seed dispersal capacity (i.e. anemochoric seeds) and higher irradiation resistance. The colonization and growth of forest epiphytes species may be facilitated along tree growth (stems and crown), as the harsher microclimate of pastures is buffered. We found a turnover partition explaining the greater part of the beta diversity, suggesting a successional process between small and large trees. The results indicate that the epiphyte species composition in smaller trees presented a different composition from the epiphyte species in greater ones. It means that pastures with large trees are more adequate for forest epiphyte species preservation, because pastures with small trees tend to harbor more generalist epiphyte species with overdominance.

Some tree size traits such as tree diameter and height in forest habitat have a controversial relationship with epiphyte richness (Zotz & Schultz, 2008), abundance (Zotz & Schultz, 2008) and biomass (Wolf, 2005). The same controversial pattern was observed in pasture trees for epiphyte richness (Flores-Palacios & García-Franco, 2006; Hietz-Seifert et al., 1996), and diversity (Kiebacher et al., 2017; Poltz, 2011). Tree height in forests presented a neutral relationship with orchids (Rosa-manzano, Luis, Zotz, & Reyes-garcía 2014), but a positive one with bromeliad abundance (Ruiz-cordova, Toledo-hernández, & Flores-palacios 2014). Poltz and Zotz (2011) analyzed the influence of tree diameter on epiphyte assemblages and found a positive relationship with diversity in pastures, but the relation was neutral (e.g. bryophyte, Kiebacher et al., 2017) or negative (e.g. lichen, Kiebacher et al., 2017) when they analyzed epiphyte groups separately. We also found varying relationships between tree size predictors and epiphyte groups (forest and generalist species). However, contrary to other trait predictors of tree size there is no controversial relationship between crown traits and epiphyte diversity in literature. The crown shows a well delimited positive relationship with epiphyte occurrence in pasture and forest (Poltz, 2011; Flores-Palacios & García-Franco, 2006; Hietz-Seifert et al., 1996). But we also found that tree crown area showed varying relationship to diversity according to epiphyte group; it presented a positive relation with forest epiphyte richness and generalist coverage, but a negative relation with generalist abundance.

We also found that tree characteristics representing habitat heterogeneity (bryophyte coverage, bark rugosity, and shedding) are essential predictors of epiphyte assemblage. The tree traits and the favorable habitat for specific epiphytes could vary along the ontogenetic stages (Taylor & Burns, 2015). The rugosity degree of tree bark, for example, ranges from smooth (initial) to very rugose (final development stage) (Anna & Jarosław, 2014) and could differently influence the epiphyte assemblages (Boelter, Dambros, Nascimento, & Zartman 2014; Vergara-Torres, Pacheco-Álvarez, & Flores-Palacios 2010; Callaway et al. 2002).

Actually, to the best of our knowledge, there is only one study relating bark rugosity and epiphyte diversity in pastures, which described a neutral effect in epiphyte diversity (Poltz & Zotz, 2011), while there are many studies on forests showing both positive (Ceballos et al., 2016; Chaves et al., 2016; Wyse & Burns, 2011) and neutral effect (Boelter et al., 2014; Duarte & Gandolfi, 2017).

In addition to the controversial results of bark rugosity, we found a clear relationship with epiphyte diversity and both bark shedding and bryophyte coverage. Bark shedding was positively related with richness of generalist species, while bryophite coverage was positively related with coverage of forest species. Bark shedding could be a predictor of habitat heterogeneity as trees with shedding and smooth bark could present different epiphyte composition (Boelter et al., 2014; Wyse & Burns, 2011). The trunk region with bark shedding could have thin bark and low water storage, thus only favoring colonization by the generalist species and increasing their richness, as found herein. On the other hand, bryophyte coverage presented a positive relationship with forest epiphyte coverage. Higher bryophyte coverage in trees could provide mechanical support to epiphyte seeds and seedling establishment, as well as humidity to their development, thereby buffering the eventual harsh microclimate (Ah-Peng et al., 2017; Werner & Gradstein, 2008). Forest epiphytes present greater richness, abundance, and size in more humid habitats, and they have high water dependence (Hietz, Winkler, Scheffknecht, & Hülber 2012). For example, Hietz et al. (2012) found a positive relationship between bryophyte coverage and germination of bromeliads in trees located both in a forest and in agricultural matrices.

2.4.2 Seed source results

We found a low influence of distance to seed source (from forest edge and/or scattered host tree) on epiphyte assemblages. Only the hypothesis that scattered phorophytes closer to one another have more generalist epiphytes was supported. We found a negative relationship between distance amongst phorophytes and coverage of generalist epiphytes. The seeds of generalist epiphyte species are mostly coming from individuals established in an open environment (Holl, 1999; Victoriano-Romero, Valencia-Díaz, Toledo-Hernández, & Flores-Palacios 2017) than from the nearest forest. Cascante-Marín et al. (2009) found that different epiphytes species had greater seed survival and growth in the forest interior when they are transplanted, indicating a good environmental condition to seed establishment and development, but a possible dispersal barrier to seed arrival and way out. On the other hand, we found unexpected relationships for both epiphyte groups. Coverage of generalist epiphyte species showed a positive relation with distance from forest fragments. On the other hand, forest epiphyte species did not show any relationship with distance from forest fragments, but we found a positive relationship with the distance among scattered host trees in pasture.

We suggested two non-mutually exclusive hypotheses to explain these unexpected results about the distance to seed source. First, seed source may not be as important as tree traits for epiphyte assemblages, at least in pastures. Dislich and Mantovani (2016) also found that the distance to seed source showed neutral or little effect on forest epiphyte assemblage and that forest tree traits were more important. Second, we hypothesize that management could have an influence on epiphyte assemblages in pastures. Farmers may maintain some isolated trees in pastures during forest removal or pasture management (Siqueira, Calasans, Furtado, Carneiro, & van den Berg 2017). Some phorophytes presenting many forest epiphyte species were possibly kept in pastures after forest cleaning and some of these phorophytes were older and available to epiphyte colonization longer than regenerating trees in pasture. However, we did not find any relationship between indirect predictors of tree age (height and diameter) and forest edge distance (results not shown) in our study, which could indicate that trees near forest fragments were older and were the matrix of the seed source.

2.4.3 Conservation issues

Knowledge about the influence of phorophyte characteristics and the distance to seed source in disturbed habitats such as pastures is essential for epiphyte conservation, mainly conservation of forest species which are more sensitive to disturbances. Based on our results, we recommend the maintenance of large trees with large crowns and rough and moist trunks in pastures, which will increase their conservation value by harboring forest epiphyte diversity. However, we also envisage a scenario where pasture trees can be enriched with forest epiphytes by transplantation (Reid et al. 2016; Duarte & Gandolfi, 2017), and manage trees which present favorable traits to a higher occurrence of forest epiphytes (richness and abundance).

Our results about epiphyte assemblages on pastures demonstrate how scattered trees could maintain some forest epiphytes, although there is a general tendency of generalist species to become dominant. Regarding epiphyte conservation, landowners and farmers should prioritize trees with larger diameter, height and crown, with rugose bark and high bryophyte coverage on the bark.

Conclusion

Our study is the first to approach forest and generalist epiphyte species separately, especially in pastures. The generalist epiphytes species are tolerant to sunny and warm microclimate, tend to be favored in disturbed habitats such as pastures, and could occur as super dominants in the assemblage. In our case, three generalist species (from 15 species total) were super dominant and represented about 92% of the sampled individuals. To avoid any bias for generalist species due to their super dominance, we analyzed the data separating the assemblage into generalists and forest species.

We strongly recommend that these groups are always analyzed separately in function of their different requirements and contrasting responses regarding tree characteristics and distance to seed source. Contrary to our expectation, the distance to forest fragments did not influence the richness or the abundance of forest epiphytes. However, many tree characteristics related to size, bark rugosity, and moisture influenced the richness and abundance of epiphytes in the pasture.

2.6 Author’s contributions

FNR conceived the ideas and designed the methodology; JPCE and MBS collected the data; JPCE, FNR and MBS analyzed the data, and interpreted the results with the contribution of AFNF and EB; JPCE drafted the article. All authors contributed critically to the article review, and gave final approval for publication.

2.7 Acknowledgements

We thank Nathalia M. Francisco, Natalia G. Costa, Renan G. Carvalho and all graduate students for assisting with fieldwork. This manuscript also greatly benefited from the comments of André R. T. Nascimento,Luiz Menini Neto and Glenda Mendieta-Leiva, for which we are grateful. The “Universidade Federal de Alfenas” provided logistical support to fieldwork. This work was supported by the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (*CAPES*) awarded to J.P.C.E. (no. 1587721) and M.S.B. (23038.006963/2011); the *Fundação de Amparo a Pesquisa do Estado de Minas Gerais* (*FAPEMIG*) (APQ-00839-15) and the *Conselho Nacional de Desenvolvimento Cientifico e Tecnológico* (*CNPq*) (306595/2014-1).

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TABLES

Table 1: Geographical coordinates and enviromental characteristics of the 15 studied pastures.

Code	Pasture	Latitude	Longitude	Trees	Density (tree/ha)	Elevation (m a.s.l.)
H47	1	21°41'S	45°31'W	31	16	874.5
P21	2	21°26'S	45°45'W	9	5	810.0
P9	3	21°12'S	45°46'W	22	11	897.7
PMT	4	21°30'S	45°52'W	157	80	884.5
P7	5	21°28'S	45°55'W	49	25	833.5
PZV	6	21°09'S	45°56'W	203	104	800.5
P4	7	21°13'S	46°05'W	14	7	790.0
P2	8	21°03'S	46°06'W	56	29	983.0
P23	9	21°18'S	46°07'W	34	17	1003.0
PD	10	21°26'S	46°08'W	20	10	861.0
P19	11	21°24'S	46°09'W	53	27	881.5
P27	12	21°20'S	46°10'W	21	11	924.5
P13	13	21°25'S	46°13'W	31	16	962.3
T3	14	21°13'S	46°20'W	45	23	876.7
T4	15	21°17'S	46°22'W	14	7	832.8

Table 2: Epiphtyte species and groups. The acronyms represent: For - forest epiphyte species, Tol - tolerant epiphyte species. The size was categorized in large (L) and small (S) to the coverage score application.

Family	Species	Size	For	Tol
Bromeliaceae	*Aechmea bromeliifolia* (Rudge) Baker	L	X	
	Billbergia porteana Brong. Ex Beer	L	X	
	Tillandsia loliacea Mart. Ex Schult. & Schult.f.	S		X
	Tillandsia pohliana Mez	S		X
	Tillandsia recurvata (L.) L.	S		X
	Tillandsia streptocarpa Baker	S		X
	Tillandsia tricholepis Baker	S		X
	Bromeliaceae sp.	S		X
Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	L		X
Orchidaceae	*Brassavola tuberculata* Hook	L	X	
	Epidendrum pseudodifforme Hoehne & Schltr.	S	X	
	Gomesa flexuosa (Lodd.) M.W.Chase & N.H.Williams	L	X	
	Lophiaris pumila (Lindl.) Braem	S	X	
	Oncidium sp.	L	X	
	Polystachya concreta (Jacq.) Garay & Sweet	S	X	
Piperaceae	*Peperomia* sp.	S	X	

Table 3: Tree characteristics separated into seed source and tree traits. The N column refers to number of observations. The N variations are in result of field limitations and/or ausent literature information.

Categories	Characteristics	N	Average	Measure unit
Seed source	Edge distance	757	57.74 ± 55.49	meters
	Scattered phorophyte distance	244	12.79 ± 16.91	meters
	Habitat heterogeneity			
Tree traits	bark	759	categorical	NA
	Bark rugosity	758	categorical	NA
	Deciduousness	695	categorical	NA
	Crown shape	740	categorical	NA
	Crown leaf density	740	categorical	NA
	Bryophyte cover	759	categorical	percentage
	Bark water absorption	399	126.05 ± 70.82	percentage
	Bark water retetion	399	5.04 ± 11.78	percentage
	Habitat availability			
	Tree height	759	9 ± 4.04	meters
	Crown volume	759	57.36 ± 83.84	square meters
	Stem height	741	1.87 ± 2.03	meters
	DBH.	759	26.1 ± 27.7	centimeters

Table 4: The beta-diversity partition analysis results. The Beta-diversity column indicate the representation of regional diversity (γ). Turnover and Nestedeness values are the beta diversity partition explained by each one, followed by the percetage representtion. The tree size predictors separeted into two approaches: two size groups, separeted by the median value, and four size groups, separeted by the quartiles.

Tree size predictors	Beta-diversity	Turnover (%)	Nestedness (%)
Two size groups			
Crown area	0.43	0.3 (70)	0.13 (30)
Diameter	0.56	0.36 (65)	0.2 (35)
Height	0.43	0.4 (92)	0.03 (8)
Four size groups			
Crown area	0.69	0.41 (59)	0.28 (41)
Diameter	0.7	0.41 (59)	0.29 (41)
Height	0.68	0.36 (53)	0.32 (47)

FIGURES

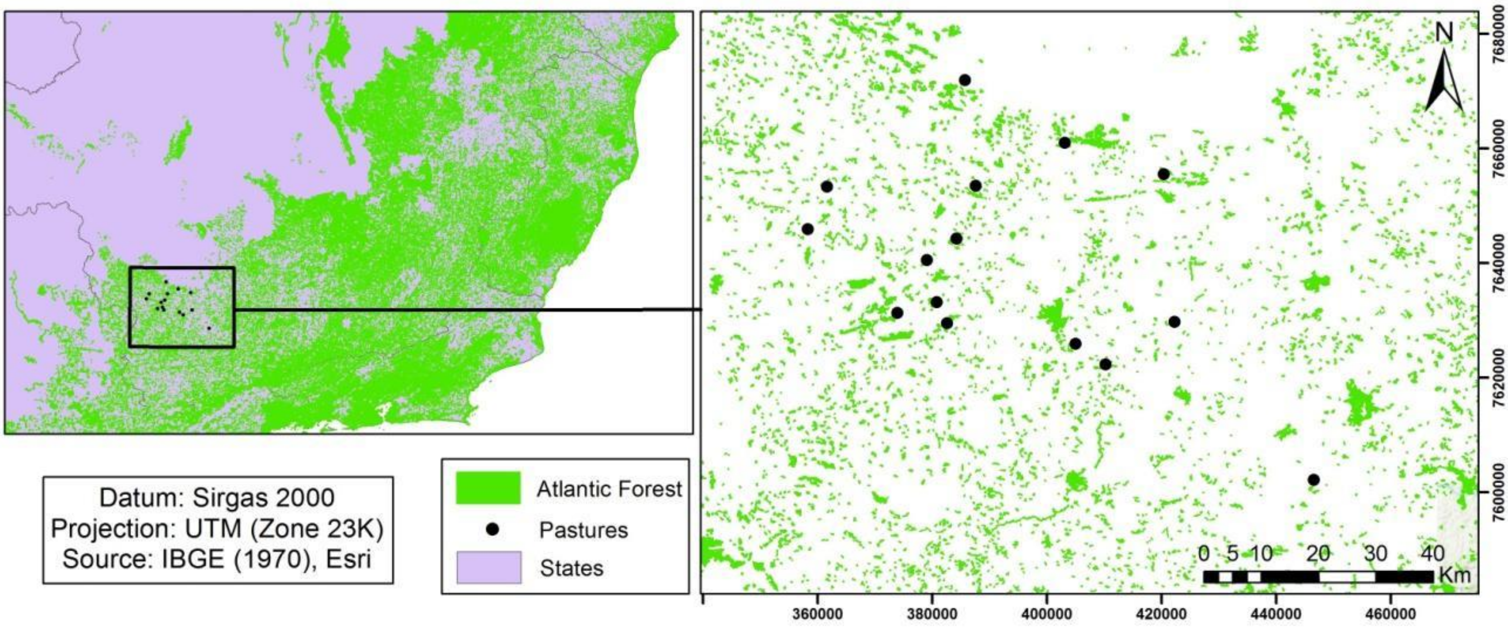

Fig. 1: Spatial localization of the 15 studied pastures, localized in Atlantic Forest area, south of Minas Gerais state, southeast of Brazil.

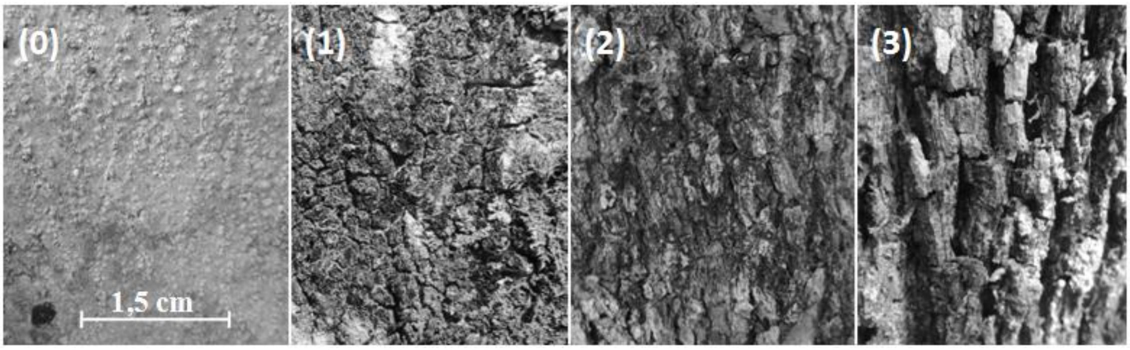

Fig.2: Bark rugosity was categorized into: (0) rugosity absent; (1) smooth rugosity; (2) superficial cracks; (3) deep cracks.

Fig.3: Crown shape categorized into four categories, according to crown openness. The number indicates crown shape: (1) columnar, (2) flabelliform, (3) globe-head, and (4) horizontal elliptical, adapted from Andrade, Salman, and Oliveira (2012).

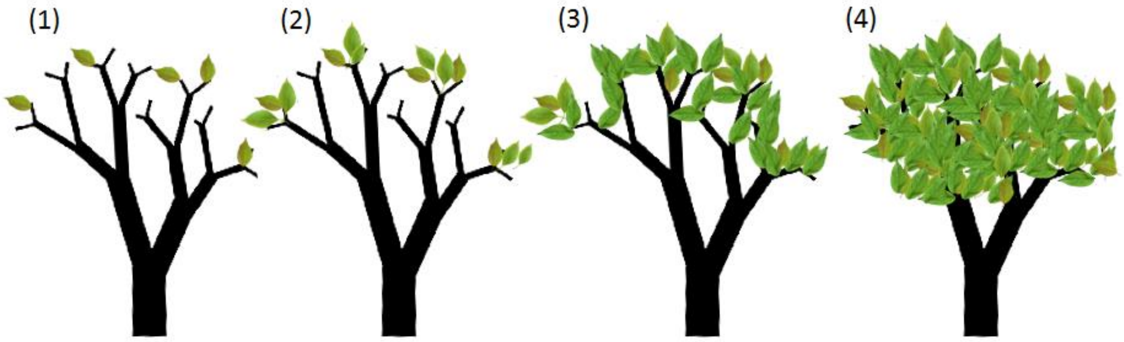

Fig. 4: Crown density categorized into four categories, according to crown leaf cover. The number indicates crown density: (1) scattered leaf predominance, (2) formation of small leaf groups, (3) crown continuous leaf coverage with trunk exposure, and (4) full crown fully covered by leaves.

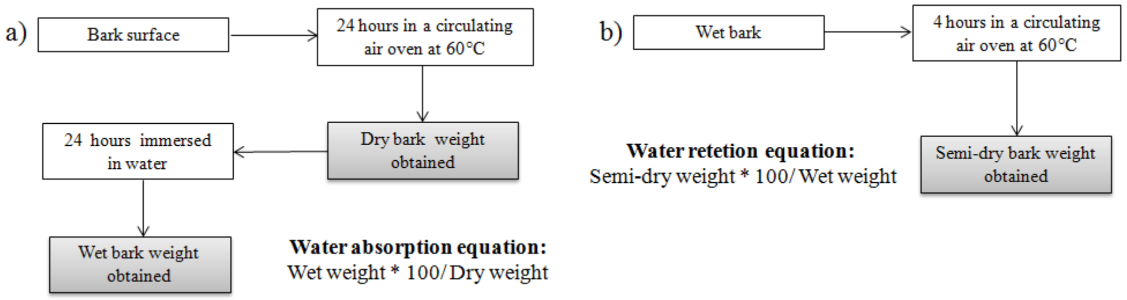

Fig. 5: Methodology to assess bark capacity of (a) water absorption and (b) retention. In the water absorption experiment, we used bark surface collected in the field, superficially in tree trunks, of 1.5 cm thick and 2cm width and length. In the water retention experiment, we used the same bark surface, after the previous experiment (wet bark). The filled text boxes indicate the values inserted in the equations, and the equations results were obtained in percentage.

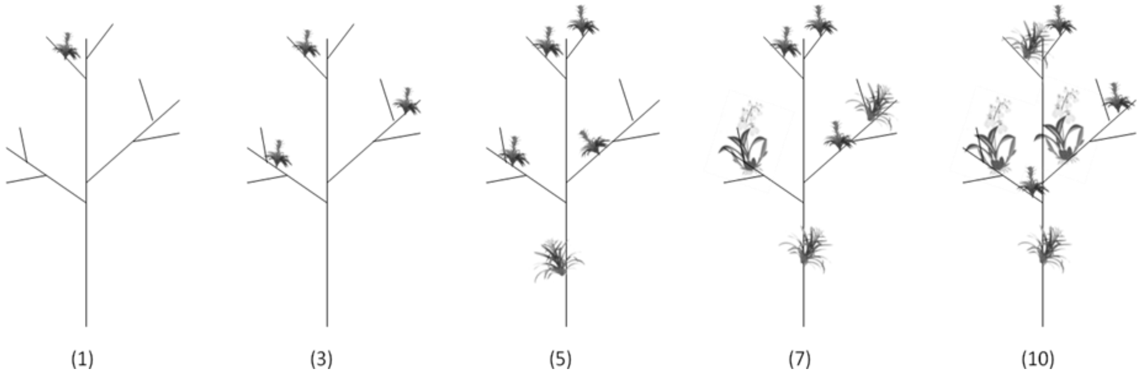

Fig. 6: Epiphyte coverage tree score: (1) one small and scattered epiphyte; (3) few small and/or one medium and scattered epiphyte; (5) several small and/or few medium epiphytes; (7) several small and medium epiphytes and/or few large epiphytes; and (10) several small, medium and large epiphytes, adapted from Kersten *et al.* (2019).

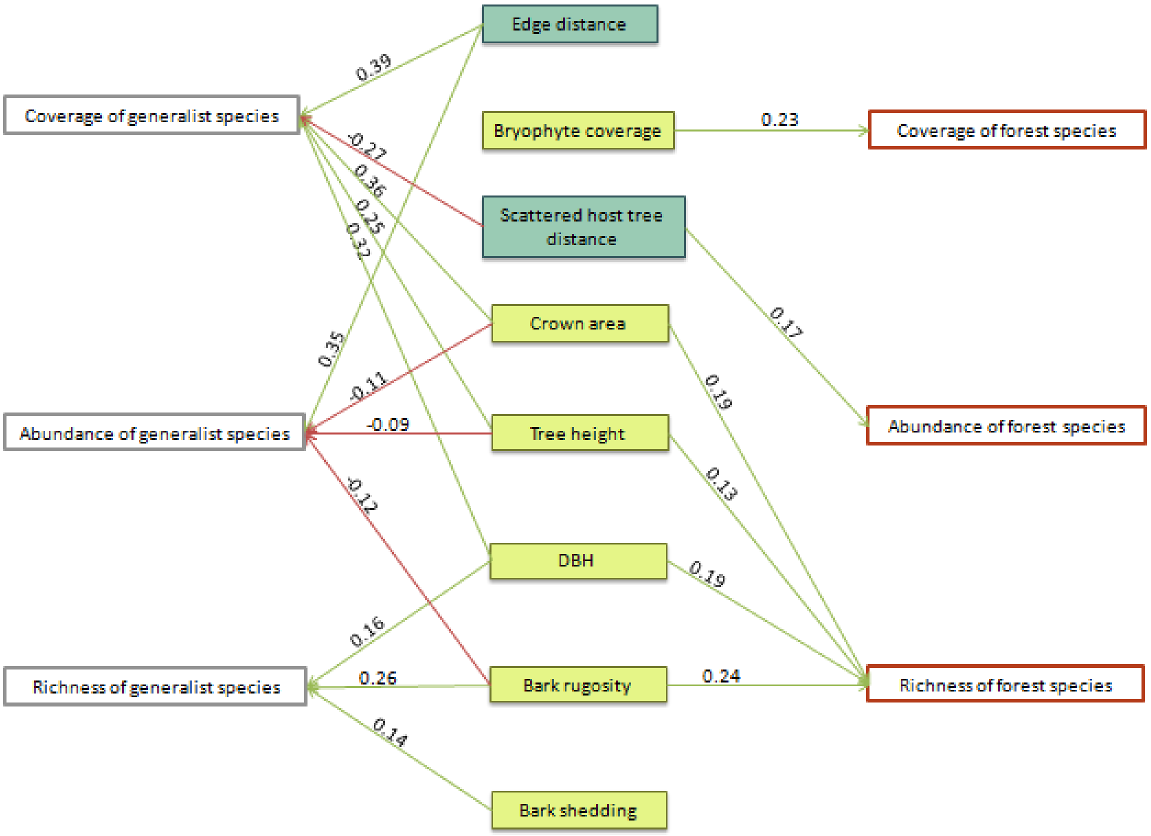

Fig. 7: All significant ($p<0.05$) relationships between measured variables. Brown boxes represent tree traits; blue boxes represent seed source limitation indicators; gray contoured boxes indicate variables for generalist epiphytes; red countoured boxes indicate variables for forest epiphytes. The values indicate the correlation coefficient (r) between variables, obtained from the path analysis, marked by the arrows, green and red represent positive and negative correlations, respectively.