INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Epífitas vasculares em ecossistemas de areia branca da Amazônia (Campinaranas): padrões de estrutura, composição e de distribuição

VIVIANE PAGNUSSAT KLEIN

Manaus, Amazonas

Setembro, 2023

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Orientadora: Drª. Maria Teresa Fernandez Piedade
Coorientadores: Dr. Adriano Costa Quaresma e Drª. Talitha Mayumi Francisco

Tese apresentada ao Programa de Pós-Graduação em Botânica, do Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Doutor em Biologia (Botânica).

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INPA INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
DIVISÃO DO CURSO
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EM BOTÂNICA

UNIDADE DE PESQUISA DO
MINISTÉRIO DA
CIÊNCIA, TECNOLOGIA,
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PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (BOTÂNICA)

DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

ATA DE DEFESA PÚBLICA DE TESE DE DOUTORADO

No dia vinte de setembro de 2023 às oito horas,horário de Manaus-AM, a discente **Viviane Pagnussat Klein**, sob orientação de **Dra. Maria Teresa Fernandez Piedade** do Instituto Nacional de Pesquisa da Amazônia e co-orientação do Dr. Adriano Costa Quaresma do Instituto Nacional de Pesquisa da Amazônia e a Dra. Talitha Mayumi Francisco, do Instituto Nacional de Mata Atlântica, defendeu publicamente sua tese de Doutorado intitulada ***Diversidade, estrutura, composição e distribuição de epífitas vasculares em ambientes de areia branca da Amazônia Central.*** A banca examinadora foi composta pelo Dr. Luiz Menini Neto da Universidade Federal de Juiz de Fora (UFJF), Dr.Gabriel Mendes Marcusso do Instituto Jardim Botânico do Rio de Janeiro (IJBRJ) e Dr. Felipe Fajardo Villela Antolin Barberena da Universidade Federal Rural da Amazônia (UFRA), tendo como suplente Dr. Charles Eugene Zartman do Instituto Nacional de Pesquisa da Amazônia (INPA). A defesa foi presidida pela orientadora, após a exposição pública do trabalho, o discente foi arguido oralmente pelos membros da Comissão Examinadora, que emitiram seus pareceres conforme indicado abaixo:

Examinador	Parecer	Assinatura
Luiz Menini Neto	(X) Aprovado ( ) Reprovado	Luiz Menini Neto
Gabriel Marcusso	(X) Aprovado ( ) Reprovado	Gabriel M. Marcusso
Felipe Fajardo Villela Antolin Barberena	(X) Aprovado ( ) Reprovado	Felipe Fajardo V. A. B.
Charles Eugene Zartman	( ) Aprovado ( ) Reprovado	

Manaus (AM), 20/09/2023

OBS: Nada mais havendo, foi lavrada a presente ata, que foi aprovada e assinada pelos membros da Comissão Examinadora, pelo orientador e pela Coordenação do Programa de Pós-Graduação em Botânica do INPA.

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Sinopse:

Neste trabalho investigou-se as comunidades de epífitas vasculares em cinco áreas de ecossistemas de areia branca (campinaranas) da Amazônia Central para verificar padrões de diversidade, composição e distribuição das espécies. Também foi analisada a estrutura e organização das interações entre as espécies de epífitas vasculares e seus respectivos forófitos. Com os resultados deste trabalho, espera-se contribuir para aumentar o conhecimento da flora presente nestes ambientes, bem como gerar informações que apoiem estratégias de conservação destes ameaçados ecossistemas amazônicos.

Palavras-chave: distribuição vertical e horizontal, forófitos, interações bióticas, redes ecológicas, resiliência.

Dedico às comunidades tradicionais
amazônicas que mantêm e preservam
este imenso patrimônio natural.

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“Tenho a impressão de ter sido uma criança
brincando à beira-mar, divertindo-me em
descobrir uma pedrinha mais lisa ou uma
concha mais bonita que as outras, enquanto
o imenso oceano da verdade continua
misterioso diante de meus olhos”

(Isaac Newton, 1687)

RESUMO

Os ecossistemas de areia branca da Amazônia, conhecidos também como campinaranas, se distribuem por extensas áreas cobrindo aproximadamente 5% do território amazônico. As condições oligotróficas dos solos, combinadas com a baixa capacidade de retenção de água, geram um forte efeito de filtragem e pressão seletiva, resultando em uma flora florística e estruturalmente diferente daquela dos demais ecossistemas amazônicos. Nos últimos anos, consideráveis avanços no conhecimento científico sobre estes ambientes foram obtidos, no entanto, estudos com foco no componente epifítico ainda são escassos, o que dificulta à inclusão desse grupo de plantas em estratégias de conservação e também obscurece o próprio entendimento da dinâmica, estrutura e funcionamento dos ecossistemas de campinaranas. Epífitas vasculares constituem um grupo diverso de plantas, com distribuição, principalmente, em regiões tropicais. Variáveis ambientais, como temperatura e precipitação, bem como as condições estruturais e composicionais da vegetação influenciam a distribuição das espécies de epífitas vasculares. Entender os fatores que determinam a dinâmica e a estrutura das comunidades de epífitas e as interações estabelecidas entre epífitas e forófitos é um dos pontos cruciais nos estudos ecológicos. Desta maneira, o objetivo geral desta tese foi investigar a estrutura, composição e distribuição das comunidades de epífitas vasculares em cinco áreas de campinaranas da Amazônia central e relacionar os padrões observados com as caraterísticas ambientais e estruturais da vegetação. Um total de 17.808 indivíduos epifíticos pertencentes a 18 famílias, 60 gêneros e 118 espécies foram registrados colonizando 486 indivíduos forofíticos. Os resultados deste estudo indicam que características intrínsecas de cada área e atributos relacionados ao tamanho e a identidade dos forófitos são fundamentais para definir a distribuição e composição das espécies de epífitas entre as áreas estudadas. As redes de interações entre epífitas-forófitos indicam que as comunidades de epífitas vasculares apresentam estrutura altamente aninhada, com baixa conectância, baixa modularidade e baixa especialização nos gradientes horizontal e vertical, porém é possível indetificar um padrão significativo de estratificação e de modularidade na distribuição vertical das espécies. Por fim, verificamos que as redes epífitas-forófitos são sensíveis a perturbações ambientais e que a retirada de uma única espécie de forófito generalista pode resultar em considerável perda das interações, reduzir a diversidade local das epífitas vasculares e levar o ecossistema ao desequilíbrio. Utilizando diferentes abordagens, a presente tese contribui para expandir o conhecimento a respeito da flora de plantas vasculares presentes nas campinarnas e fornece importantes ferramentas para embasar estratégias de conservação e manejo destes ecossistemas amazônicos.

ABSTRACT

The white sand ecosystems of the Amazon, also known as campinaranas, are distributed over extensive areas of land covering approximately 5% of the Amazon territory. The oligotrophic conditions of the soils, combined with the low water retention capacity, generate a strong filtering effect and selective pressure, resulting in a flora that is structurally and floristically different from that of other Amazonian ecosystems. In recent years, considerable advances in scientific knowledge about these environments have been achieved, however, studies focusing on the epiphytic component are still scarce, which makes it difficult to include this group of plants in conservation strategies and also obscures the understanding of the dynamics itself, structure and functioning of Campinaranas ecosystems. Vascular epiphytes constitute a diverse group of plants, distributed mainly in tropical regions. Environmental variables, such as temperature and precipitation, as well as the structural and compositional conditions of the vegetation, influence the distribution of vascular epiphyte species. Understanding the factors that determine the dynamics and structure of epiphyte communities and the interactions established between epiphytes and phorophytes is one of the crucial points in ecological studies. Thus, the general objective of this thesis was to investigate the structure, composition and distribution of vascular epiphyte communities in five campinarnas areas of the central Amazon and relate the observed patterns with the environmental and structural characteristics of the vegetation. A total of 17,808 epiphytic individuals belonging to 18 families, 60 genera and 118 species were recorded colonizing 486 phorophytic individuals. The results of this study indicate that the intrinsic characteristics of each area and attributes related to the size and identity of the phorophytes are fundamental to defining the distribution and composition of epiphyte species among the areas studied. Networks of interactions between epiphytes and phorophytes indicate that vascular epiphyte communities have a highly nested structure, with low connectance, low modularity and low specialization in the horizontal and vertical gradient, but it is possible to identify a significant pattern of stratification and modularity in vertical distribution of the species. Finally, we identified that epiphyte-phorophyte networks are sensitive to environmental disturbances and that the removal of a single species of generalist phorophyte can result in a considerable loss of interactions, reduce the local diversity of vascular epiphytes and lead the ecosystem to imbalance. Using different approaches, this thesis contributes to expanding knowledge about the flora of vascular plants present in Campinarnas and provides an important tool to support conservation and management strategies for these Amazonian ecosystems.

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1. INTRODUÇÃO GERAL

1.1 Epífitas vasculares: características gerais

Epífitas vasculares constituem um grupo de plantas taxonomicamente, morfologicamente e ecologicamente diverso. São definidas como plantas que germinam e enraízam de forma não parasitária sobre outras plantas (Zotz, 2016), desta forma, utilizam essas plantas (forófitos) apenas para suporte estrutural. Diferentes categorias ecológicas foram propostas para definir as formas de vidas das epífitas vasculares. Os sistemas de classificações incluem: o relacionamento da espécie com o forófito (acidental, facultativa, hemiepífita primaria e secundária, holoepífita); hábito de crescimento (reptantes, bulbosas ou arbustivas); relação com a umidade (poiquiloídricas e homoídricas) e o grau de exposição à luminosidade (plantas de sol ou plantas de sombra) (Pittendrigh, 1948; Benzing, 1990; Zotz 2016). Após uma ampla revisão Zotz (2013) propôs uma nova classificação, onde epífitas são separadas ecologicamente em dois grandes grupos: **Holoepífitas** – plantas que germinam e desenvolvem todo o seu ciclo sobre o forófitos. As holoepífitas são representadas, principalmente, por orquídeas, bromélias e samambaias; e **Hemipífitas** – plantas que germinam sobre o forófito, mas posteriormente estabelecem contato com o solo através de raízes adventícias. Exemplos deste grupo incluem as figueiras (e.g., gênero *Ficus*) e os mata-paus (e.g., gênero *Clusia*). As hemiepífitas secundárias, que anteriormente faziam parte do grupo de epífitas vasculares, foram realocadas em uma categoria ecologia à parte, as videiras nômades (Zotz, 2013).

As epífitas vasculares compreendem uma significativa fração da diversidade vegetal, representando mundialmente aproximadamente 10% da riqueza global de plantas (Zotz et al., 2021). As epífitas também são componentes chaves para o funcionamento dos ecossistemas, pois atuam em importantes processos ecológicos, como ciclagem de nutrientes e acúmulo de biomassa (Nadkarni et al., 2004), interceptação das águas das chuvas (Van Stan et al. 2015, Hargis et al. 2019) e no fornecimento de alimento e abrigo para a fauna especializada de dossel (Melnychuk & Srivastava, 2002, Stuntz et al., 2002, McCracken & Forstner, 2014). Além destas funções, as epífitas também adicionam diversidade e complexidade estrutural ao dossel das florestas (Zotz, 2016).

1.2 Epífitas vasculares: representatividade taxonômica

Epífitas vasculares são taxonomicamente diversas e estão incluídas em todos os grandes grupos de traqueófitas (Lycophyta, Monilophyta, Gimnospermas e Angiospermas). Em uma primeira lista global de epífitas vasculares Zotz *et al.* (2021) incluíram 79 famílias e 31.311 espécies de epífitas vasculares. O epífitismo é dominado por Angiospermas (90%), tem representantes entre as samambaias (9,84%), mas é praticamente ausente entre as Gimnospermas (0,006%) (Kersten, 2010; Zotz et al., 2021). Embora as angiospermas abriguem a maioria dos táxons, a participação proporcional não é regular dentro do grupo, onde as monocotiledôneas são dominantes. Orchidaceae é a família que obteve o maior sucesso em colonizar o dossel, aproximadamente 75% das espécies de epífitas vasculares (20.956 spp.) são orquídeas (Zotz et al., 2021). Bromeliaceae (1.943 spp.; 6,2%) se destaca como a segunda família mais representativa entre as epífitas (Figura 1). Entre as eudicotiledôneas, Gesneriaceae (616 spp.; 2,0%.) e Ericaceae (531 spp.; 1,7%) são as mais representativas. Entre as Magnoliídeas, Piperaceae merece destaque como uma das famílias com o maior númeo de representantes epifíticos (509 spp.; 1,6%). As samambaias são represesentadas principalmente por Polypodiaceae (1.450 spp.; 4,6%), Hymenophyllaceae (433 spp.; 1,4%) e Dryopteridaceae (424 spp.; 1,4%) (Figura 1).

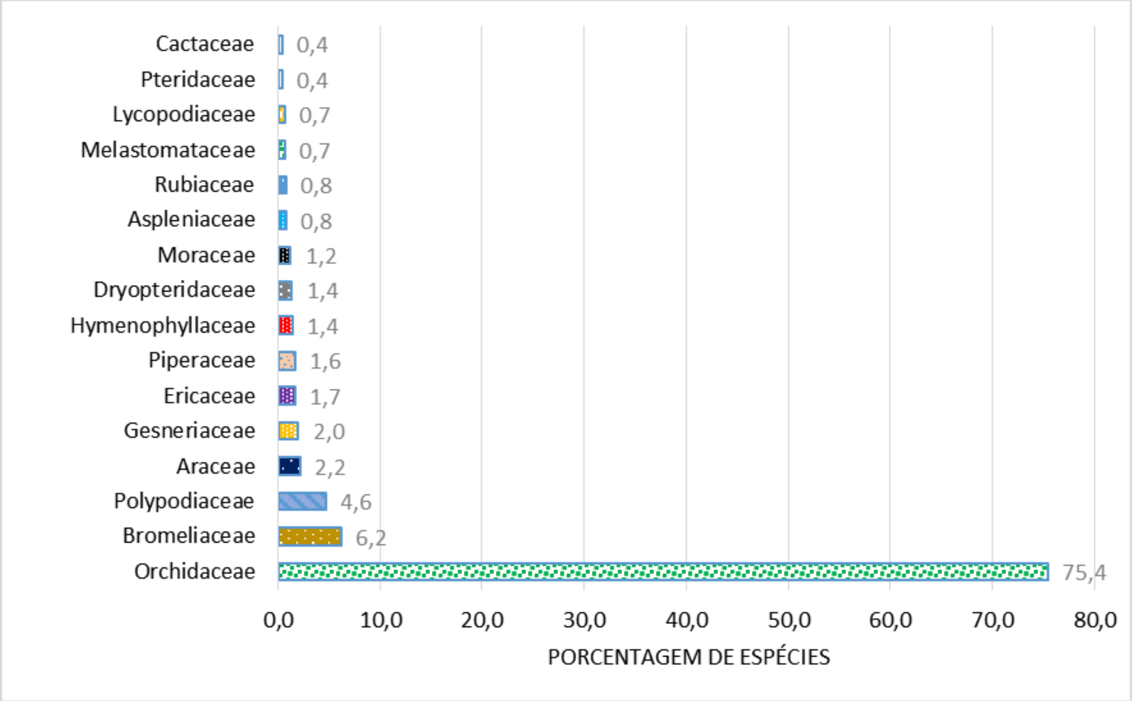

Figura 1. Representatividade taxonômica das principais famílias de epífitas vasculares. Dados obtidos de Zotz et al. (2021).

No domínio amazônico, as epífitas vasculares podem representar até 10% da flora de plantas vasculares, compreendendo aproximadamente 1.200 espécies (hemi e holoepífitas), distribuídas em 255 gêneros e 60 famílias (Flora do Brasil, 2023). A representatividade das epífitas amazônicas está principalmente concentrada em cinco famílias botânicas, Orchidaceae (588 spp.), Bromeliaceae (88 spp.), Polypodiaceae (71 spp.), Araceae (43 spp.) e Dryopteridaceae (24 spp.), que são responsáveis por cerca de 70% da diversidade da riqueza de espécies neste domínio (Flora e Funga do Brasil, 2023).

1.3 Epífitas vasculares: padrões de diversidade e de distribuição

Um dos objetivos centrais em ecologia é entender os fatores que estabelecem e mantêm padrões de biodiversidade. Em grandes escalas espaciais a distribuição das epífitas vasculares é influenciada por inúmeras características ambientais, como precipitação, umidade relativa do ar, temperatura e pressão atmosférica, sendo as regiões tropicais os principais centros de diversidade do grupo (Gentry & Dodson, 1987; Zotz, 2016). Entretanto, em pequenas escalas a distribuição das espécies está relacionada às características locais, como microclima, disponibilidade de recursos, condições estruturais e de preservação dos ambientes (Wagner et al., 2015; Petter et al., 2021). As epífitas vasculares são estruturalmente dependentes dos forófitos que disponibilizam substrato e uma variedade de ambientes com diferentes micro-habitats em uma única árvore (Sanger & Kirkpatrick, 2016), de maneira que é esperado que variações na composição e na estrutura da vegetação tenham forte efeito na distribuição do grupo (Wagner et al., 2015). Correlações positivas entre o tamanho e a idade dos forófitos são relatadas frequentemente (Zotz & Vollrath, 2003; Flores-Palacios & García-Franco, 2006; Quaresma et al., 2020; Francisco et al., 2021), porque o tamanho dos forófitos integra um conjunto complexo de condições ambientais e microclimáticas que desempenham um papel fundamental no estabelecimento e desenvolvimento das comunidades epifíticas (Francisco et al., 2021; Sáyago et al., 2013).

Outras características intrínsecas dos forófitos, como propriedades físicas e químicas da casca, arquitetura dos ramos e densidade da madeira e fenologia foliar (Callaway et al., 2002; Sáyago et al., 2013; Wagner et al., 2015; Woods et al., 2015) variam entre as espécies arbóreas e também podem influenciar fortemente a distribuição e composição das epífitas vasculares (Burns & Zotz, 2010; Wagner et al., 2015). Embora a especificidade estrita nas interações envolvendo epífitas-forófitos não seja um padrão frequentemente relatado (Alves et al., 2008; Sáyago et al., 2013; Wagner et al., 2015), a preferência de espécies epífitas por determinados táxons de árvores hospedeiras já foi evidenciada (Callaway et al., 2002; Francisco et al., 2018; Laube & Zotz, 2006; Quaresma et al., 2017; Barberena et al., 2019), sugerindo que algumas espécies de árvores apresentam conjuntos de caraterísticas estruturais e microclimáticas que as torna melhores forófitos que outras (Francisco et al., 2018; Zhao et al., 2015). Além das variações horizontais, as florestas também apresentam acentuados gradientes de variações microclimáticas verticais (Krömer et al., 2007; Sanger & Kirkpatrick, 2016). Já se sabe que nas partes mais elevadas do dossel a luminosidade e a temperatura são maiores, ao passo que a umidade é menor do que no solo da floresta (Benzing, 1995), de maneira que as variações impostas pelo gradiente podem selecionar grupos de espécies mais adaptadas às dadas condições e serem fatores preponderantes na distribuição das espécies (Johansson, 1974; Agudelo et al., 2019).

Considerando que comunidades ecológicas são formadas por diferentes tipos de associações entre espécies e que inúmeros fatores influenciam a composição e distribuição das comunidades de epífitas vasculares, identificar os fatores que impulsionam essas interações e as espécies associadas é fundamental para entender como os ecossistemas funcionam e determinar ações em prol da conservação e da biodiversidade (Taylor et al., 2016; Hu et al., 2021; Francisco et al., 2018). Neste sentido, o uso das teorias de redes ecológicas complexas, utilizando um conjunto específico de métricas (conectividade, especialização, modularidade, aninhamento e robustez), pode ser uma ferramenta útil para descrever as interações entre espécies e para compreender os níveis de organização, estrutura e dinâmica das interações entre epífitas e forófitos (Francisco et al., 2018; Delmas et al., 2019). Abordagens de rede são usadas para entender a organização de diferentes sistemas ecológicos, como teias alimentares (Keyes et al., 2021), interações mutualísticas (Mello et al., 2019), interações antagônicas (Morris et al., 2014) e, mais recentemente, em interações comensais envolvendo epífitas-forófitos (Burns, 2007; Francisco et al. 2018; Francisco et al. 2019; Zotarelli et al. 2019; Couto et al. 2022). Entre os estudos realizados, dois arranjos na estrutura das interações epífitas-forófitos parecem consistentes: a distribuição aninhada e a baixa especialização das interações (Francisco et al., 2019; Couto et al., 2022). Uma rede com estrutura aninhada indica que espécies especialistas interagem com espécies generalistas, resultando em um padrão de especialização assimétrica (Bascompte et al., 2003; Taylor et al., 2016), ao passo que, a baixa especialização indica que as espécies de epífitas têm baixa especificidade nas interações com as espécies de forófitos (Francisco et al., 2019; Newman, 2006; Taylor et al., 2016). Além das abordagens convencionais, outras métricas de redes, como a robustez, nos permitem simular a retirada de espécies altamente conectadas do sistema, e avaliar a fragilidade e tolerância de um sistema natural em relação a perturbações, fornecendo informações valiosas para apoiar planos de gestão e conservação da biodiversidade (Dunne et al., 2002; Memmont et al., 2004). Embora as análises de redes ecológicas tenham se mostrado uma importante ferramenta para o entendimento dos padrões e processos que estruturam as comunidades naturais, estas métricas ainda não foram utilizadas para os ecossistemas amazônicos em geral, sendo este estudo o pioneiro no uso dessa abordagem para as campinaranas da região.

2. CARACTERIZAÇÃO DAS ÁREAS DE ESTUDO

Os ecossistemas de areia branca, também conhecidos como campinaranas amazônicas, são ambientes que ocorrem exclusivamente no domínio amazônico, se distribuem irregularmente por aproximadamente 334.879 km^2, correspondendo a uma cobertura de cerca de 5% da região (Adeney et al., 2016). Grandes áreas contínuas destes ecossistemas são observadas principalmente no norte da Amazônia, associadas às bacias dos rios Negro e Branco, enquanto no restante da Amazônia se distribuem na forma de ilhas de diversos tamanhos imersas em uma matriz de outros ecossistemas florestais, principalmente ecossistemas de terra firme e de igapós (Prance, 1996). Os solos são caracterizados por serem arenosos (Podzóis ou Espodossolos), fortemente lixiviados, deficientes em nutrientes, ácidos e com altos níveis de alumínio em algumas regiões (Anderson, 1981; Coomes & Grubb 1996; Adeney et al., 2016; Capurucho et al., 2020). Além disto, estes solos apresentam saturação hídrica sazonal, com alagamento do sistema radicular e exposição do lençol freático em alguns pontos durante a estação chuvosa, e déficit hídrico (seca) durante a estação menos chuvosa (Anderson, 1981; Guimarães & Bueno, 2016). Estas condições edáficas estressantes promovem forte efeito de filtragem e pressão seletiva resultando em uma biota especializada, com alto endemismo filogenético e distinta dos demais ambientes amazônicos (Stropp et al., 2011; Fine & Baraloto, 2016; Vicentini, 2016).

A vegetação presente nestes ambientes apresenta diferenças na estrutura e composição, quando comparada aos ecossistemas adjacentes. Os ecossistemas de areia branca são formados por diferentes fitofisionomias, que variam desde ambientes florestados, formados por grandes árvores que podem ultrapassar os 20 metros altura, até fitofisionomias gramíneo-lenhosas onde predominam plantas herbáceas (Veloso et al., 1991), sendo as diferenças estruturais da vegetação proporcionadas principalmente por variações na profundidade do lençol freático (Demarchi et al., 2022). Floristicamente, apresentam baixa riqueza de espécies, alta densidade de indivíduos, dominância de algumas espécies em particular, alto número de linhagens endêmicas e elevadas quantidades de epífitas (Figura 2; Vicentini, 2016; Capurucho et al., 2020). Determinar padrões de distribuição e composição de espécies nestes ecossistemas tem sido o objetivo constante de muitas pesquisas ecológicas. Avanços consideráveis foram obtidos no conhecimento dos componentes arbóreo e arbustivo (e.g., García-Villacorta et al., 2016; Guevara et al., 2016), entretanto, o entendimento das interações entre os demais constituintes da flora com as características ambientais continuam pouco compreendidas para estes ecossistemas.

A Amazônia Central apresenta clima equatorial pluvial com precipitação média anual de 2.077 ± 438,3 mm (período analisado 1975-2005) e temperatura média anual de 27 °C (Carneiro & Trancoso, 2007). A região apresenta duas estações bem definidas; uma estação marcada por fortes chuvas que se estendem de dezembro a maio, com picos de precipitação nos meses de março e abril (média mensal de 298,4 e 278,7 mm, respectivamente), seguidos por uma estação seca durante os meses de junho a outubro, sendo agosto e setembro os mais secos, com média mensal de 72,0 mm (Demarchi et al., 2022). Este estudo foi conduzido em cinco área de ecossistemas de campinaranas da Amazônia Central, próximos a cidade de Manaus, Amazonas (Figura 3a).

2.1 Reserva Asframa (AR)

A Asframa (Figura 3b) é uma área de proteção particular pertencente à Associação dos Funcionários da Suframa, fundada em 1979 com o objetivo de promover a interação e o bem-estar dos servidores. A reserva está situada no Km 98 da rodovia BR 174, ao norte da cidade de Manaus, Amazonas, (Lat. 2°08’12” S, Long. 59°59’42’’ W), distante aproximadamente 110 km da capital. Próximo à sede da associação, a reserva apresenta vegetação arbustiva e arbórea marcada por clareiras estabelecidas pela ação antrópica com a finalidade de desenvolver atividades de lazer nos entornos das cachoeiras presentes no local (Vilas Boas et al. 2018). No interior da reserva é possível encontrar ambientes preservados de florestas de terra firme, mata ciliar e campinaranas. A vegetação de campinarana se distribui por aproximadamente 0,8 km^2, apresenta altura média do dossel de 14,2 m, área basal de 32,81 m^2/ha e 132,14 t/ha de biomassa (Tabela 1). Em uma visita prévia à área, foi constatado que o ambiente apresenta grande abundância de epífitas vasculares.

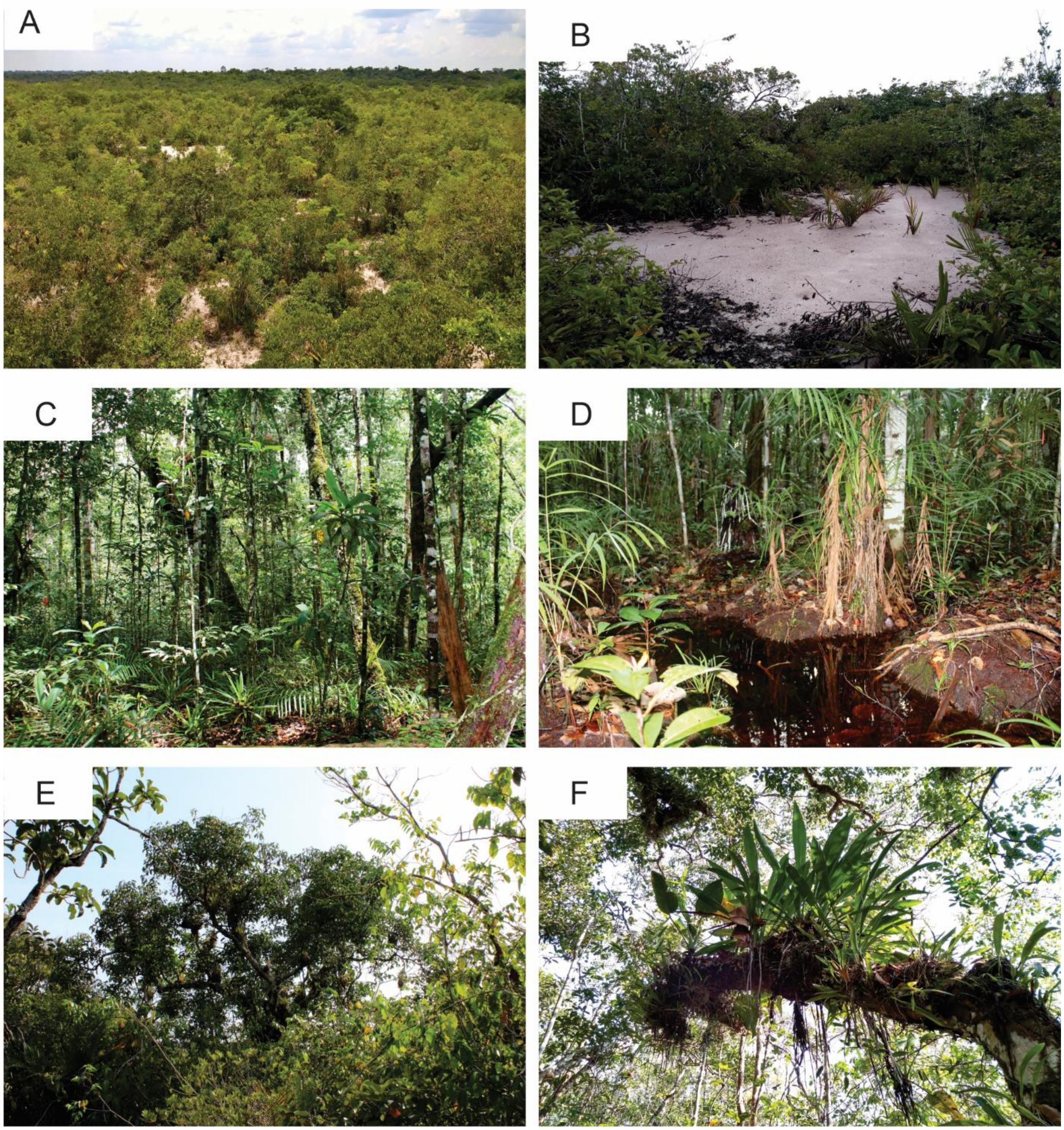

Figura 2. Ecossistemas de areia branca (Campinaranas amazônicas). A) Visão geral das campinaranas. B) Manchas de solo de areia branca descobertos em meio á vegetação. C) Sub-bosque das formações florestadas. D) Afloramento do lençol freático na estação chuvosa. E) Destaque para a espécie arbórea, *Aldina heterophylla* Spruce ex Benth. F) Grande quantidade de epífitas presentes sobre os forófitos.

2.2 Reserva Alto Cuieiras (ACR)

A base Alto Cuieiras (Figura 3c) faz parte do Mosaico de Unidades de Conservação do baixo Rio Negro, uma das maiores áreas protegidas da Amazônia. A base de pesquisa é coordenada pelo Instituto Nacional de Pesquisas da Amazônia (INPA) e está localizada às margens do Rio Cuieiras, distante aproximadamente 80 km da cidade de Manaus, Amazonas (Lat. 2°34’06” S, Long. 60°19’15” W). Nos entornos da base é possível encontrar florestas de terra firme, floresta de igapó e de campinaranas. A vegetação de campinarana estudada, se estende por aproximadamente 1,2 km^2, apresenta um dossel com altura média de 12,4 m, área basal de 19,71 m^2/ha e 214,27 t/ha de biomassa (Tabela 1).

2.3 Reserva Biológica da Campina (CBR)

A Reserva Biológica de Campina (Figura 3d) é uma unidade de conservação gerenciada pelo Instituto Nacional de Pesquisas da Amazônia (INPA). Está localizada às margens da rodovia BR 174, no Km 44, cerca de 50 km ao norte da cidade de Manaus, Amazonas (Lat. 2º35'19” S, Long. 60º01'59” W). A reserva possui 900 ha, sendo formada por florestas de terra-firme e campinaranas (Luizão, 1995). As florestas de campinaranas estão distribuídas em aproximadamente 1,5 m^2, o dossel tem altura média de 10,4 m, área basal de 17,98 m^2/ha e 95,31 t/ha de biomassa (Tabela 1). As áreas florestadas de campinaranas da CBR são dominadas pelas espécies arbóreas *Aldina heterophylla* Spruce ex Benth (Fabaceae) e *Pradosia schomburgkiana* (A.DC.) Cronquist (Sapotaceae) (Anderson et al. 1975). As epífitas vasculares são relatadas como muito abundantes e diversificadas na área, principalmente representadas pela família Orchidaceae (Braga & Braga 1975).

2.4 Reserva de Desenvolvimento Sustentável do Rio Negro (RDS - Rio Negro)

A RDS – Rio Negro (Figura 3e) também faz parte do Mosaico de Unidades de Conservação do Baixo Rio Negro; foi criada em 2008 e atualmente é administrada pelo Departamento de Mudanças Climáticas e Gestão de Unidades de Conservação da Secretaria Estadual de Meio Ambiente (DEMUC). A reserva está localizada aproximadamente 150 km da cidade de Manaus, Amazonas (Lat. 3°04’11” S, Long. 60°45’07” W). A RDS - Rio Negro contém em seus limites extensas áreas alagadas por florestas de igapó, florestas de terra-firme, formações pioneiras com influência agropastoril e campinaranas (IDESAM, 2016). A vegetação de campinaranas se estende por aproximadamente 3,2 km^2, apresenta dossel com a média de 9,1 m de altura, área basal de 10,90 m^2/ha e 51,34 t/ha de biomassa (Tabela 1). As espécies arbóreas com maiores indícies de valor de importância (IVI) são *A. heterophylla, Caraipa densifolia* Mart. (Calophyllaceae), *Adiscanthus fusciflorus* Ducke (Rutaceae), *Dimorphandra vernicosa* Spreng. ex Benth. (Fabaceae) e *Pagamea coriacea* Spruce ex Benth. (Rubiaceae) (Farroñay, 2019). Entre as epífitas vasculares, diversas espécies de Bromeliaceae e Orchidaceae são reportadas para a área (Farroñay, 2019).

2.5 Reserva de Desenvolvimento Sustentável Uatumã (RDS Uatumã)

A RDS Uatumã (Figura 3f) foi criada em junho de 2004 como forma de amenizar os impactos ambientais gerados em função da construção da Usina Hidrelétrica de Balbina (UHE Balbina), situada no rio Uatumã, município de Presidente Figueiredo (01º 55'S e 59º 28'O), e que inundou uma área de 300.000 hectares (IDESAM, 2009). A RDS Uatumã possui 424.430 hectares, está localizada a 330 m de Manaus, nos municípios de São Sebastião do Uatumã e Itapiranga (2º0'- 2º40'S; 58º0'- 59º20'O), e é constituída por extensas áreas de igapó, florestas de terra-firme e campinaranas. A floresta de campinarana estudada se localiza próximo á Torre ATTO (Amazonian Tall Tower Observatory), ocupa uma área aproximada de 4,2 km^2, apresenta dossel com a média de 13,4 m de altura, área basal de 13,83 m^2/ha e 89,12 t/ha de biomassa (Tabela 1). As espécies mais abundantes são *Emmotum orbiculatum* (Benth.) Miers (Metteniusaceae) e *P. schomburgkiana* (Demarchi et al. 2022).

Tabela 1: Características gerais das cinco áreas de campinaranas estudadas. Valores de área basal e biomassa foram estimados por hectare (Capitulo 1). AR – Reserva Asframa; ACR – Reserva Alto Cuieiras; CBR – Reserva Biológica da Campina; RNSDR – Reserva de Desenvolvimento Sustentável do Rio Negro; USDR – Reserva de Desenvolvimento Sustentável do Uatumã.

	AR	ACR	CBR	RNSDR	USDR
Distância da cidade de Manaus, AM (km)	110	80	50	150	200
Tamanho da campinarana (km^2)	0,8	1,2	1,5	3,2	4,2
Distância média da terra-firme circundante (m)	380	216	320	156	438
Altura média do dossel (m)	14,2	12,4	10,4	9,1	13,4
Área Basal (m^2/ha)	32,81	19,71	17,98	10,90	13,83
Biomassa (t/ha)	132,14	214,27	95,31	51,34	89,12

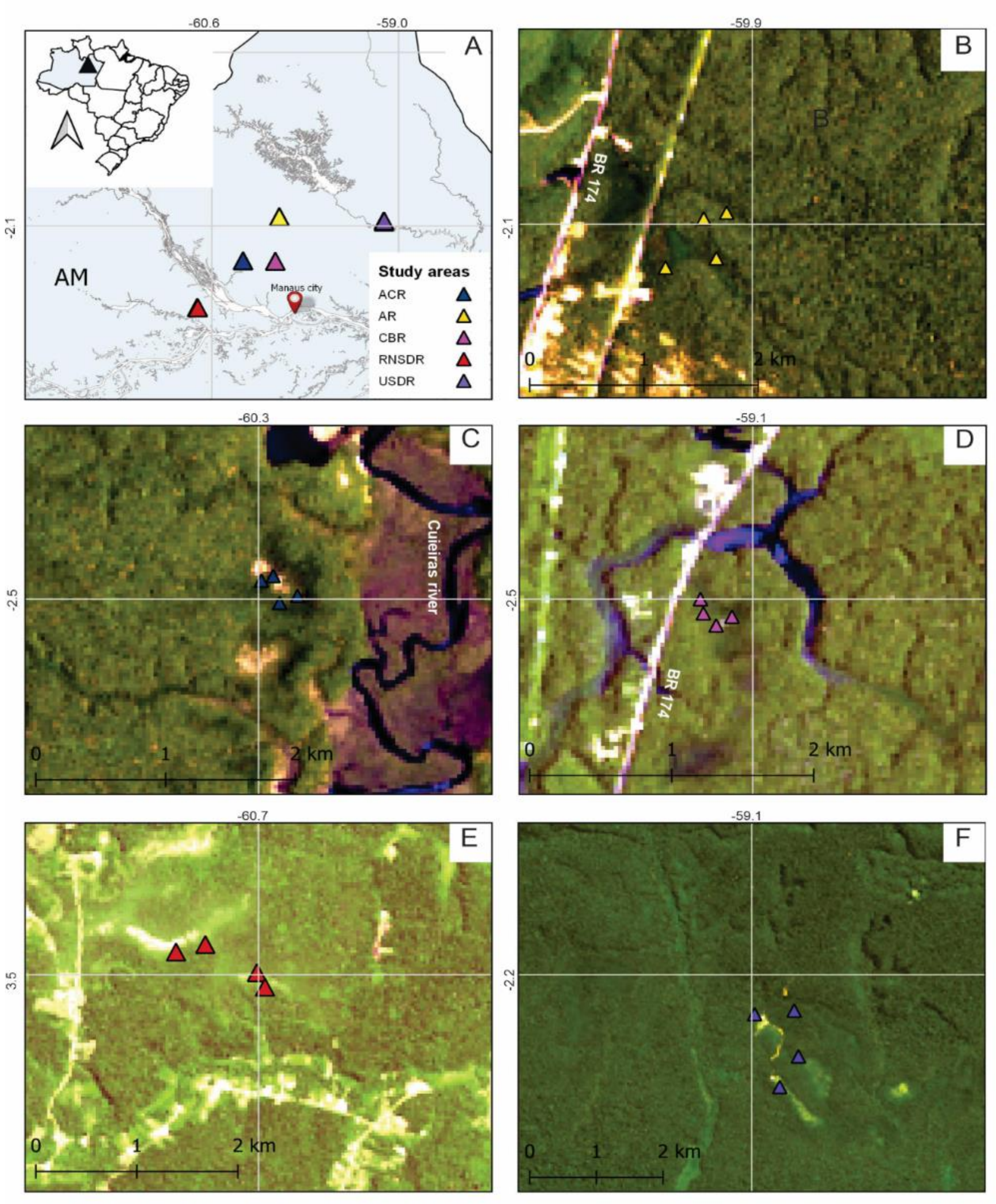

Figura 3. Localização das áreas de estudo em cinco ecossistemas de areia branca (campinaranas) da Amazônia central. A: Distribuição geral dos pontos de coleta no estado do Amazonas, Brasil. B: Reserva Asframa (AR). C: Reserva Alto Cueiras (ACR). D: Reserva Biológica da Campina (CBR). E: Reserva do Desenvolvimento Sustentável do Rio Negro (RNSDR). F: Reserva do Desenvolvimento Sustentável do Uatumã (USDR). Os pontos das parcelas estão indicados por triângulos de diferentes cores.

5. OBJETIVO GERAL

Esta tese teve como objetivo geral investigar a estrutura, composição e distribuição das comunidades de epífitas vasculares em cinco ecossistemas de areia branca (campinaranas) da Amazônia Central e relacionar os padrões observados com as características ambientais e estruturais da vegetação.

5.1. OBJETIVOS ESPECÍFICOS

A tese foi dividida em 5 capítulos, onde no **capítulo 1** foi verificada a composição das espécies de epífitas vasculares em cinco áreas de campinaranas, analisado a similaridade florística entre as áreas e relacionado a composição das espécies com variáveis ambientais e estruturais vegetação. No **capítulo 2** foi avaliado quais caraterísticas dos forófitos influenciam a riqueza, abundância e composição das espécies de epífitas vasculares nos gradientes verticais e horizontais. Já no **capítulo 3,** utilizando abordagem baseada na teoria de redes ecológicas complexas, se investigou a estrutura das interações entre epífitas e forófitos e a estabilidade do sistema a perturbações ambientais. No **capítulo 4** é apresentado um *checklist* e descrito detalhadamente como estão organizadas as comunidades de epífitas vasculares presentes em uma das áreas estudadas. Por fim, no **capítulo 5** é apresentado um guia fotográfico para auxiliar na identificação das espécies de epífitas vasculares presentes nas campinaranas da Amazônia central estudadas.

5.1.1. Objetivos específicos do Capítulo 1

1. Analisar se a composição de epífitas vasculares difere entre as áreas de campinaranas estudadas.

2. Verificar se a assembléia epífita é geograficamente estruturada, com áreas próximas compartilhando um maior número de espécies.

3. Identificar as espécies características de cada área estudada.

4. Avaliar se o tamanho da área estudada, distância da matriz florestal adjacente e as características estruturais da vegetação arbórea influenciam a composição e distribuição das comunidades de epífitas vasculares nas áreas estudadas.

5.1.2. Objetivos específicos do Capítulo 2

1. Avaliar se as características estruturais (altura, diâmetro e densidade da madeira) e a identidade taxonômica dos forófitos influenciam a distribuição vertical e horizontal das epífitas vasculares;

2. Analisar se a distribuição vertical das epífitas vasculares apresenta um padrão de estratificação e modularidade;

3. Identificar espécies ou grupos de epífitas indicadoras de cada uma das zonas ecológicas verticais dos forófitos.

5.1.3. Objetivos específicos do Capítulo 3

1. Investigar os padrões gerais de organização das comunidades de epífitas vasculares em cinco campinaranas da Amazônia central.

2. Analisar a estrutura e robustez das redes de interações epífitas-forófitos nas áreas de estudo utilizando métricas específicas baseadas na teoria de redes ecológicas.

3.Identificar as espécies de forófitos mais importantes para manter a estrutura e robustez das redes nos locais estudados.

5.1.4. Objetivos específicos do Capítulo 4

1. Descrever a flora das epífitas vasculares que ocorrem nas diferentes fitofisionomias de campinaranas encontradas na Reserva de Desenvolvimento Sustentável do Uatumã (RDS do Uatumã), no estado do Amazonas, Brasil.

2. Analisar quantitativamente a estrutura das comunidades de epífitas e calcular o valor de importância epifítica (IVE) das espécies para duas das fitofisionomias de campinaranas presentes na área.

5.1.5. Objetivos específicos do Capítulo 5

1. Elaborar um guia de campo contendo o registro fotográfico das espécies de epífitas vasculares presentes em cinco áreas de campinaranas da Amazônia central.

CAPÍTULO 1

Viviane Pagnussat Klein, Talitha Mayumi Francisco, Layon Oreste Demarchi, Jeisiane Santos da Silva, Adriano Costa Quaresma e Maria Teresa Fernandez Piedade. **Islands in the middle of the forest: size, distance and tree structure drives vascular epiphytes composition in Amazonian white-sand ecosystems.** Artigo em revisão no Brazilian Journal of Botany.

RESUMO

Fatores ambientais e características associadas às comunidades arbóreas influenciam os padrões de diversidade, composição e distribuição de plantas estruturalmente dependentes, como as epífitas vasculares. Neste estudo, verificamos a composição florística, estrutural e espacial de comunidades de epífitas vasculares presentes em cinco áreas de ecossistemas de areia branca (WSEs; campinaranas) na Amazônia Central, os quais estão localizados em unidades de conservação (UCs) e distantes aproximadamente 100 km entre si. Testamos as seguintes hipóteses: (1) a composição florística das epífitas vasculares difere entre as áreas dos WSEs e é possível encontrar espécies típicas em cada área, (2) as comunidades epífitas são geograficamente estruturadas, com áreas próximas compartilhando um maior número de espécies, e (3) o tamanho da área, a distância da matriz florestal adjacente e a estrutura da vegetação arbórea influenciam a composição e distribuição das comunidades epífitas vasculares nos WSEs estudados. Em 1,25 ha de WSE florestado, foram realizadas medições estruturais da vegetação, medidas do tamanho da mancha de WSE e da distância das parcelas aos ambientes adjacentes e todas as epífitas vasculares foram identificadas e quantificadas. Nossos resultados indicam que o tamanho dos WSE, a distância de ambientes adjacentes, a altura média do dossel e a área basal das espécies arbóreas influenciam a distribuição de epífitas vasculares nos WSEs, e que a composição de espécies difere entre os WSEs, mesmo que estejam geograficamente próximos. Além disso, observamos que as comunidades possuem estruturação geográfica, com áreas próximas compartilhando maior número de táxons entre si; entretanto, as espécies características e o valor de importância epifítica são diferentes entre as áreas.

Palavras-chave: Campinaranas, estrutura comunitária, conservação, floresta tropical

ABSTRACT

Environmental factors and characteristics associated with tree communities influence patterns of diversity, composition, and distribution of structurally dependent plants, such as vascular epiphytes. In this study, we verified the floristic, structural and spatial composition of vascular epiphyte communities present in five white-sand ecosystems (WSEs) in the Central Amazon that are located in conservation units (CUs) and are approximately 100 km apart in order to test the following hypotheses: (1) the floristic composition of vascular epiphytes differs between areas of WSEs and presents typical species in each of them, (2) the epiphytic communities is geographically structured, with nearby areas sharing a greater number of species, and (3) the size of the area, the distance from the adjacent forest matrix and the structure of the arboreal vegetation influence the composition and distribution of the vascular epiphytic communities in the WSEs of the study. In 1.25 ha of forested WSE, structural measurements of the vegetation, measurements of the size of the WSE and the distance of plots to adjacent environments were taken and all vascular epiphytes were identified and quantified. Our results indicate that WSE size, distance from adjacent environments, average canopy height and basal area of tree species influence the distribution of vascular epiphytes in WSEs, and that the species composition differs among WSEs, even if they are geographically close. In addition, we observed that the communities have geographical structuring, with nearby areas sharing a greater number of taxa among themselves; however, the characteristic species and the epiphytic importance value are different between the areas.

Keywords: Campinaranas, community structure, conservation, tropical forest

1. Introduction

One of the central points in ecological studies is to understand the factors responsible for generating and maintaining patterns of species diversity and distribution. Habitat heterogeneity is historically proposed as one of the factors that most drives species diversity in a given environment (Simpson 1949; MacArthur and Wilson 1967). This hypothesis postulates that structurally complex habitats have more ecological niches and consequently a greater variety of resources, which allows the coexistence of different species (Bazzaz 1975). In most habitats, the microclimatic and structural characteristics of the landscape are determined by plant communities, which exert considerable influence on patterns of distribution and interactions among species (Lawton 1983; McCoy and Bell 1991).

The effect of arboreal vegetation is even more prominent in structurally dependent organisms, as is the case with epiphytic plants. Vascular epiphytes are defined as non-parasitic plants that depend on the structure and mechanical support provided by other plant species, the phorophytes, which provide a substrate and a diversity of microhabitats for their establishment (Benzing 1990; Zotz 2016). Vascular epiphytes comprise a significant fraction of plant diversity, mainly in tropical forests, where they make up 52% of the local richness of vascular flora in mountainous forests (Kelly et al. 2004), while representing approximately 10% of global plant richness (Zotz et al. 2021). Epiphytes are also key components to the proper functioning of ecosystems, since they perform important ecological functions and add structural complexity to the forest canopy (Zotz 2016). Vascular epiphytes are influenced by distinct abiotic and biotic factors. On a geographical scale at the landscape level, the availability of water is one of the main limitations to the establishment of these plants, with the greatest diversity of epiphytes recorded in places with higher rainfall and fewer months of drought (Kreft et al. 2004; Mendieta-Leiva et al. 2020). On a local scale, multiple factors interfere with the establishment, development, and survival of species of vascular epiphytes (Einzmann and Zotz 2016). Among the primary factors, microclimatic conditions are usually cited (e.g., temperature, humidity, radiation, atmospheric pressure, winds) (Johansson 1974; Hietz and Hietz-Seifert 1995; Gotsch et al. 2017), as well as characteristics associated with tree communities (Taylor and Burns 2015; Wagner and Zotz 2020). Vegetation structure is an important predictor of diversity, as structured forests have trees of different sizes, ages and ontogenetic stages (Woods et al. 2019). Positive correlations between epiphyte richness and abundance with phorophyte size are well-established patterns (Quaresma et al. 2020; Wagner and Zotz 2020; Francisco et al. 2021). The size of the phorophytes integrates several fundamental ecological characteristics for epiphytes (Francisco et al. 2021), such as greater availability of area for colonization, a greater length of time in the environment and greater environmental heterogeneity within the canopy (Woods et al. 2015). Soil edaphic conditions are also important in the structuring of epiphytic communities, since they directly influence the structure and composition of the communities of host trees (Boelter et al. 2014; Ding et al. 2016).

The Amazon region encompasses a vast environmental heterogeneity, which influences the patterns of diversity and distribution of species. Among the environments that make up the Amazon domain are the white-sand ecosystems (WSEs) or “campinaranas”, which are irregularly distributed over approximately 334,879 km^2, and cover about 5% of the Amazon basin (Adeney et al. 2016). Large continuous areas of WSEs are observed mainly in the north of the Amazon, associated with the Negro and Branco River basins, while in the rest of the Amazon these environments are distributed in the form of islands of different sizes that are immersed in a matrix of other forest ecosystems, mainly *terra-firme* ecosystems (Prance 1996). The soils of the WSEs are characterized by being sandy (Podzols or Spodosols), extremely leached and poor in nutrients (Mendonça et al. 2015), with seasonal water saturation, flooding of the root system and exposure of the groundwater in some points during the rainy season, and a water deficit during the dry season (Anderson 1981). These stressful edaphic conditions promote a strong filtering effect and selective pressure that results in a specialized biota, with high phylogenetic endemism and distinct floristic composition when compared to other Amazonian environments (Stropp et al. 2011; Adeney et al. 2016). In addition, variations in soil texture, fertility and water saturation are observed within WSEs (Damasco et al. 2013; Demarchi et al. 2022), and these variations are considered the main reason for differences observed in the structure, composition and distribution of tree species (Damasco et al. 2013; Targhetta et al. 2015; Demarchi et al. 2018).

Given the close relationship between epiphytes and their phorophytes (Wagner et al. 2015), and considering the fragmented nature of WSEs in regions of the Central Amazon (Adeney et al. 2016), it is possible that different areas have different phorophyte composition and, consequently, the associated epiphytes community is also different. To analyze this issue, we designed this study, which was general objective of which was to verify whether the composition and structure of vascular epiphytes communities vary between the areas studied. Three hypotheses were tested: (1) the floristic composition of vascular epiphytes differs between areas of WSE and presents typical species in each of them, (2) the epiphyte communities is geographically structured, with nearby areas sharing a greater number of species, and (3) the size of the area, the distance from the adjacent forest matrix and the structural characteristics of the arboreal vegetation influence the composition and distribution of the communities of vascular epiphytes in WSE. According to the patterns that have previously been found for tree communities in WSEs (Damasco et al. 2013; Demarchi et al. 2018; Costa et al. 2020), we assume that the floristic composition of vascular epiphytes presents differences between the studied areas and that geographically closer areas share a greater number of species (MacArthur and Wilson 1963; Costa et al. 2020). In addition, we predicted that environmental characteristics and structural characteristics of vegetation influence the distribution patterns and composition of vascular epiphytes between the studied sites (Zotz 2016).

2. Materials and methods

2.1 Study areas – The Central Amazon has a pluvial equatorial climate (RADAM Brasil 1978), with an average annual rainfall of 2,077 ± 438.3 mm (analyzed period 1975-2005) and an average annual temperature of 27.0 °C (Carneiro and Trancoso 2007). The region has two well-defined seasons: a season marked by heavy rainfall, which extends from December to May with precipitation peaks in the months of March and April (monthly average of 298.4 and 278.7 mm, respectively), and a dry season, during the months of June to October, with August and September being the driest, both with a monthly average of 72.0 mm (Demarchi et al. 2022). The islands of WSEs are widely distributed in the region and have phytophysiognomies that range from forested areas, with trees up to 25 m high, to open phytophysiognomies, with predominance of herbaceous vegetation (Veloso et al. 1991). This variation is directly related to soil fertility and water saturation levels of each of these sites (Damasco et al. 2013; Targhetta et al. 2015).

This study was conducted in five forested WSEs, all inserted in conservation units (CUs), approximately 100 km apart, located near the city of Manaus, Amazonas state (Fig. 1):

Asframa Reserve (AR); Alto Cuieiras Reserve (ACR); Campina Biological Reserve (CBR); Rio Negro Sustainable Development Reserve (RNSDR) and Uatumã Sustainable Development Reserve (USDR). Detailed information on the areas studied is presented in Table 1.

2.2 Data collection and processing – In five areas of WSE, 1.25 ha of the tree component were inventoried. Four plots of 25 × 25 m were established randomly, with a minimum distance of 100 m between them, totaling 0.25 ha sampled in each CU. We recorded, identified and measured the circumference and height of all trees with diameter at breast height (DBH) of ≥ 10 cm. All vascular epiphytes (sensu Zotz et al. 2021) were identified and quantified with the aid of binoculars (Bushnell H2O, 10X42, FOV 305FT), a camera with close-up lenses and techniques of tree climbing in the phorophytes. We considered an epiphytic individual, any plant or group of plants geographically distinguishable from each other (Sanford 1968). Seedlings with undefined botanical characteristics were disregarded in the sampling. The fertile specimens collected were herborized and incorporated into the collection of the Herbarium of the National Institute for Amazonian Research (Herbarium INPA, acronym according to Thiers 2023), in the city of Manaus (Amazonas). For classification of the nomenclature, we followed the system proposed by the Angiosperm Phylogeny Group (APG IV 2016) and Pteridophyte Phylogeny Group (PPG I 2016).

The measurements of DBH (cm), total height (m) and wood density (g/cm^3) of the trees were used to calculate the basal area (m^2/ha), biomass (t/ha) and the average canopy height. Wood density values were obtained via the PELD/MAUA project database and the Global Wood Density database (Zanne et al. 2009). Basal area and biomass estimates were calculated following allometric models of estimates for tropical regions (Cunha et al. 2013;

Chave et al. 2014). For the average canopy height, the measurements of the individual height of each tree were used and the average height per plot was calculated.

High resolution satellite images followed by a calculation of the area were used to verify the coverage area (size) of the studied WSEs. The images were obtained from the Sentinel-2 (MSI Level-1C) satellite with a resolution of 10 m, available on the European Space Agency (ESA) Copernicus portal (https://scihub.copernicus.eu). The composition of the images was constructed using Band 3 (Green, Resolution 10 m), Band 4 – (Red, Resolution 10 m) and Band 8 (NIR, Resolution 10 m). The difference in spectra reflects the height of the vegetation and allowed us to establish the boundaries of the areas. The images were processed in QGIS software (QGIS Development Team) and the area calculation was performed using the function '$geometry'. Using the same processed images from the Sentinel satellite, we measured the distance (in meters) from the center point of each plot to the nearest point of *terra-firme* forest, in four directions. The distance between the two environments was defined as the average of the four measurements. The measurements were processed in the QGIS software using the algorithm "Distance to the Nearest Central Point".

2.3 Data analysis – The diversity of tree species and vascular epiphytes was calculated using Fisher's Alpha Diversity index (Fisher et al. 1943). The normality and homoscedasticity of the data were tested using the Shapiro-Wilk and Levene tests, respectively. In order to determine whether the diversity of vascular epiphytes differed between the sampled sites, an analysis of variance (ANOVA) was performed and then paired comparisons using Tukey's test.

The Mantel test (Legendre and Legendre 2012) based on a Euclidean distance matrix of geographic space and the Jaccard dissimilarity matrix of epiphytic species composition was used to examine whether the composition was related to the geographical location of the study areas. The statistical significance test for the Mantel correlation was based on 10,000 permutations. To observe the taxonomic similarity between the studied areas, grouping analyses were performed based on a presence and absence matrix (Jaccard index), and the unweighted pair group method with arithmetic mean (UPGMA) as the algorithm of the linkage method. The cophenetic correlation coefficient was used to measure the degree of fit between the cluster and the original similarity matrix (Borcard et al. 2011); and a Venn diagram was used to represent the number of unique and shared species among the sampled areas (Venn 1881).

Possible differences in the composition of epiphytic species among the WSEs were verified via ANOSIM similarity analysis, with 999 permutations (Clarke, 1993) and graphed with non-metric multidimensional scaling (NMDS), using the Bray-Curtis distance (Bray and Curtis 1957), which was reduced into two axes of an NMDS. To identify the relative contribution of individual species to the dissimilarity observed among the WSEs, percentage similarity was used (SIMPER, Clarke 1993). This analysis uses paired comparisons among the sampled groups and indicates the average contributions of each species to the overall average dissimilarity (Clarke 1993). The similarity percentage is based on the decomposition of the Bray-Curtis dissimilarity index. ANOSIM and SIMPER were calculated using the probabilistic significance obtained through 1,000 permutations. To analyze the effect of the environmental variables on the species composition we calculated the variance inflation factor (VIF), wherein highly correlated variables with VIF>5 were excluded (Petrie 2016). After selection, environmental variables (distance from the surrounding forest and size of areas of WSE) and structural variables of vegetation (mean canopy height, basal area, tree density and tree diversity) were used as linear predictors. The relationships were tested by means of the *envfit* function (Fits an Environmental Vector or Factor onto an Ordination), of the vegan package (Oksanen et al. 2022). The *envfit* function fits environmental vectors into an order and calculates multiple regressions of the variables with the ordering axes (environmental and structural vegetation variables are used as dependents and the selected ordering axes as explanatory variables). The original function provides a table with normalized regression coefficients (R^2), and significance based on the original permutation. Values of the coefficient of determination and the significance of the data were tested using permutation tests (999 permutations). All analyses were performed in R environment (R Core Team 2021) with the Vegan package (Oksanen et al. 2022) and VennDiagram (Chen 2022).

Quantitative data regarding the abundance of epiphytic species on the respective phorophytes were used to observe the structure of the communities of vascular epiphytes in the studied WSEs. The quantitative participation of epiphytic species was evaluated considering the absolute and relative frequencies of epiphyte occurrence on individual phorophytes (FAi and FRi) and on specific phorophytes (FAj and FRj). To obtain the epiphytic importance value index (IVe) of each species, the equations proposed by Waechter (1998) were used. The IVe was calculated because it provides important ecological information about the ability of species to colonize different substrates through reproduction, dispersion and establishment in the environment (Waechter 1998).

3. Results

3.1 Vascular epiphytes at the regional-level – In five areas of WSE, 486 individuals were recorded, which were distributed in 29 families, 39 genera and 52 species of phorophytes. Fabaceae Lindl. was the family with the highest number of phorophytic species (12 spp.), followed by Sapotaceae Juss. and Myrtaceae Juss, with four species each. *Myrcia* DC. (4 spp., Mytaceae) and *Licania* Aubl. (3 spp., Chrysobalanaceae) were the most representative genera. Vascular epiphytes were represented by 17,808 individuals, distributed in 18 families, 60 genera and 118 species (Table 2). The richest evolutionary lineage was monocots with five families and 82 species, which contributed 69.5% of the total species richness. Ferns were represented by eight families and 25 species (21.2%) and eudicots by five families and 11 species (9.3%). Orchidaceae (62 spp.), Bromeliaceae (12 spp.) and Polypodiaceae (10 spp.) were the richest families in species, concentrating 71% of the total species richness in the WSEs studied. The most representative epiphytic genera were *Epidendrum* L. (11 spp., Orchidaceae), *Maxillaria* Ruiz & Pav. (11 spp., Orchidaceae), *Aechmea* Ruiz & Pav. (7 spp., Bromeliaceae) and *Elaphoglossum* Schott ex J.Sm. (5 spp., Dryopteridaceae).

The richness of epiphytic species on individual phorophytes ranged from 1 to 31, while the number of individuals ranged from 1 to 704. On average, each phorophyte had 37 vascular epiphytes. The species *Aldina heterophylla* Spruce ex Benth (Fabaceae) was the phorophyte that hosted a higher number of epiphyte species, 105 species and 13,378 individuals, respectively. The cluster analysis showed the formation of three groups, which presented low floristic similarity at the regional level (Fig. 2a). Only 18 species of vascular epiphytes (15%) are shared among all the studied areas (Fig. 2b). The Mantel test indicated a positive and significant spatial correlation between geographic distance and vascular epiphyte composition ($r = 0.5587$; $p < 0.05$). The composition of vascular epiphytes differed significantly between the sampled WSEs (ANOSIM, $R = 0.51$; $p = 0.001$). The average canopy height, the size of the WSE, the distance from the studied plot to the surrounding *terra-firme* forest and the basal area of the tree community were significantly related to the structure of the vascular epiphyte community (Fig. 3; Table 3). The SIMPER analysis indicated that 106 species of epiphytes contributed significantly to the observed differences in floristic composition among the five areas (Table S1). In the paired comparisons between areas, a greater number of indicative species was observed for the USDR, reflecting the pattern of difference observed in the cluster analysis (Fig. 2a).

In general, vascular epiphytes in WSEs have few dominant species and many species with low number of individuals. Six species, *Prosthechea aemula* (Lindl.) W. E. Higgins (IVe = 5.64, Fig. 4A, Orchidaceae), *Codonanthopsis crassifolia* (H. Focke) Chautems & Mat. Perret (IVe = 5.64, Fig. 4B, Gesneriaceae), *Brassavola martiana* Lindl. (IVe = 4.94, Fig. 4C, Orchidaceae), *Elaphoglossum discolor* (Kuhn) C. Chr. (IVe = 4.69, Fig. 4D, Dryopteridaceae), *Maxillaria lutescens* Scheidw. (IVe = 4.13, Fig. 4E; Orchidaceae) and *Cattleya wallisii* (Linden) Linden ex Rchb.f. (IVe = 3.49, Fig. 4F, Orchidaceae), presented the highest values of epiphytic importance for the WSEs (Table 4). In addition to being widely distributed on the phorophytes, these six species accounted for more than half of the total abundance of epiphytes recorded (53.1%). In contrast, most species (65 spp., 55%) presented less than 20 individuals, representing only 2.4% of the total abundance of epiphytes.

3.2 Vascular epiphytes at the local-level -Richness (F = 6.32; p = 0.03), diversity (F = 9.07; p = 0.0006) and number of epiphyte families (F = 7.922; p =0.001), as well as phorophyte species richness (F = 3.089; p = 0.048), differed significantly between the WSE sites studied (Fig. 5). The sites with the highest epiphytes species richness and diversity were ACR (71 spp. and α-Fisher = 8.22) and AR (66 spp. and α-Fisher = 8.8), respectively. Similarly, the species with the highest IVe values are different between sites (Table S2). Only *Brassavola martiana* (Orchidaceae) and *Codonanthopsis crassifolia* (Gesneriaceae) are among the 10 species with the highest IVe values in all areas. The Alto Cuieiras Reserve presented more expressive values of individuals (5,615) families (15), genera (39) and epiphytic species (71), occupying 132 phorophytes. On the other hand, the lowest representativeness was observed in RDS Uatumã, where we recorded 1,174 individuals, 10 families, 26 genera and 42 species, of epiphytes, occupying 95 phorophytes. Individual values by area and the species with the highest IVe for the sampled sites are represented in Table S2.

4. Discussion

Although WSEs are distributed over approximately 5% of the Amazon region (Adeney et al. 2016), little is known about the ecological patterns of richness, abundance and composition of vascular epiphytes in these environments. The results of this study indicate that the flora of vascular epiphytes presents expressive species richness and high abundance of individuals, which contributes substantially to the increase in plant diversity in these environments. We show that the distribution of epiphytes is influenced by environmental and structural variables of the vegetation; in addition, we show that the communities have geographical structuring, in which nearby areas share a greater number of taxa among themselves. However, the species composition differs between the areas of WSE, despite being geographically close. These results show that factors that are intrinsic to each landscape, such as the size of the area and proximity of the surrounding forest, also have an effect on the distribution of the species.

The vascular epiphyte families with a greater number of species in this study (Orchidaceae, Bromeliaceae and Polypodiaceae) are also the richest worldwide (Zotz 2013; Taylor et al. 2021), especially in Neotropical regions (Zotz et al. 2021). The most species-rich genera in WSEs, *Epidendrum* and *Maxillaria*, are prominent in the Neotropical region, including the Amazonian domain (Pinheiro and Cozzolino 2013; Quaresma et al. 2022). *Epidendrum* is one of the richest genera of Orchidaceae, represented by approximately 1,400 species, and has a wide distribution in the Neotropical region, consisting mainly of epiphytic species (Pinheiro and Cozzolino 2013; Chase et al. 2015). Similarly, *Maxillaria* is one of the most diverse and species-rich genera of Neotropical orchids, most of which are epiphytes (Chase et al. 2015). The WSEs are traditionally recognized for having low species richness, when compared to other Amazonian ecosystems (Stropp et al. 2011). However, for vascular epiphytes, the species richness recorded in this study is very similar to the values reported for *terra-firme* forests (122 spp.; Boelter et al. 2014), and flooded environments of the Central Amazon (96 spp.; Quaresma et al. 2020) and higher than the values observed in the WSEs of Guyana (67 spp.; ter Steege and Cornelissen 1989), of the southwest of the Brazilian Amazon (7 ssp.; Gottsberger and Morawetz 1993), of Venezuela (12 spp.; Coomes and Grubb 1996) and the Central Amazon (68 spp.; Mari et al. 2016). However, it is worth highlighting that the sampling effort between the highlighted studies may reflect the differences observed in the number of species between the sites studied.

The distribution of vascular epiphytes in WSEs reflects the general pattern of plant distribution in tropical forests, with few very abundant species, while most species are represented by few individuals (Richard 1996*). Prosthechea aemula* and *Codonanthopsis crassifolia* had the highest IVe and, in addition to being abundant in the WSEs, these species are also generalists in the occupation of phorophytes, occupying an average of 58% of phorophyte species. *P. aeumula* is recurrently reported as the most abundant species in the WSEs of the Central Amazon (Braga 1982; Mari et al. 2016; Klein et al. 2022), where it forms large clusters of individuals that almost entirely cover the thickest branches of the phorophytes. The representativeness of *C. crassifolia* has also been evidenced in WSEs (Klein et al. 2022) and in other Amazonian ecosystems (Quaresma et al. 2017). The high representativeness of these taxa in the WSEs reinforce the idea that the distribution of vascular epiphytes is density-dependent and suggest competitive advantages when compared to rare species (Janzen et al. 2020). Although the WSEs harbor endemic species and lineages of fungi (Singer and Araujo 1979), bryophytes (Lisboa 1976) and angiosperms (Fine and Baraloto 2016), few species of vascular epiphytes are restricted to the WSEs (Mari et al. 2016; Klein et al 2022), suggesting that many species of vascular epiphytes may be shared with other adjacent forest ecosystems (Nieder et al. 2000).

The WSEs showed significant differences in species composition. Studies have shown that the composition of epiphytes differs between dry and flooded coastal sandy forests (Quaresma and Jardim 2014), between environments of floodplains and flooded forests (Quaresma et al. 2017) and between biogeographic regions of the Amazon (Quaresma et al. 2022). Our study indicated that the compositional variation of vascular epiphytes also occurs between areas that are geographically very close to the Amazon. Although the WSEs of the Central Amazon are considered similar in origin and environmental conditions (Capurucho et al. 2020), small variations in soil microclimatic and edaphic characteristics can alter the diversity, composition and structure of its arboreal vegetation (Damasco et al. 2013; Demarchi et al. 2018, 2022), which may also influence the distribution of the associated epiphytic assemblage (Burns and Zotz 2010). Epiphytes are plants that are structurally dependent on phorophytes, which provide substrate and a diversity of microclimatic conditions and microhabitats (Woods et al. 2015). Although specificity in interactions between epiphytes and phorophytes are rarely reported (Francisco et al. 2018), some species of epiphytes may show preferences for certain traits of phorophytes (Callaway et al. 2002; Barberena et al. 2019; Francisco et al. 2021). In this sense, variations in the composition of tree species can play an important role in determining the composition and species diversity of epiphytes (Wagner et al. 2015; Ding et al. 2016).

The distribution of epiphytic species in the WSEs was significantly explained by structural variables of vegetation (average canopy height and basal area). Vegetation structure is related to a number of factors that are predictors of diversity in epiphyte communities, such as habitat availability, branch structure, colonization time, and microclimatic heterogeneity (Woods et al. 2015). The basal area is directly related to the size of the trees (Chave et al. 2014). Positive relationships between epiphyte diversity and phorophyte size are already well established (Wagner et al. 2015) because the size of the phorophyte combines a set of complex factors that are closely related to the distribution of vascular epiphytes (Francisco et al. 2021). Large trees have been available in the environment for longer and provide a greater area for colonization and establishment of epiphytes, in addition to presenting greater structural heterogeneity and microclimatic variations within the crown, which allows different groups of epiphytes to establish themselves (Woods et al. 2015). Similarly, the height of the forest canopy also contributed to the formation of distinct microhabitats, since environmental conditions such as relative humidity, vapor pressure deficit and brightness gradients vary from the crown to the base of the tree trunk (Hietz and Hietz-Seifert 1995; Cardelús and Chazdon 2005).

In the Central Amazon, the WSEs have an insular distribution, unequal size and are surrounded by other types of vegetation, which in the case of the studied areas are *terra-firme* forests (Adeney et al. 2016). Our results show that the size of the WSEs and the distance between the plots and the surrounding *terra-firme* forest significantly influenced the composition of vascular epiphytes. The area effect and degree of connectivity between the "islands" is historically proposed as a precursor to species diversity (MacArthur and Wilson 1963). Larger areas offer greater surface area for colonization and generally greater environmental heterogeneity, which provides for the coexistence of species and, consequently, increases local richness (Potts et al. 2004; Udy et al. 2021). Despite our results showing evidence related to the theory of island biogeography (MacArthur and Wilson 1963), WSEs cannot be thought of as isolated islands, since in the lowlands of the Amazonian plains, several species of surrounding ecosystems such as *terra-firme* and the flooded forest environments can colonize these areas (Damasco et al. 2013, Janzen et al. 2020); therefore, future studies are necessary to tetst this hypothesis for the epiphytic component in a context of WSE environments.

The vegetation structure of *terra-firme* forests, which is formed mainly by tall and dense trees and harbors rich and diverse communities of vascular epiphytes (Stropp et al. 2011; Boelter et al. 2014), can facilitate seed dispersal and act as propagule sources for contiguous environments (Thomson et al. 2011). Whereas most, or part, of the large epiphytic taxa disperse their reproductive structures by wind (e.g., orchids, bromeliads, and ferns), proximity between environments may result in dispersal of propagules via mass effect of surrounding habitats (Shmida and Wilson 1985). However, although most of the species recorded in this study have small reproductive structures and are supposedly suitable for wind dispersal (Benzing 1990), long-distance dispersal does not seem to be as effective for the studied environments, since the floristic similarity between WSE islands was low and only 18 species (15%) were shared among all the studied areas, while 41 species (35%) occur exclusively in one of the studied areas. In fact, different Amazonian ecosystems share greater similarity in the composition of vascular epiphytes, when belonging to the same biogeographic region, than the same environment in a different biogeographic region (Quaresma et al. 2022). This distribution pattern was also evidenced for the tree communities of WSEs, with greater floristic similarity with surrounding forests being observed (but not with non-white sand forests) than between geographically distant WSEs (García-Villacorta et al. 2016).

Although the WSEs studied are all located in the same biogeographic region, and in geographically relatively close areas, the flora of vascular epiphytes presented geographically structured distribution, in which nearby areas share a greater number of taxa. In the Central Amazon, WSEs have an insular distribution, which is possibly one of the limiting factors for the dispersion and sharing of propagules between sites (Costa et al. 2020). Although there is no biological barrier that limits long-distance dispersal for most epiphytes, the effectiveness of dispersal is directly related to the distance from the source of the propagule (Werner and Gradstein 2008) and possibly depends on the density of adult reproductive individuals (Janzen et al. 2020). In addition, success in the process of dispersal of propagules is only one of the stages of successful colonization (Einzmann and Zotz 2016), since species with high dispersion rates can reach other areas, but do not establish themselves due to the intrinsic conditions of each landscape, or even because they do not find a suitable phorophyte for propagule fixation, thus increasing floristic differentiation between areas, even on a small scale (Quaresma et al. 2022).

In recent years, anthropogenic actions have caused immense changes and fragmentation of Amazonian vegetation, including in the WSEs. The use of land for agricultural activities, logging, burning, sand extraction and the growth of cities are among the main threats to the WSEs (Adeney et al. 2016). These activities alter the structure of the environment, endanger all the associated components, and also compromise the ecosystem services provided (Nadkarni et al. 2004). Historically, WSEs have not been considered a high priority in conservation policies, given the low number of conservation units that cover this type of habitat (Adeney et al. 2016). However, it is recognized that WSEs have many lineages and endemic species, which indicates their extreme ecological importance (Fine and Baraloto 2016). We suggest that future studies in these environments should consider other landscape metrics to better understand the processes that shape and structure the composition and distribution of vascular epiphytes. In addition, we observed that the epiphytic flora is different among the WSE “islands”, even the geographically close ones, which reinforces the need for effective conservation measures that consider the particularities of each landscape, as well as all the ecological components present in this complex and unique Amazonian ecosystem.

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Author contributions

All authors participated in the elaboration and writing of the manuscript. VPK, ACQ, and MTFP designed the survey. VPK, JS, LDO and ACQ carried out the field collections. VPK and TMF organized and performed the statistical analyses. All the authors drafted and critically revised the manuscript. All authors have read and approved the manuscript.

Declarations

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

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List of Tables

Table 1 General characteristics of the five areas of white-sand ecosystems (WSEs) studied. Values referring to species diversity (α-Fisher's); the richness and abundance of trees refers to the total area (0.25 ha) sampled per habitat. Basal area and biomass values were estimated per hectare. AR – Asframa Reserve; ACR – Alto Cuieiras Reserve; CBR – Campina Biological Reserve; RNSDR – Rio Negro Sustainable Development Reserve; USDR – Uatumã Sustainable Development Reserve. Vegetation types: TF – *terra-firme* forest; GF – gallery forest; FF – flooded forest; WSE – white sand ecossystem.

Location	AR	ACR	CBR	RNSDR	USDR
Distance from Manaus (km)	110	80	50	150	200
WSE area (km^2)	0.8	1.2	1.5	3.2	4.2
Average distance from the surrounding TF (m)	380	216	320	156	438
Biomass (t/ha)	132.14	214.27	95.31	51.34	89.12
Basal area (m^2/ha)	32,81	19.71	17.98	10.90	13.83
Vegetation types	TF, WSE, GF	TF, FF, WSE	TF, WSE	TF, FF, WSE	TF, FF, WSE

Table 2 Vascular epiphytes species present in the study areas in white-sand ecosystems of the Central Amazon. Values 0 and 1 represent the presence or absence of the species in the area. (AR) Asframa Reserve, (ACR) Alto Cuieiras Reserve, (CBR) Campina Biological Reserve, (RNSDR) Rio Negro Sustainable Development Reserve; (USDR) Uatumã Sustainable Development Reserve.

Group	Botanical Family	Vascular Epiphyte Species	AR	ACR	CBR	RNSDR	USDR
F	Aspleniaceae	Asplenium sp.	1	0	0	0	0
E	Dryopteridaceae	*Elaphoglossum discolor* (Kuhn) C.Chr.	1	1	1	1	0
R		*Elaphoglossum glabellum* J.Sm.	1	1	1	1	0
N		*Elaphoglossum obovatum* Mickel	1	1	1	1	1
S		*Elaphoglossum plumosum* (Fée) T.Moore	1	1	1	1	1
		Elaphoglossum raywaense (Jenman) Alston	0	0	1	0	0
	Hymenophyllaceae	*Hymenophyllum polyanthos* (Sw.) Sw.	1	1	1	1	1
		Trichomanes crispum L.	0	0	1	0	1
		Trichomanes martiusii C.Presl	1	1	0	0	0
		Trichomanes spruceanum Hook.	1	1	0	0	0
	Lindsaeaceae	*Lindsaea lancea* (L.) Bedd.	1	1	0	0	0
	Nephrolepidaceae	*Nephrolepis rivularis* (Vahl) Mett. ex Krug	0	1	0	0	0
	Polypodiaceae	*Cochlidium furcatum* (Hook. & Grev.) C.Chr.	1	1	1	0	0
		Cochlidium pumilum C.Chr.	1	0	0	0	0
		Cochlidium serrulatum (Sw.) L.E.Bishop	0	1	0	1	0

		Microgramma baldwinii Brade	1	1	1	1	1
		Microgramma percussa (Cav.) de la Sota	0	0	0	1	0
		Moranopteris nana (Fée) R.Y. Hirai & J. Prado	1	0	1	1	1
		Pleopeltis bombycina (Maxon) A.R.Sm	1	0	0	0	0
		Pleopeltis hirsutissima (Raddi) de la Sota	0	0	1	1	0
		Serpocaulon attenuatum (Humb. & Bonpl. ex Willd.) A.R. Sm.	0	1	1	1	0
		Serpocaulon sessilifolium (Desv.) A.R.Sm.	0	0	0	1	0
	Pteridaceae	*Hecistopteris pumila* (Spreng.) J.Sm.	1	1	0	0	0
		Vittaria lineata (L.) Sm.	0	0	0	1	0
	Schizaeaceae	*Actinostachys pennula* (Sw.) Hook.	1	1	1	0	1
ANGIOSPERM	Araceae	*Anthurium bonplandii* Bunting	0	1	0	0	0
		Anthurium eminens Schott	1	0	0	0	1
		Anthurium gracile (Rudge) Lindl.	1	1	1	1	1
		Anthurium obtusum (Engl.) Grayum	1	0	0	0	1
		Philodendron melinonii Brongn. ex Regel	1	1	0	0	0
		Philodendron pulchrum G.M.Barroso	0	1	1	0	1
	Bromeliaceae	*Aechmea bromeliifolia* (Rudge) Baker	1	0	0	0	1
		Aechmea huebneri Harms	0	1	0	1	1
		Aechmea longifolia (Rudge) L.B.Sm. & M.A.Spencer	0	1	0	0	0
		Aechmea mertensii (G.Mey.) Schult. & Schult.f.	0	0	1	1	1

S		*Aechmea rodriguesiana* (L.B.Sm.) L.B.Sm.	0	1	0	0	0
		Aechmea setigera Mart. ex Schult. & Schult.f.	0	1	1	0	0
		Aechmea vallerandii (Carrière) Erhardt, Götz & Seybold	0	0	1	0	0
		Araeococcus micranthus Brongn.	0	0	0	1	0
		Guzmania brasiliensis Ulle	1	1	0	1	0
		Mezobromelia pleiosticha (Griseb.) Utley & H.Luther	0	0	0	1	0
		Tillandsia adpressiflora Mez	1	1	1	1	1
		Tillandsia bulbosa Hook.f.	0	0	0	1	0
	Burmanniaceae	*Apteria aphylla* (Nutt.) Barnhart ex Small	0	0	0	1	0
	Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	0	1	1	1	0
	Clusiaceae	*Clusia insignis* Mart.	1	1	1	1	1
		Clusia nemorosa G.Mey.	1	1	1	1	1
		Clusia penduliflora Engl.	1	0	0	0	0
		Clusia spathulaefolia Engl.	1	1	0	0	0
		Clusia ucamira J.E. Nascim. & Bittrich	1	1	0	0	0
	Cyclanthaceae	*Ludovia lancifolia* Brongn.	0	1	1	1	1
	Gesneriaceae	*Codonanthopsis crassifolia* H. Focke) Chautems & Mat. Perret	1	1	1	1	1
		Codonanthopsis dissimulata (H.E.Moore) Wiehler	1	1	1	0	0
		Codonanthopsis ulei Mansf.	1	1	1	1	0
	Moraceae	*Ficus mathewsii* (Miq.) Miq.	0	0	0	1	0

Orchidaceae	*Acianthera miqueliana* (H.Focke) Pridgeon & M.W.Chase	1	1	0	0	0
	Aganisia cyanea (Schltr.) Rchb.f.	1	0	0	0	0
	Batemannia colleyi Lindl.	0	1	0	0	0
	Bifrenaria longicornis Lindl.	1	1	1	1	1
	Bifrenaria venezuelana C.Schweinf.	0	1	0	0	0
	Brassavola martiana Lindl.	1	1	1	1	1
	Bulbophyllum setigerum Lindl.	0	0	0	1	0
	Campylocentrum fasciola (Lindl.) Cogn.	1	0	0	0	0
	Cattleya wallisii (Linden) Linden ex Rchb.f.	1	1	1	1	1
	Caularthron bicornutum (Hook.) Raf.	0	1	1	1	1
	Dichaea picta Rchb.f.	1	0	0	1	0
	Encyclia chloroleuca (Hook.) Neumann	1	1	1	1	0
	Encyclia conchaechila (Barb.Rodr.) Porto & Brade	0	0	0	0	1
	Encyclia mapuerae (Huber) Brade & Pabst	1	1	1	1	1
	Epidendrum apuahuense Mansf.	0	0	0	0	1
	Epidendrum bahiense Rchb.f.	1	1	1	1	1
	Epidendrum carpophorum Barb.Rodr.	1	1	0	1	1
	Epidendrum compressum Griseb.	0	1	1	0	0
	Epidendrum micronocturnum Carnevali & G.A.Romero	1	1	1	1	1
	Epidendrum microphyllum Lindl.	1	1	0	0	1

Epidendrum orchidiflorum (Salzm.) Lindl.	0	0	0	1	0
Epidendrum rigidum Jacq.	1	1	1	1	0
Epidendrum schlechterianum Ames	1	0	1	1	0
Epidendrum sculptum Rchb.f.	0	0	1	0	0
Epidendrum strobiliferum Rchb.f.	1	1	1	1	1
Eriopsis sceptrum Rchb.f. & Warsz.	0	0	0	0	1
Hylaeorchis petiolaris (Schltr.) Carnevali & G.A.Romero	0	1	0	0	0
Jacquiniella globosa (Jacq.) Schltr.	1	0	0	0	0
Macroclinium mirabile (C. Schweinf.) Dodson	0	0	1	0	0
Madisonia kerrii (Braga) Luer	1	1	0	0	0
Maxillaria brasiliensis Brieger & Illg	1	1	1	0	0
Maxillaria desvauxiana Rchb.f.	0	1	1	0	0
Maxillaria obtusa (Lindl.) Molinari	0	1	0	0	0
Maxillaria kegelii Rchb.f.	1	0	0	0	1
Maxillaria lutescens Scheidw.	1	1	1	1	0
Maxillaria parviflora (Poepp. & Endl.) Garay	1	0	1	1	1
Maxillaria pendens Pabst	1	1	1	1	0
Maxillaria subrepens (Rolfe) Schuit. & M.W.Chase	0	1	0	1	0
Maxillaria superflua Rchb.f.	1	1	1	1	1
Maxillaria tenui Lindl.	0	1	0	0	0

Maxillaria uncata Lindl.	0	1	1	1	0
Notylia aromatica Barker ex Lindl.	0	0	1	0	0
Octomeria grandiflora Lindl.	1	1	0	0	1
Octomeria taracuana Schltr.	1	0	0	0	0
Octomeria yauaperyensis Barb.Rodr.	0	1	0	0	0
Orleanesia amazonica Barb.Rodr.	0	1	1	0	0
Pabstiella yauaperyensis (Barb.Rodr.) F.Barros	0	1	0	0	0
Polystachya concreta (Jacq.) Garay & Sweet	1	0	0	1	0
Polystachya stenophylla Schltr.	1	0	0	1	1
Prosthechea aemula (Lindl.) W.E.Higgins	1	1	1	1	1
Prosthechea crassilabia (Poepp. & Endl.) Carnevali & I.Ramírez	0	0	1	1	1
Rodriguezia lanceolata Ruiz & Pav.	1	0	1	1	0
Rudolfiella aurantiaca (Lindl.) Hoehne	0	0	0	1	1
Scaphyglottis sickii Pabst	1	0	0	0	0
Scaphyglottis stellata Lodd. ex Lindl.	1	0	0	0	0
Scuticaria steelei (Hook.) Lindl.	1	0	1	0	0
Sobralia bletiae Rchb.f.	0	0	1	0	0
Sobralia granitica G.A.Romero & Carnevali	0	0	0	0	1
Sobralia sessilis Lindl.	0	1	1	0	0
Specklinia picta (Lindl.) Pridgeon & M.W.Chase	0	1	1	1	0

	Trichosalpinx orbicularis (Lindl.) Luer	1	1	0	1	0
	Vanilla bicolor Lindl.	0	1	0	0	0
Urticaceae	*Coussapoa asperifolia* Trécul	1	1	0	0	0

Table 3 Relationship of environmental variables (distance from the surrounding forest and size of areas) and structural of forests (average canopy height, alpha tree diversity, basal area, tree density) of WSEs of the Central Amazon with the first two axes of non-metric multidimensional scaling (NMDS). Significance values obtained by permutation tests (999 permutations). * Indicates significance values.

Variables	NMDS1	NMDS2	R^2	Pr(>r)
Size of WSE forest patches	0.93292	0.36008	0.5436	0.001**
Distance from surrounding forest	0.78715	-0.61676	0.4966	0.002***
Tree density	-0.00664	-0.99998	0.1168	0.339
Tree alpha diversity	-0.99986	-0.01702	0.1362	0.275
Basal area	-0.47956	-0.87751	0.3610	0.026*
Average canopy height	-0.01349	-0.99991	0.5626	0.003**

Table 4 Structural parameters of the ten main species of vascular epiphytes in five areas of white-sand ecosystems of the Central Amazon. Abe – absolute abundance of epiphyte species; Nip – number of phorophytes occupied by the epiphyte species; Spi – number of phorophytes species occupied by the species epiphytes; FAi – absolute frequency of the epiphyte species on the individual phorophyte; FRi relative frequency of the epiphyte species on the individual phorophyte; FAj – absolute frequency of epiphytic species in specific phorophytes; FRj – relative frequency of the epiphyte species on the specific phorophyte; IVe - epiphytic importance value.

Vascular epiphyte species	Botanical family	Abe	Nip	Spi	FAi	Fri	FAj	FRj	IVe
Prosthechea aemula	Orchidaceae	4,130	162	30	33.4	7.13	57.6	4.14	5.64
Codonanthopsis crassifolia	Gesneriaceae	725	159	31	32.8	7.00	59.6	4.28	5.64
Brassavola martiana	Orchidaceae	1,027	146	25	30.1	6.43	48.0	3.45	4.94
Elaphoglossum discolor	Dryopteridaceae	452	122	29	25.2	5.37	55.7	4.00	4.69
Maxillaria lutescens	Orchidaceae	2516	106	26	21.9	4.67	50.0	3.59	4.13
Cattleya wallisii	Orchidaceae	613	102	18	21.0	4.49	34.6	2.48	3.49
Epidendrum strobiliferum	Orchidaceae	903	91	18	18.8	4.01	34.6	2.48	3.24
Elaphoglossum glabellum	Dryopteridaceae	641	85	23	17.5	3.74	44.2	3.17	3.46
Tillandsia adpressiflora	Bromeliaceae	685	79	19	16.3	3.48	36.54	2.62	3.05
Elaphoglossum obovatum	Dryopteridaceae	357	68	18	14.0	2.99	34.6	2.48	2.74

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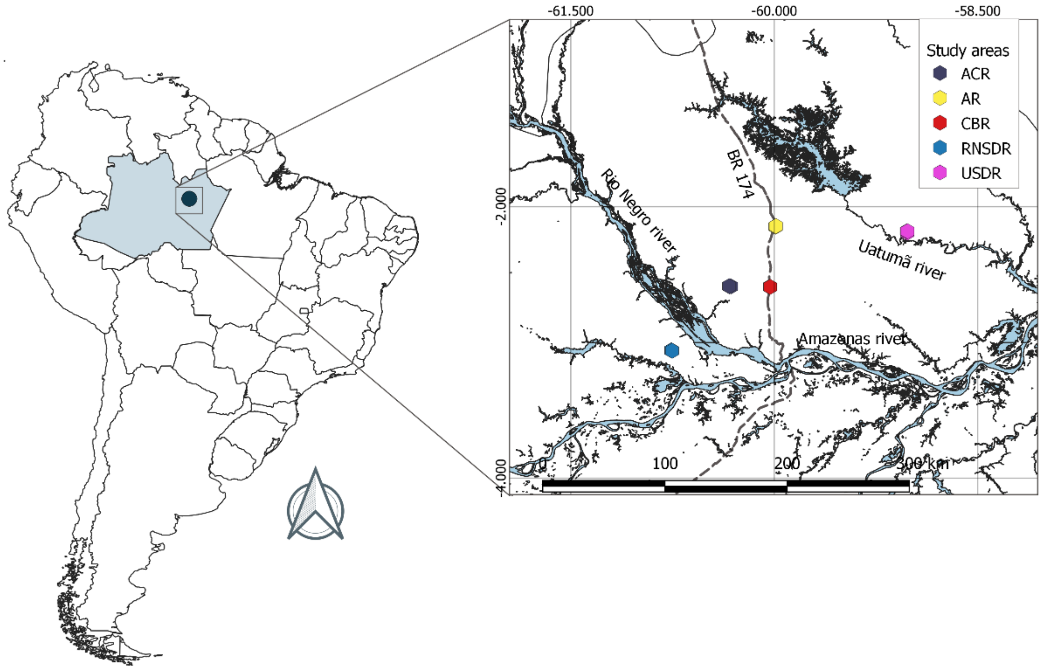

Fig. 1 Location of the five study areas of white-sand ecosystems (WSE) in the Central Amazon; AR – Asframa reserve; ACR – Alto Cuieiras reserve; CBR – Campinas Biological Reserve; RNSDR – Rio Negro Sustainable Development Reserve; USDR – Uatumã Sustainable Development Reserve

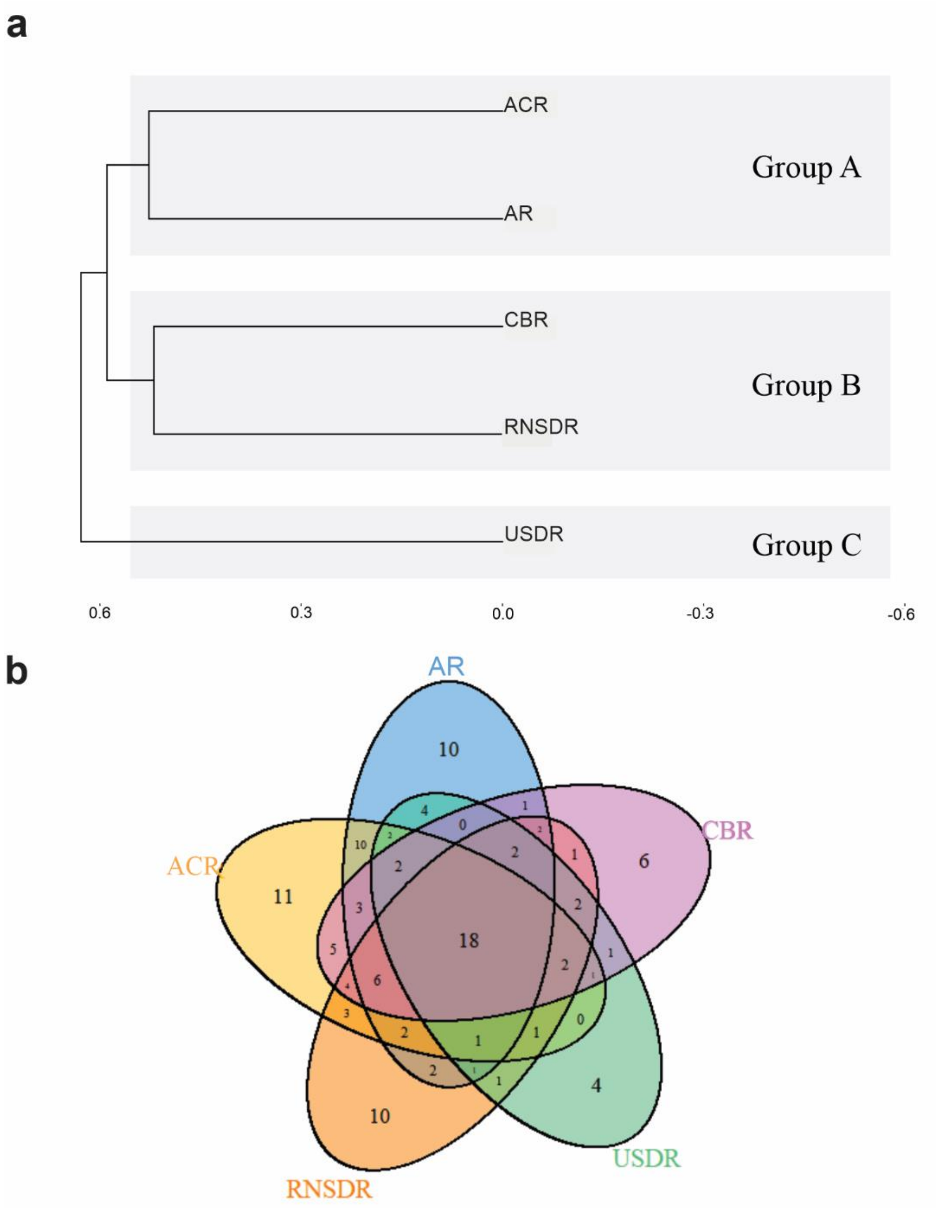

Fig. 2 (a) Floristic similarity dendogram of the vascular epiphytes present in five Amazonian white-sand systems (WSEs) based on the Jaccard similarity index. Cophenetic correlation coefficient r = 0.76. (b) Venn diagram – representation of the number of shared species and unique species from each of the sampled WSE sites in the Central Amazon. AR – Asframa reserve; ACR – Alto Cuieiras reserve; CBR – Campinas Biological Reserve; RNSDR – Rio Negro Sustainable Development Reserve; USDR – Uatumã Sustainable Development Reserve

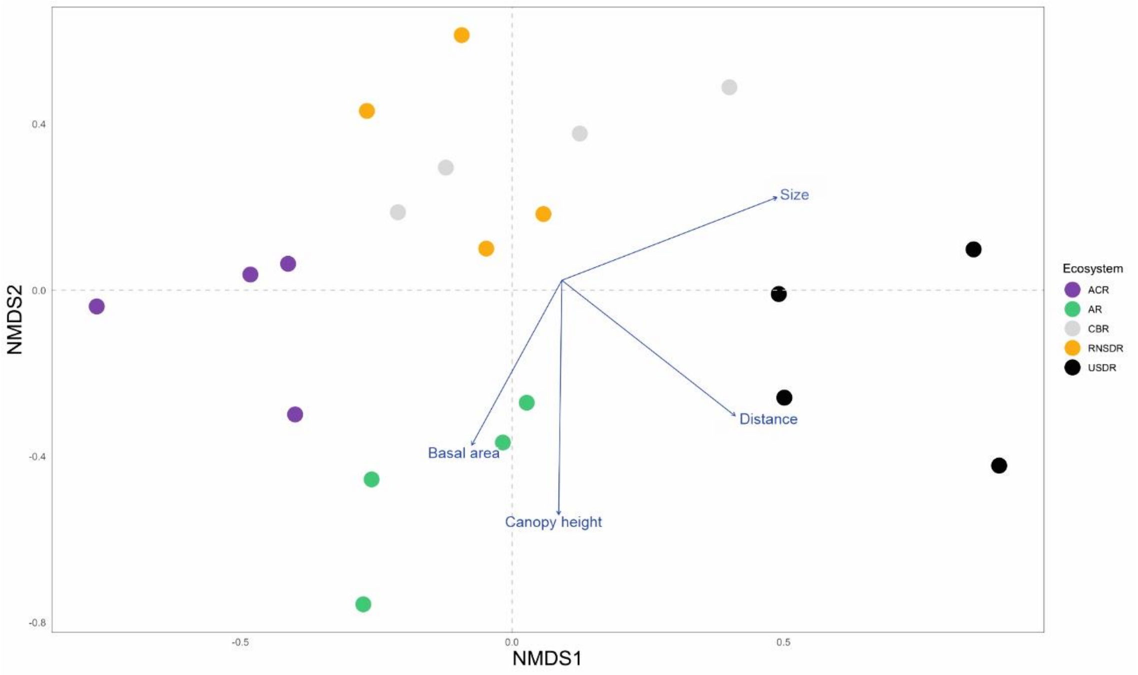

Fig. 3 Non-metric multidimensional scaling (NMDS) analyses based on dissimilarities calculated using the Bray–Curtis index the composition of vascular epiphytes present in five areas of white-sand ecosystems of the Central Amazon. The environmental variables and vegetation structure were adjusted using the *envfit* function (Oksanen et al. 2022). Variables that presented statistical significance were associated with the ordering and were represented together with the distribution of the studied areas. AR – Asframa reserve; ACR – Alto Cuieiras reserve; CBR – Campinas Biological Reserve; RNSDR – Rio Negro Sustainable Development Reserve; USDR – Uatumã Sustainable Development Reserve

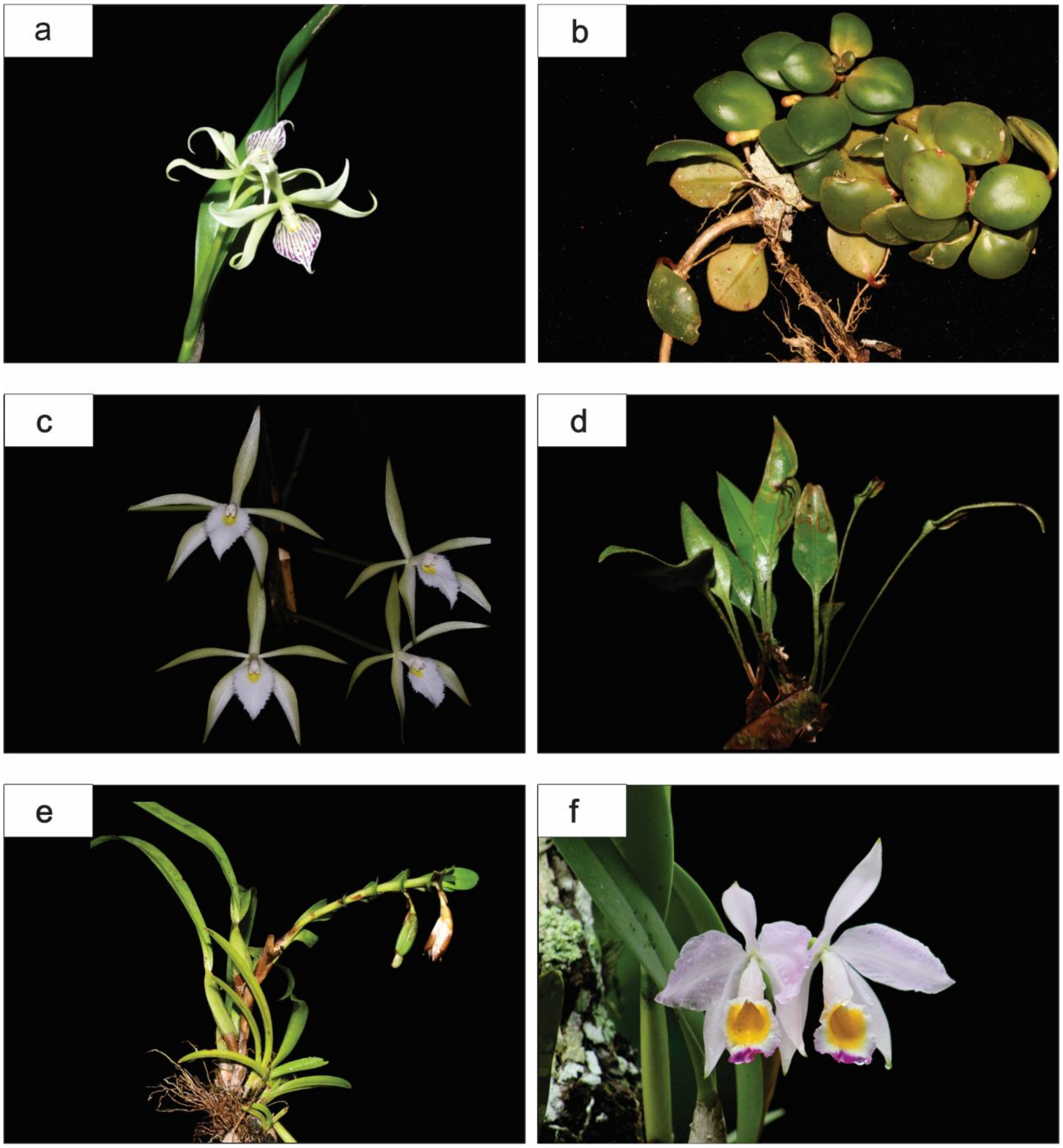

Fig. 4 Vascular epiphyte species with the highest value of epiphytic importance (IVe) in white-sand ecosystems of the Central Amazon. (a) *Prosthechea aemula* (Lindl.) W.E. Higgins; (b) *Codonanthopsis crassifolia* (H.Focke) Chautems & Mat. Perret; (c) *Brassavola martiana* Lindl.; (d) *Elaphoglossum discolor* (Kuhn) C.Chr.; (e) *Maxillaria lutescens* Scheidw; (f) *Cattleya wallisii* (Linden) Linden ex Rchb.f.

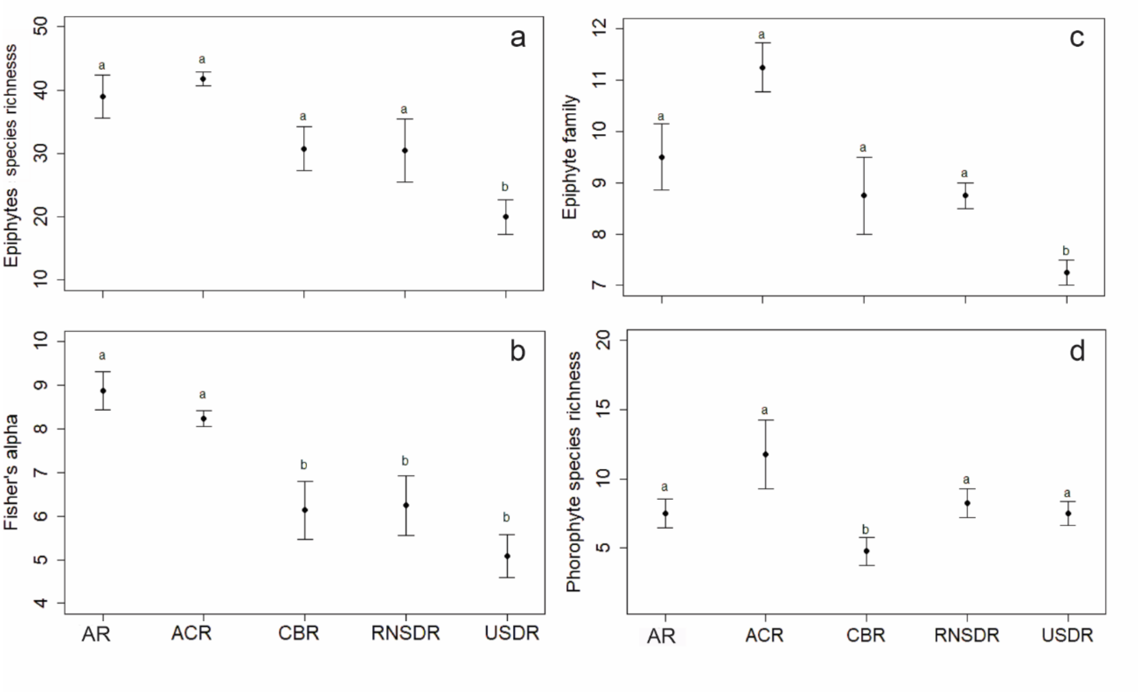

Fig. 5 Observed differences (a) Epiphyte species richness, (b) Alpha diversity, (c) Number of vascular epiphyte families and (d) Phorophyte species richness in white-sand ecosystems of the Central Amazon. AR – Asframa reserve; ACR – Alto Cuieiras reserve; CBR – Campinas Biological Reserve; RNSDR – Rio Negro Sustainable Development Reserve; USDR – Uatumã Sustainable Development Reserve

Supplementary Information (SI)

Table SI1 List of vascular epiphyte species reported by simper analysis that significantly ($P \leq 0.05$) contributed to the dissimilarity between the studied white sand ecosystems (WSEs). Analysis was performed in pairs. (AR) Asframa Reserve, (ACR) Alto Cuieiras Reserve, (CBR) Campina Biological Reserve, (RNSDR) Rio Negro Sustainable Development Reserve; (USDR) Uatumã Sustainable Development Reserve.

	Species	average	sd	ratio	ava	avb	cumsum	p value
Contrast: AR x ACR	*Epidendrum compressum*	0.024	0.013	1.79	0	58.2	0.589	0.002
	Anthurium bonplandii	0.001	0.001	1.44	0	3.8	0.96	0.005
	Aechmea huebneri	0.003	0.002	1.33	0	7.2	0.929	0.005
	Pabstiella yauaperyensis	0.025	0.029	1.05	0	64	0.558	0.007
	Speclinia picta	0.043	0.029	1.44	0	105.2	0.34	0.020
	Maxillaria obtusa	0.001	0.001	0.78	0	2.2	0.975	0.027
	Epidendrum bahiense	0.015	0.011	1.36	4.25	37.8	0.682	0.031
	Octomeria surinamensis	0.015	0.016	0.88	0.25	30.8	0.702	0.035
	Maxillaria camaridii	0.135	0.082	1.632	69.5	376.	0.174	0.039
	Epidendrum rigidum	0.006	0.006	0.99	2.5	12.8	0.902	0.048
Contrast: AR x RNSDR	*Epidendrum carpophorum*	0.005	0.004	1.27	8.5	0.2	0.891	0.008
	Maxillaria subrepens	0.020	0.016	1.24	0	41.8	0.698	0.015
	Maxillaria brasiliensis	0.013	0.014	0.98	25.2	0	0.805	0.017
	Clusia penduliflora	0.003	0.003	1.046	4.25	0	0.935	0.018
	Pleopeltis bombycina	0.001	0.001	0.925	1	0	0.988	0.018
	Rodriguesia lanceolata	0.008	0.007	1.031	1	15.2	0.865	0.023
	Epidendrum schlechterianum	0.009	0.006	1.395	6.75	16	0.856	0.024
	Trichomanes spruceanum	0.001	0.001	1.222	2	0	0.983	0.030
	Vittaria lineata	0.000	0.000	0.909	0	0.8	0.993	0.033
	Scaphyglottis sickii	0.020	0.023	0.876	34.25	0	0.724	0.035
	Anthurium eminens	0.001	0.001	2.11	1.75	0	0.986	0.037
	Microgramma percursa	0.000	0.000	0.853	0	0.8	0.995	0.038
	Aganisia cyanea	0.000	0.001	0.712	0.5	0	0.994	0.044

	Scuticaria steelei	0.001	0.002	0.926	2.5	0	0.978	0.043
Contrast: AR x USDR	*Scaphyglottis sickii*	0.0290	0.028	1.011	34.25	0	0.662	0.001
	Maxillaria brasiliensis	0.0188	0.016	1.124	25.25	0	0.8	0.001
	Epidendrum carpophorum	0.0083	0.005	1.576	8.5	0.25	0.846	0.001
	Clusia penduliflora	0.0041	0.003	1.214	4.25	0	0.918	0.001
	Elaphoglossum discolor	0.0522	0.033	1.545	52	2.75	0.465	0.002
	Pleopeltis bombycina	0.0012	0.001	1.098	1	0	0.984	0.003
	Cochlidium pumilum	0.0021	0.254	0.855	2.75	0	0.963	0.004
	Aganisia cyanea	0.0005	0.002	0.792	0.5	0	0.995	0.004
	Codonanthopsis crassifolia	0.0703	0.050	1.399	108.7	18.5	0.266	0.005
	Codonanthopsis ulei	0.0079	0.009	0.863	10	0	0.875	0.005
	Acianthera miqueliana	0.0027	0.004	0.635	2	0	0.942	0.005
	Anthurium obtusum	0.0097	0.011	0.871	12	0.25	0.825	0.006
	Madisonia kerrii	0.0193	0.029	0.639	14	0	0.777	0.001
	Trichomanes spruceanum	0.0019	0.001	1.403	2	0	0.975	0.001
	Scuticaria steelei	0.0021	0.001	1.051	2.5	0	0.97	0.001
	Asplenium sp.	0.0001	0.002	0.555	0.25	0	1	0.001
	Jacquiniella globosa	0.0001	0.000	0.555	0.25	0	1	0.001
	Hymenophyllum polyanthos	0.0242	0.025	0.943	28.25	0.25	0.754	0.001
	Maxillaria kegelii	0.0031	0.004	0.68	2.25	0.5	0.936	0.001

Philodendron melinonii	0.0021	0.002	0.942	2.5	0	0.96	0.001
Octomeria taracuana	0.0024	0.004	0.543	1.75	0	0.952	0.002
Campylocentrum fasciola	0.0003	0.006	0.543	0.25	0	0.998	0.002
Scaphyglottis stellata	0.000	0.005	0.555	0.5	0	0.998	0.002
Maxillaria parviflora	0.026	0.022	1.175	34.5	1	0.694	0.004
Epidendrum strobiliferum	0.058	0.036	1.617	68.5	7	0.337	0.004
Epidendrum microphylum	0.007	0.007	1.101	7.75	3.75	0.865	0.007
Clusia ucamira	0.001	0.001	1.505	2.25	0	0.979	0.010
Clusia spathulaefolia	0.002	0.002	0.894	2	0	0.968	0.010
Maxillaria pendens	0.011	0.005	1.92	13.25	0	0.813	0.011
Bifrenaria longicornis	0.001	0.001	1.283	0.75	2	0.981	0.012
Elaphoglossum plumosum	0.031	0.032	0.813	41.75	3.75	0.591	0.014
Tillandsia adpressiflora	0.076	0.072	1.01	83.25	32.7	0.092	0.016
Hecistopteris pumila	0.002	0.004	0.543	1.75	0	0.949	0.019
Encyclia chloroleuca	0.002	0.002	0.816	2.25	0	0.957	0.019
Dichaea picta	0.0006	0.001	0.555	1	0	0.992	0.025
Sobralia granitica	0.005	0.006	0.864	0	6	0.897	0.031
Aechmea bromeliifolia	0.0004	0.007	0.648	0.25	0.25	0.997	0.031
Anthurium eminens	0.001	0.006	1.659	1.75	0.75	0.986	0.032
Epidendrum apuahuense	0.001	0.002	0.777	0	1.5	0.972	0.045

Contrast: AR x CBR	*Epidendrum carpophorum*	0.0051	0.003	1.668	8.5	0	0.883	0.018
	Prosthechea aemula	0.2074	0.060	3.411	2.75	355.	0.264	0.025
	Aechmea vallerandii	0.0032	0.003	1.031	0	6.8	0.924	0.025
	Codonanthopsis crassifolia	0.0518	0.038	1.35	108.7	11.8	0.4	0.029
	Clusia penduliflora	0.0025	0.002	1.21	4.25	0	0.945	0.036
	Epidendrum sculptum	0.0007	0.009	0.786	0	1.2	0.99	0.044
	Pleopeltis bombycina	0.0007	0.006	1.123	1	0	0.991	0.048
Contrast: ACR x RNSDR	*Epidendrum compressum*	0.0236	0.013	1.7115	58.2	0	0.65	0.002
	Anthurium bonplandii	0.0016	0.001	1.3698	3.8	0	0.963	0.005
	Pabstiella yauaperyensis	0.0250	0.024	1.0369	64	0	0.615	0.011
	Aechmea huebneri	0.0033	0.002	1.2502	7.2	0.2	0.935	0.018
	Epidendrum bahiense	0.0152	0.011	1.3036	37.8	2.8	0.695	0.031
	Maxillaria camaridii	0.1331	0.078	1.6878	376.5	90	0.198	0.039
	Maxillaria cf. obtusa	0.0011	0.001	0.756	2.2	0	0.975	0.043
	Octomeria surinamensis	0.0145	0.017	0.8514	30.8	0	0.717	0.045
Contrast: ACR x USDR	*Pabstiella yauaperyensis*	0.0323	0.029	1.1113	64	0	0.586	0.000
	Epidendrum compressum	0.0308	0.015	2.0579	58.2	0	0.623	0.000
	Aechmea huebneri	0.0045	0.003	1.2566	7.2	0.5	0.928	0.000
	Maxillaria camaridii	0.2038	0.074	2.7461	376.5	0	0.248	0.000
	Anthurium bonplandii	0.0021	0.001	1.4533	3.8	0	0.962	0.000

Maxillaria cf. obtusa	0.0015	0.001	0.7838	2.2	0	0.968	0.000
Aechmea rodriguesiana	0.0009	0.001	0.6705	2	0	0.983	0.000
Octomeria yauaperyensis	0.0007	0.001	0.6822	1	0	0.986	0.000
Cochlidium serrulatum	0.0093	0.012	0.7679	12	0	0.825	0.000
Octomeria surinamensis	0.0196	0.021	0.9123	30.8	1	0.757	0.000
Nephrolepis cf. rivularis	0.0001	0.000	0.5573	0.2	0	1	0.001
Speclinia picta	0.0542	0.034	1.5702	105.2	0	0.433	0.002
Vanilla bicolor	0.0050	0.009	0.557	10.5	0	0.916	0.002
Hylaeorchis petiolaris	0.0004	0.008	0.5522	0.5	0	0.994	0.002
Aechmea longifolia	0.0002	0.004	0.5522	0.2	0	0.998	0.002
Epidendrum rigidum	0.0079	0.009	0.8673	12.8	0	0.878	0.002
Maxillaria tenui	0.0025	0.004	0.5537	3.2	0	0.957	0.002
Batemannia colleyi	0.0002	0.005	0.5537	0.2	0	0.999	0.002
Epidendrum bahiense	0.0180	0.012	1.428	37.8	6.75	0.779	0.002
Trichosalpinorbicularis	0.0178	0.028	0.6158	24	0	0.801	0.003
Ludovia lancifolia	0.0019	0.002	0.7886	3	0.25	0.964	0.004
Actinostachys pennula	0.0093	0.014	0.6367	11.5	0.25	0.836	0.020
Bifrenaria venezuelana	0.0005	0.001	0.5537	0.8	0	0.991	0.026
Maxillaria desvauxiana	0.0004	0.004	0.9572	0.8	0	0.993	0.026
Clusia ucamira	0.0015	0.001	1.1041	2.8	0	0.97	0.029

	Epiphyllum phyllanthus	0.0011	0.008	1.3044	2.2	0	0.975	0.029
	Orleanesia amazonica	0.0007	0.001	0.5537	1	0	0.987	0.035
	Trichomanes martiusii	0.0078	0.014	0.5537	10	0	0.888	0.048
Contrast: ACR x CBR	*Epidendrum compressum*	0.0221	0.013	1.6754	58.2	2	0.664	0.007
	Anthurium bonplandii	0.0015	0.001	1.4901	3.8	0	0.962	0.007
	Aechmea huebneri	0.0033	0.002	1.3998	7.2	0	0.925	0.016
	Pabstiella yauaperyensis	0.0242	0.022	1.0596	64	0	0.631	0.02
	Epidendrum bahiense	0.0149	0.010	1.4033	37.8	1.5	0.714	0.033
Contrast: RNSDR x USDR	*Epidendrum schlechterianum*	0.0132	0.006	1.9641	16	0	0.832	0.003
	Rodriguesia lanceolata	0.0102	0.009	1.0844	15.2	0	0.874	0.003
	Polystachya concreta	0.0054	0.009	0.5872	2.8	0	0.919	0.004
	Vittaria lineata	0.0005	0.004	0.9421	0.8	0	0.993	0.005
	Microgramma percursa	0.0004	0.005	0.876	0.8	0	0.994	0.005
	Maxillaria subrepens	0.0262	0.019	1.3241	41.8	0	0.683	0.009
	Bifrenaria longicornis	0.0020	0.001	1.3847	0	2	0.971	0.001
	Serpocaulon sessilifolium	0.0006	0.001	0.5519	0.8	0	0.988	0.001
	Bulbophyllum setigerum	0.0002	0.004	0.5519	0.2	0	0.997	0.001
	Tillandsia bulbosa	0.0002	0.004	0.5519	0.2	0	0.998	0.001
	Apteria aphylla	0.0003	0.005	0.5558	0.5	0	0.996	0.002
	Ficus mathewsii	0.0001	0.002	0.5558	0.2	0	0.999	0.002

	Araeococcus micranthus	0.0001	0.002	0.556	0.2	0	0.999	0.002
	Epidendrum orchidiflorum	0.0001	0.002	0.556	0.2	0	1	0.002
	Mezobromelia pleiosticha	0.0001	0.002	0.556	0.2	0	1	0.002
	Epidendrum strobiliferum	0.0614	0.033	1.8368	92	7	0.481	0.003
	Prosthechea aemula	0.2387	0.120	1.9878	378.8	84	0.316	0.005
	Rudolfiella aurantiaca	0.0013	0.001	1.0051	1	1	0.98	0.011
	Epidendrum apuahuense	0.0020	0.003	0.6363	0	1.5	0.968	0.027
	Sobralia granitica	0.0054	0.007	0.7685	0	6	0.926	0.037
	Serpocaulon attenuatum	0.0026	0.004	0.6504	4.5	0	0.962	0.042
Contrast: RNSDR x CBR	*Brassavola martiana*	0.0514	0.033	1.5576	26.5	115.2	0.416	0.027
	Maxillaria subrepens	0.0187	0.014	1.249	41.8	0	0.702	0.033
	Aechmea vallerandii	0.0031	0.003	0.9985	0	6.8	0.943	0.037
	Cattleya wallisii	0.0422	0.037	1.124	24.2	81.5	0.553	0.040
	Epidendrum schlechterianum	0.0080	0.005	1.5951	16	0.5	0.855	0.045
	Rodriguesia lanceolata	0.0070	0.006	1.082	15.2	1.2	0.904	0.046
Contrast: USDR CBR	*Cattleya wallisii*	0.0770	0.042	1.8141	0.5	81.5	0.401	0.000
	Aechmea vallerandii	0.0042	0.003	1.0805	0	6.8	0.937	0.000
	Anthurium gracile	0.0108	0.009	1.1717	1.5	13	0.827	0.000
	Epidendrum sculptum	0.0010	0.001	0.8436	0	1.2	0.981	0.000

Brassavola martiana	0.0686	0.027	2.4885	28.5	115.	0.492	0.000
Pleopeltis hirsutissima	0.0008	0.001	0.7333	0	0.8	0.988	0.001
Elaphoglostum raywaense	0.0002	0.005	0.5563	0	0.5	0.998	0.001
Sobralia bletiae	0.0002	0.005	0.5563	0	0.5	0.998	0.001
Maxillaria uncata	0.0049	0.006	0.7561	0	7.5	0.913	0.002
Notylia aromatica Barker ex Lindl.	0.0007	0.001	0.5502	0	0.8	0.99	0.002
Macroclinium miralis	0.0010	0.001	0.5547	0	1.5	0.98	0.002
Encyclia mapuerae	0.0041	0.005	0.7767	0.25	3.8	0.943	0.002
Moranopteris nana	0.0193	0.024	0.8	1.25	20	0.772	0.004
Elaphoglossum glabellum	0.0614	0.054	1.1294	0	94.8	0.572	0.006
Sobralia sessilis	0.0050	0.009	0.5563	0	9	0.906	0.006
Trichomanes crispum	0.0053	0.008	0.616	0.5	9	0.892	0.008
Prosthechea aemula	0.2270	0.116	1.9458	84	355.	0.299	0.011
Clusia insignis	0.0048	0.004	1.1286	1.5	6	0.925	0.016
Cochlidium furcatum	0.0008	0.000	0.9195	0	1	0.987	0.018
Philodendron pulchrum	0.0015	0.002	0.734	0.25	2.5	0.969	0.025
Microgramma baldwinii	0.0136	0.014	0.9133	5	14.8	0.813	0.034
Aechmea mertensii	0.0019	0.001	0.9593	1	1.8	0.962	0.042

Table SI-2 Structural parameters of the five main species of vascular epiphytes in white-sand ecosystems of the Central Amazon. Abe – absolute abundance of epiphyte species; Nip – number of phorophytes occupied by the epiphyte species; Spi – number of phorophytes species occupied by the species epiphytes; FAi – absolute frequency of the epiphyte species on the individual phorophyte; FRi relative frequency of the epiphyte species on the individual phorophyte; FAj – absolute frequency of epiphytic species in specific phorophytes; FRj – relative frequency of the epiphyte species on the specific phorophyte; IVe - epiphytic importance value. (AR) Asframa Reserve, (ACR) Alto Cuieiras Reserve, (CBR) Campina Biological Reserve, (RNSDR) Rio Negro Sustainable Development Reserve; (USDR) Uatumã Sustainable Development Reserve.

	Vascular epiphyte species	Botanical family	Abe	Nip	Spi	FAi	FRi	FAj	FRj	IVe
AR	*Codonanthopsis crassifolia*	Gesneriaceae	435	54	12	54.0	10.8	80.0	6.7	8.7
	Tillandsia adpressiflora	Bromeliaceae	333	18	5	18.0	3.6	33.3	2.8	3.2
	Maxillaria lutescens	Orchidaceae	278	11	1	11.0	2.2	6.7	0.5	1.3
	Epidendrum strobiliferum	Dryopteridaceae	274	22	4	22.0	4.4	26.7	2.2	3.3
	Brassavola martiana	Orchidaceae	251	33	8	33.0	6.6	53.3	4.4	5.5
ACR	*Maxillaria lutescens*	Orchidaceae	1506	72	24	54.5	10.0	88.9	6.3	8.1
	Elaphoglossum glabellum	Dryopteridaceae	234	42	17	31.8	5.8	63.0	4.5	5.1
	Prosthechea aemula	Orchidaceae	846	39	18	29.5	5.4	66.7	4.7	5.1
	Elaphoglossum discolor	Dryopteridaceae	135	35	16	26.5	4.8	59.3	4.2	4.5
	Codonanthopsis crassifolia	Gesneriaceae	100	34	15	25.7	4.7	55.6	3.9	4.3
CBR	*Prosthechea aemula*	Orchidaceae	1422	46	6	68.6	11.5	66.7	5.1	8.3
	Brassavola martiana	Orchidaceae	461	35	5	52.2	8.7	55.6	4.2	6.5
	Cattleya wallisii	Orchidaceae	326	31	6	46.2	7.7	66.7	5.1	6.4
	Elaphoglossum glabellum	Dryopteridaceae	379	28	6	41.7	7.0	66.7	5.1	6.0
	Elaphoglossum discolor	Dryopteridaceae	64	20	4	29.8	5.0	44.4	3.4	4.2

RNSDR	*Prosthechea aemula*	Orchidaceae	1515	53	10	58.8	12.9	62.5	6.0	9.4
	Epidendrum strobiliferum	Orchidaceae	368	33	6	36.6	8.0	37.5	3.6	5.8
	Brassavola martiana	Orchidaceae	106	27	8	30.0	6.5	50.0	4.8	5.6
	Codonanthopsis crassifolia	Gesneriaceae	69	25	8	27.7	6.0	50.0	4.8	5.4
	Cattleya wallisii	Orchidaceae	97	21	7	23.3	5.1	43.8	4.2	4.6
USDR	*Codonanthopsis crassifolia*	Gesneriaceae	74	27	10	28.4	10.4	62.5	7.5	8.9
	Elaphoglossum obovatum	Dryopteridaceae	148	26	10	27.3	10.0	62.5	7.5	8.8
	Brassavola martiana	Orchidaceae	114	28	6	29.4	10.8	37.5	4.5	7.6
	Tillandsia adpressiflora	Bromeliaceae	131	23	8	24.2	8.9	50.0	6.0	7.4
	Prosthechea aemula	Orchidaceae	336	21	8	22.1	8.1	50.0	6.0	7.0

CAPÍTULO 2

Viviane Pagnussat Klein, Adriano Costa Quaresma, Talitha Mayumi Francisco, Randolpho Dias-Terceiro e Maria Teresa Fernandez Piedade. **Características estruturais e a identidade das árvores influenciam a distribuição horizontal e vertical das epífitas vasculares em ecossistemas de areia branca (campinaranas) da Amazônia central.** Artigo formatado para o Journal of Vegetation Science.

RESUMO

Questões: É postulado que as condições ambientais e microclimáticas influenciam a composição e distribuição das epífitas vasculares, entretanto, estas relações foram insuficientemente avaliadas para os ecossistemas amazônicos de areia branca (WSE), assim, perguntamos: As características dos forófitos (altura, diâmetro e densidade da madeira) e sua identidade taxonômica influenciam a distribuição vertical e horizontal das epífitas vasculares? A distribuição vertical das epífitas apresenta um padrão de estratificação e modularidade? É possível identificar espécies indicadoras das zonas ecológicas verticais?

Localização: Este estudo foi conduzido em cinco áreas de ecossistemas de areia branca (WSE) localizados na Amazônia Central, distantes aproximadamente 100 km entre si.

Metodologia: Identificamos e quantificamos todas as epífitas vasculares em parcelas de 25 x 25 metros em um total de 1.25 ha de WSEs. Todas as árvores com diâmetros superiores a 10 cm foram identificadas, mensuradas (DAP – diâmetro a altura do peito e altura) e valores da densidade da madeira foram atribuídos. As árvores foram divididas em quatro zonas ecológicas, duas no fuste (ZI e ZII) e duas na copa (ZIII e ZIV). Modelos lineares generalizados de efeito misto (GLMM) foram utilizados para verificar a relação das características dos forófitos com a distribuição vertical e horizontal das epífitas. Testes de hipóteses e análises de rede ecológica foram usados para avaliar a estrutura e a estratificação das epífitas no gradiente vertical. O índice de valor de espécies indicadoras (Indval) foi utilizado para identificar as espécies características de cada zona ecológica.

Resultados: A identidade taxonômica, a altura e o DAP dos forófitos influenciaram a composição e distribuição das epífitas vasculares. A rede vertical apresentou estrutura aninhada, baixa especialização complementar e foi modular. A riqueza, abundância e a composição de espécies variou significativamente entre as zonas ecológicas, demostrando um padrão de estratificação e modularidade. Espécies de samambaias foram indicadoras das zonas do fuste, e as espécies de orquídeas dominaram as demais zonas dos forófitos.

Conclusão: Padrões de composição e de distribuição das epífitas vasculares em WSE são influenciados pelo tamanho e identidade dos forófitos, desta forma, a preservação de

espécies-chaves de forófitos, especialmente indivíduos de grandes tamanhos, são essenciais para a manutenção da biodiversidade nestes ecossistemas.

Palavras-chaves: Campinaranas amazônicas, Heterogenidade de microhabitats, Holoepífitas, Redes ecológicas, Tamanho das árvores, Zonas de Johansson

1 | INTRODUÇÃO

Sistemas ecológicos são formados por conjuntos específicos de organismos que interagem entre si e formam redes complexas de interações (Bascompte, 2009). Por mais de um século, ecólogos vêm descrevendo padrões de riqueza, abundância e de distribuição espacial das espécies (McGill et al., 2007), entretanto, as interações ecológicas estabelecidas entre espécies ainda permanecem como um componente fundamental a ser avaliado. Por definição, interação ecológica é a relação estabelecida entre duas ou mais espécies (interespecíficas) ou dentro da mesma espécie (intraespecífica) (Schoener, 1990). As interações entre espécies são, portanto, um componente-chave da biodiversidade a ser analisado, pois agrega informações sobre dinâmica ecológica dentro das comunidades (Jordano, 1987).

Grupos de espécies interagem entre si direta ou indiretamente formando diversas associações ecológicas. Estudos teóricos e práticos se voltaram majoritariamente a analisar as interações antagonistas tais como parasitismos, competição, predação e herbivoria, e as mutualísticas entre espécies (e.g. Bascompte et al. 2003; Bellay et al. 2015; Mello et al., 2015), ao passo que, outras interações, como as interações comensais estabelecidas entre epífitas e árvores foram pouco exploradas. Epífitas vasculares constituem um grupo diverso de plantas, formado por aproximadamente 30.000 espécies, distribuídas, principalmente, nas regiões tropicais (Zotz el al., 2021, Taylor et al. 2021). As epífitas são definidas como plantas que germinam e crescem sobre outras plantas (forófitos), utilizando-as apenas como suporte estrutural e fixação (Zotz, 2016). Considerando a dependência das epífitas por um suporte arbóreo/arbustivo, as características estruturais dos forófitos como o tamanho (Flores-Palacios & García-Franco, 2006; Francisco et al., 2021; Quaresma et al., 2020; Zotarelli et al., 2019), a idade (Johansson et al. 2007; Zotz & Vollrath, 2003), a diversidade de microhabitats dentro dos forófitos (Sayago et al., 2013; Woods et al., 2015), densidade da madeira (Cebalos et al. 2016; Sáyago et al. 2013), a estabilidade e capacidade de retenção de água na casca e a fenologia da árvore (Callaway et al., 2002; Einzmann et al. 2014; Sáyago et al., 2013), influenciam os padrões de composição e distribuição das epífitas vasculares. Tendo em vista que as condições estruturais variam entre os indivíduos e entre espécies de forófitos, as epífitas podem ser fortemente influenciadas pela composição das comunidades vegetais (Burns & Zotz, 2010; Laube & Zotz, 2006; Wagner et al., 2015). Compreender como essas relações se estabelecem e o grau de especificidade das interações é uma parte importante do “quebra-cabeça da diversidade” (Kitching, 2006).

Variações microclimáticas da base do fuste até os ramos mais finos da copa também são consideradas um dos principais fatores que influenciam a germinação, o estabelecimento e, consequentemente, a distribuição de epífitas dentro dos forófitos (Cardelús & Chazdon, 2005; Krömer et al., 2007; Sanger & Kirkpatrick, 2016). Já se sabe que nas partes mais elevadas do dossel a luminosidade e a temperatura são maiores, ao passo que a umidade é menor do que no solo da floresta (Benzing 1995). Somado a isso, a estrutura da árvore também apresenta diferenças verticais (Benzing, 2004). Nas regiões da copa, geralmente os ramos estão dispostos mais horizontalmente, o que pode aumentar a fixação das epífitas e favorecer o acúmulo de humos nas bifurcações dos galhos, onde as epífitas podem germinar e se estabelecer (Sanger & Kirkpatrick, 2015; Woods et al., 2015). Tendo em vista a complexidade de fatores que se estabelecem nos forófitos, numerosos estudos foram desenvolvidos para entender como as epífitas se distribuem ao longo dos gradientes verticais (e.g Sanger & Kirkpatrick, 2016), no entanto, a atual compreensão sobre os padrões de distribuição de espécies é baseado principalmente em medidas de presença e ausência das espécies ou em números de indivíduos por zonas ecológicas (Krömer et al. 2007), ainda carecendo de informações sobre os padrões que estruturam tais interações.

Considerando que as condições microclimáticas variam verticalmente e que as espécies de epífitas podem refletir distintas respostas fisiológicas, morfológicas e ecológicas (Agudelo et al., 2019; Johansson, 1974), o uso da teoria de redes ecológicas pode ser uma ferramenta útil para compreender os níveis de organização, estrutura e dinâmica das interações entre as espécies (Francisco et al., 2019; Sáyago te al., 2013). Em redes epífitas-forófitos, a estrutura aninhada é um padrão comumente relatado (Burns, 2007) e indica que espécies especialistas interagem com espécies generalistas, resultando em um padrão de especialização assimétrica (Bascompte et al., 2003; Taylor et al. 2016). Por outro lado, redes com estrutura especializada ou modular indicam que as espécies utilizam os recursos de maneira diferenciada e refletem respostas de algumas espécies de epífitas a diferentes gradientes microclimáticas (Francisco et al., 2019; Newman, 2006; Taylor et al., 2016). Um padrão modular é caracterizado pela divisão da rede em módulos ou compartimentos, em que as espécies de um módulo estão mais densamente conectadas entre si do que com as demais espécies da rede (Dormann & Strauss, 2014). Neste contexto, a modularidade pode ser usada para analisar a estratificação vertical e indicar como as epífitas vasculares respondem aos distintos gradientes microclimáticos e estruturais dos forófitos (Francisco et al., 2019).

Neste sentido este trabalho foi concebido para investigar a distribuição das comunidades de epífitas vasculares nos gradientes horizontais (entre forófitos) e verticais (da base até a copa das árvores) em cinco áreas de WSE da Amazônia Central. Nos propomos a responder três perguntas específicas: 1) Características dos forófitos (altura, DAP e densidade da madeira) e a identidade taxonômica dos forófitos influenciam a distribuição vertical e horizontal das epífitas vasculares? 2) A distribuição vertical das epífitas vasculares apresenta um padrão de estratificação e modularidade? 3) É possível identificar espécies ou grupos de epífitas indicadoras de cada uma das zonas ecológicas dos forófitos? Epífitas vasculares são estruturalmente dependentes dos forófitos com os quais mantêm uma estreita relação (Wagner & Zotz, 2020; Zotz, 2016), desta maneira, presumimos que caraterísticas das espécies e dos indivíduos forofíticos moldem a distribuição horizontal das epífitas vasculares. Considerando que as florestas tropicais apresentam alta estratificação vertical e variações microclimáticas são estabelecidas da base à copa do forófito (Krömer et al., 2007; Wagner et al., 2015), assumimos que a distribuição das espécies de epífitas vasculares do tronco até os ramos finos não se dá de maneira aleatória e a composição de espécies apresentará um padrão de estratificação e modularidade (Franscisco et al., 2019; Woods et al., 2018). Também prevemos que as variações ambientais impostas pelo gradiente vertical selecionem determinados grupos ou espécies com diferentes estratégias adaptativas (Agudelo et al., 2019; Petter et al., 2016).

2 | MÉTODOS

2.1 | Área de estudo e coleta dos dados

Entre os ambientes que compõem o Domínio Amazônico, os ecossistemas de areia-branca (WSE), também conhecidos como campinaranas, são ambientes de distribuição restrita a região amazônica. Se caracterizam por apresentam solos arenosos de baixíssima fertilidade, vegetação escleromórfica e composição florística única, com uma biota caracteristicamente pobre em espécies, porém rica em endemismos (Adeney et al., 2016; Anderson, 1981; Prance, 1996; Vicentini, 2004). Este estudo foi realizado em áreas de WSE localizadas em cinco Unidades de Conservação (UCs) da Amazônia Central, próximas à cidade de Manaus, Amazonas, abrangendo uma área amostral de 4.500.00 km^2 (Figura 1).

A região apresenta temperatura média anual de 27 °C e a precipitação média anual é de 2.077 ± 438,3 mm (período analisado 1975-2005), com duas estações bem definidas, uma estação chuvosa, que se estende nos meses de dezembro a maio, e uma estação seca de junho a outubro (Carneiro & Trancoso, 2007). Na Amazônia central, os WSEs têm distribuição dispersa, em geral ocorrendo como pequenas manchas em forma de ilhas de vegetação cercadas pela floresta de terra-firme, pois seguem à distribuição fragmentada dos solos arenosos onde ocorrem (Capurucho et al., 2020). As áreas de WSE estudadas apresentam vegetação florestada, com dossel médio de 12 metros de altura e dominância de algumas espécies arbóreas, especialmente *Aldina heterophylla* Spruce ex Benth. (Fabaceae), *Manilkara bidentata* (A.DC.) A.Chev. (Sapotaceae), *Pradosia schomburgkiana* (A.DC.) Cronquist, e *Sacoglottis mattogrossensis* Malme (Humiriaceae) (Costa et al., 2020; Demarchi et al., 2022; Targhetta et al., 2015; Vicentini, 2004).

Em cada WSE estabelecemos quatro parcelas (25 x 25 metros), totalizando 0.25 ha de vegetação inventariada por WSE. As parcelas foram dispostas aleatoriamente, mantendo uma distância mínima de 100 m entre elas. Todas as espécies arbóreas com diâmetro a altura do peito (DAP) superior a 10 cm foram identificadas e mensuradas quanto a altura total e o diâmetro. Valores referentes a densidade básica da madeira das espécies foram obtidos nos bancos de dados do projeto PELD/MAUA e do Global Wood Density (Zanne et al., 2009). Valores de biomassa foram calculados para todos os indivíduos arbóreos (Chave et al., 2014; Finger, 1993). Todas as árvores foram escaladas, usando técnicas apropriadas de alpinismo (Nadkarni, 1988). Em cada árvore, todos os indivíduos de epífitas vasculares (sensu Zotz et al., 2021) foram identificados e quantificados. Espécies de hábito preferencialmente terrestre, como *Lindsaea lancea,* foram inseridas na nossa amostragem quando encontradas em mais de um forófito e ocupando diferentes zonas de distribuição. Consideramos um indivíduo, qualquer planta ou grupo de plantas geograficamente distinguíveis entre si (Sanford, 1968).

Plântulas com características botânicas ainda indefinidas foram desconsideradas na amostragem.

Para quantificar a abundância das espécies no gradiente vertical, os forófitos foram divididos em quatro zonas ecológicas verticais (adaptado de Johansson, 1974; Figura 2): base do tronco (ZI) – região compreendida desde superfície do solo até 1 m de altura; tronco alto (ZII) – região que se estende acima de 1 m de altura até a emissão das primeiras bifurcações; copa interna (ZIII) – compreende a região onde estão presentes os ramos primários mais grossos e verticalizados da árvores; copa externa (ZIV) – região mais externa da copa, que compreende os ramos mais jovens e finos. Matrizes com dados binários de presença e ausência e com dados ponderados de abundância registrada de cada espécie de epífita foram elaboradas para analisar as interações entre as espécies e a zona ecológica de ocorrências.

Para a identificação das espécies, utilizamos literatura específica (Mez, 1891, 1892, 1894; Hoehne, 1949; Pabst e Dungs 1975, 1977; Croat, 1988; Zuquim et al., 2007), comparação com exsicatas disponíveis em herbários e em plataformas digitais e, sempre que possível, confirmação junto a especialistas do grupo. Nomes válidos e sinonímia para as espécies de forófitos e de epífitas foram verificados e seguem a proposta da Flora e Funga do Brasil (2023). Para classificação taxonômica das monocotiledôneas e eudicotiledôneas seguimos o sistema hierárquico proposto pelo Grupo de Filogenia de Angiospermas (APG IV, 2016); para samambaias e licófitas foi seguido o sistema proposto pelo Grupo de Filogenia de Pteridófitas (PPG I, 2016). O material botânico testemunho das espécies férteis foi coletado, herborizado e incorporado à coleção do Herbário do Instituto Nacional de Pesquisas da Amazônia (Herbário INPA, siglas conforme Thiers, 2021), departamento de Botânica, na cidade de Manaus (AM).

2.2 | Análises estatísticas

Utilizamos o Teste de Shapiro-Wilk para avaliar a distribuição dos dados (Shpairo and Wilk, 1965). Testamos a independência das variáveis preditoras usando o coeficiente de correlação de Spearman ($r > 0.7$; $P < 0.05$). Modelos lineares generalizados de efeitos mistos (GLMMs) com a distribuição “Poisson” foram utilizados para investigar os efeitos dos forófitos sobre a riqueza, abundância e composição das epífitas vasculares nos gradientes horizontais e verticais (Crawley, 2002). A composição de espécies foi resumida por Análise de Coordenadas Principais (PCoA) utilizando a classificação baseada na dissimilaridade entre as amostras calculadas pelo índice de Bray-Curts (Austin, 2013). A dissimilaridade estendida foi utilizada devido à grande dissimilaridade entre as amostras (Oksanen et al., 2011). Incluímos nos modelos como fatores fixos a altura, DAP, densidade da madeira das espécies, identidade taxonômica das espécies arbóreas e as zonas ecológicas (utilizadas apenas para os modelos verticais). A área de coleta e o indivíduo forofítico foram considerados fatores aleatórios (Bolker et al., 2008). Quinze modelos exploratórios simples e aditivos foram criados para investigar as interações entre variáveis preditoras para cada variável resposta. Ajustamos os modelos pelo critério de máxima verossimilhança Akaike (AIC) que compara e seleciona o modelo de melhor ajuste. Para verificar a dispersão dos resíduos, realizamos testes baseados em simulação de over/underdispersion. Realizamos todas as análises estatísticas no ambiente R (version 4.2.3, R core team, 2023) usando os pacotes bbmle (Bolker, 2022), DHARMa (Harti, 2022), lme4 (Bates et al., 2015), MuMIn (Barton, 2020).

Utilizamos o teste não paramétrico de Kruskal-Wallis (Kruskal & Wallis, 1952) e o teste de comparações múltiplas de Dunn (Dunn, 1964) para verificar diferenças na riqueza e abundância de epífitas nas zonas ecológicas dos forófitos (ZI, ZII, ZIII e ZIV). O valor indicador (Indval) foi utilizado para verificar a ocorrência de espécies indicadoras de cada zona ecológica (Dufrêne & Legendre, 1997). Este índice leva em consideração dois parâmetros: a especificidade da espécie, que é obtida através da razão da abundância média das espécies em termos de abundância sobre todos os grupos amostrados, e a fidelidade, que é a proporção de locais em que uma determinada espécie está presente dentro dos grupos. Utilizando a combinação de dados de abundância e os valores de presença e ausência das espécies, o Indval expressa para cada espécie o valor indicador em relação à tipologia dada, que representa a probabilidade de a espécie ser encontrada naquela tipologia (Podani & Csányi, 2010). Consideramos como indicadora a espécie que apresentou frequência superior a 50% ($P \leq 0.05$) em uma das zonas ecológicas. As análises foram conduzidas no ambiente R, utilizando o pacote Labdsv (Roberts, 2023).

A estrutura e a dinâmica das interações entre as espécies de epífitas vasculares e as zonas ecológicas foram avaliadas utilizando os descritores característicos para análises de redes ecológicas: conectância, aninhamento, índice de especialização complementar e modularidade. Conectância (C) é uma métrica que indica a porcentagem de interações observadas dentro do total de interações possíveis (Jordano, 1987). Para analisar o grau de aninhamento da rede foi utilizado a métrica de NODF (metric based on overlap and decreasing fill). O valor de NODF varia de zero (redes não aninhadas) a 100 (redes perfeitamente aninhadas). Para testar a significância de NODF usamos o modelo nulo de CE com 1000 permutações (Bascompte et al., 2003). O índice de especialização complementar (H2') foi calculado para verificar o grau de especialização da rede vertical; essa métrica é adequada, pois nos nos permite avaliar a seletividade das espécies em relação aos recursos disponíveies (Blüthgen et al., 2006). O modelo nulo de Patefield (1000 permutações aleatórias) foi utilizado para testar a significância de H2' (Blüthgen et al., 2006). Usamos a modularidade (Q) para examinar o grau de especialização de nicho na ocupação nas zonas ecológicas dos forófitos. Redes com alta modularidade possuem conexões densas entre os nós dentro dos módulos, mas conexões esparsas entre os nós em diferentes módulos. Valores de Q próximos a zero indicam ausência de estrutura modular na rede, ao passo que, valores mais próximos ao um, podem indicar que as espécies estão estruturadas em subgrupos (módulos) de preferência semelhante (Newman, 2006; Dormann & Strauss, 2014). A modularidade (Q) foi estimada usando o algoritmo QuanBiMo (Dormann & Strauss, 2014) e testada a significância de Q usando modelos nulos com 1.000 randomizações (Patefield, 1981). Utilizamos o teste de correlação de Mantel (Legendre & Legendre, 2012) com 10.000 randomizações para verificar a correlação entre os módulos e as zonas ecológicas, a partir de uma matriz ponderada das epífitas dentro de seus respectivos módulos (gerados pelo algoritmo QuanBiMo) e uma matriz que pondera as epífitas nas zonas ecológicas dos forófitos.

As métricas de rede foram calculadas usando o pacote "bipartite" (Dormann, Gruber & Frund, 2008) no ambiente estatístico R, versão 4.0.1 (R Core Team 2022.) A significância do índice de aninhamento (NODF) foi testada no programa ANINHADO 3.0.2 (Guimarães & Guimarães, 2006). Para visualização das interações da rede vertical, utilizamos como parâmetros a força das interações (baseado na abundância de indivíduos) entre o conjunto de arestas e o conjunto de nós. As inferências das interações foram visualizadas e ilustradas usando o software Gephi versão 0.10.1 (Jacomy et al., 2014).

3 | RESULTADOS

3.1| Distribuição horizontal – Considerando as cinco WSE inventariadas, registramos um total de 17.808 indivíduos epifíticos pertencentes a 18 famílias, 60 gêneros e 118 espécies, colonizando 486 indivíduos forófiticos (80% do total de árvores inventariadas), compreendendo 52 espécies, 39 gêneros e 29 famílias de forófitos (Tabela S1). Holoepífitas foram predominantes, representando 91% (108 spp.) das espécies registradas. As espécies de Orchidaceae, *Prosthechea aemula* (Lindl.) W.E.Higgins (4.130 indiv., 23%), *Maxillaria lutescens* Scheidw. (2.516 indiv., 14%) e *Brassavola martiana* Lindl. (1.027 indiv., 6%), foram as mais abundantes e juntas representaram 43% do total de indivíduos amostrados. A riqueza de espécies sobre os forófitos individuais variou de 1 – 31, ao passo que, o número de indivíduos variou de 1 – 704.

A altura, o DAP e a identidade taxonômica do forófito influenciaram significativamente a distribuição das epífitas vasculares no gradiente horizontal. O melhor modelo que incluiu altura, DAP e a espécie do forófito (variáveis de efeito fixo), os indivíduos forofíticos e o local de coleta (variáveis de efeito aleatório) explicou 72% da variação da riqueza (P<0,001) e 98% da variação da abundância de indivíduos (P<0,001; Tabela 1). Para a composição das espécies, o modelo incluindo altura, DAP e a espécie do forófito (variáveis de efeito fixo) e os indivíduos forofíticos (variável de efeito aleatório), foi o de melhor ajuste e explicou 99% da composição de espécies (P<0,001; Tabela 1). Para a composição de espécies, a altura dos forófitos (P < 0,0001) foi a única variável de efeito significativo (Tabela S1, Figure S1). A densidade da madeira não teve efeito significativo na distribuição das epífitas vasculares.

As espécies forofíticas, *Aldina heterophylla* Spruce ex Benth. (Fabaceae), *Leptobalanus latus* (J.F.Macbr.) Sothers & Prance (Chrysobalanaceae), *Licania canescens* Benoist (Chrysobalanaceae), *Peltogyne catingae* Ducke (Fabaceae), *Protium heptaphyllum* (Aubl.) Marchand (Burseraceae), *Schoepfia clarkii* Steyerm (Schoepfiaceae), *Ternstroemia dentata* (Aubl.) Sw (Pentaphylacaceae) e *Vitex duckei* (Lamiaceae) Huber foram as espécies arbóreas preditoras da riqueza de epífitas nas WSEs estudadas (Tabela S1). Essas mesmas espécies, com adição de *Myrcia umbraticola* (Kunth) (Myrtaceae) E.Lucas & C.E.Wilson e *Ouratea spruceana* Engl (Ochnaceae), foram as preditoras da abundância de epífitas (Tabela S1).

3.2| Distribuição vertical – A zona ecológica ZIII apresentou maior riqueza de espécies (98 spp.) enquanto que a zona ZIV exibiu maior abundância de indivíduos (7.075 indiv.). A maior abundância de epífitas em ZIV foi relacionada a quatro espécies abundantes, *P. aemula* (2.107 indiv.), *M. lutecences* (1.019 indiv.), *Epidendrum strobilifereum* Rchb.f. (726 indiv.) e *B. martiana* (678 indiv.), ambas Orchidaceae, que juntas representam 64% dos indivíduos presentes nesta zona. As regiões do fuste (ZI e ZII), foram dominadas por samambaias, as quais representaram 58% do número total de indivíduos presentes nessas duas zonas. Dryopteridaceae foi mais abundante em número de indivíduos em ZI (4 spp.; 784 indiv.), representando 54% da abundância de epífitas. Nas demais zonas (ZII, ZIII e ZIV), Orchidaceae prevaleceu, representando até 84% da abundância total de indivíduos. A riqueza de espécies (Qui-quadrado = 149,59; $P < 0,001$) e a abundância de epífitas (Qui-quadrado = 182,04; $P < 0,001$) diferiram significativamente entre as zonas verticais (Figura 3). O modelo da interação entre as variáveis altura, DAP, espécie de forófito, as zonas ecológicas (variáveis de efeito fixo) e os indivíduos forofíticos (variável de efeito aleatório) foi o que apresentou menores valores de AIC (Tabela 1) e explicou 71% da variação da riqueza ($P<0,001$), 96% da variação da abundância de indivíduos ($P<0,001$) e 60% da variação na composição de espécies no gradiente vertical ($P<0,001$; Tabela 1). Valores de significância dos modelos encontram-se disponíveis na Tabela S1.

As análises de estrutura da rede de interação vertical entre as epífitas e as zonas ecológicas demostraram uma rede altamente conectada (C = 0,65), aninhada (NODF = 48,5; $P < 0,01$), pouco especializada (H2' = 0,24, $P < 0,05$) e pouco modular (Q = 0,26; $P < 0,02$). As epífitas vasculares foram agrupadas em três módulos, em que 84 espécies foram compartilhadas entre dois ou mais módulos e 34 espécies (28%) foram exclusivas de apenas um módulo (Figura 4, Tabela 2). O módulo 1 (correspondente às zonas do fuste) agrupou duas zonas ecológicas ZI e ZII, e foi composto por 45 espécies (38%), das quais 15 foram exclusivas para este módulo. O módulo 2, formado por ZIII, apresentou 52 espécies (44%) associadas, das quais 15 espécies são exclusivas. O módulo 3, formado pela zona ZIV, apresentou 21 espécies (18%) associadas e apenas quatro espécies exclusivas. O teste de Mantel reportou correlação positiva entre a formação de módulos e as zonas ecológicas dos forófitos (r = 0,93; $P < 0,00001$).

A análise de espécies indicadoras (Indival) demostrou a presença de nove espécies indicadoras no gradiente vertical (Figura 5). Duas espécies de samambaias, *Elaphoglossum discolor* (Kuhn) C.Chr. e *Elaphoglossum plumosum* (Fée) T.Moore (Dryopteridaceae) foram indicadoras de ZI; *Maxillaria parviflora* (Poepp. & Endl.) Garay (Orchidaceae) foi indicadora de ZIII; e seis espécies, *Brassavola martiana*, *Caularthron bicornutum* (Hook.) Raf., *Encyclia chloroleuca* (Hook.) Neumann *Epidendrum micronocturnum* Carnevali & G.A.Romero, *E. strobiliferum* Rchb.f. (Orchidaceae) e *Tillandsia adpressiflora* Mez (Bromeliaceae) foram indicadoras da ZIV. A zona ecológica ZII não apresentou nenhuma espécie indicadora.

4 | DISCUSSÃO

Epífitas são estruturalmente dependentes das árvores/arbustos, e características intrínsecas dos forófitos como tamanho, idade e disposição dos ramos influenciam na distribuição das espécies epifíticas (Wagner et al., 2015). Os resultados do presente estudo mostraram que características estruturais relacionadas, principalmente, ao tamanho das árvores e à identidade do forófito influenciam os padrões horizontais e verticais de riqueza, abundância e composição das comunidades de epífitas vasculares em WSEs da Amazônia central. Também identificamos diferenças na distribuição vertical das epífitas em relação às zonas ecológicas estabelecidas nos forófitos, com maior riqueza e abundância de epífitas nas regiões da copa dos forófitos. As análises da rede vertical, demostraram que as interações entre as epífitas e as zonas ecológicas apresentaram estrutura aninhada e altamente conectada, porém pouco especializada e modular. As espécies foram distribuídas em três módulos dentro dos forófitos, sendo possível identificar distintos grupos de espécies ocupando diferentes zonas das árvores.

Nossos resultados mostraram que caraterísticas relacionadas ao tamanho do forófito (DAP e altura) influenciaram a distribuição das espécies de epífitas. A relação positiva entre riqueza e abundância de epífitas vasculares e o tamanho do forófito é um padrão comumente relatado por diversos estudos que envolvem as interações epífitas-forófitos (Callaway et al., 2002; Clemente-Arenas et al., 2021; Francisco et al., 2021; Obermüller et al., 2012; Quaresma et al., 2020; Wagner & Zotz, 2019; Zhao et al., 2015). O tamanho de um forófito pode integrar características ecológicas importantes, como um conjunto muito diversificado de condições ambientais e microclimáticas que desempenham um papel fundamental na determinação da estrutura das comunidades epifíticas (Francisco et al., 2021; Sáyago et al., 2013). Geralmente o tamanho do forófito está associado com a idade da árvore (Zotz & Vollrath, 2003), e assim, árvores mais velhas possuem mais chances de serem colonizadas, provavelmente devido a maior exposição à chuva de sementes por um maior período de tempo (Zhao et al., 2015). Além disto, grandes forófitos possuem maiores superfície de área, em comparação com árvores menores, proporcionando maior disponibilidade de espaço para colonização e estabelecimento das epífitas (Wagner et al., 2015).

Embora a densidade da madeira esteja associada a maior estabilidade e resistência dos ramos, condições que podem favorecer as epífitas (Easdale, 2006; Sáyago et al. 2013), neste estudo, não observamos efeito significativo dessa variável na distribuição das epífitas vasculares em WSE. Acreditamos que isto pode ser parcialmente explicado pela influência de algumas espécies em particular. Por exemplo, *Aldina heterophylla* foi o forófito que manteve maior interação com as epífitas em WSE, mas é uma espécie que apresenta uma densidade da madeira não muito elevada (0,65 g/cm3). Sendo assim, acreditamos que um conjunto de traços, relacionados principalmente a disponibilidade de area para colonização, disposição dos ramos horizontais e características do ritidoma estão entre os principais fatores que garantem o sucesso na germinação e estabelecimento das epífitas vasculares (Wagner et al. 2015). Estudos realizados em regiões subtropicais da Argentina, também não encontraram efeitos significativos dessa variável na frequência das interações entre epífitas-forófitos (Ceballos et al. 2016). Desta maneira, acreditamos que um conjunto de caraterítsicas, principalmente associadas a (Sáyago et al. 2013).

Os modelos utilizados indicaram que a identidade do forófito é um importante preditor para a distribuição das epífitas vasculares em WSE. Uma vez que as espécies de epífitas dependem estruturalmente dos forófitos, variações nas propriedades físicas e químicas da casca, no tamanho e na idade, na arquitetura dos ramos da copa e na fenologia das espécies de forófitos podem influenciar fortemente o estabelecimento e desenvolvimento das comunidades de epífitas vasculares (Burns & Zotz, 2010; Wagner et al., 2015). Ainda que a especificidade estrita nas interações envolvendo epífitas-forófitos não seja um padrão frequentemente relatado (Alves et al., 2008; Sáyago et al., 2013; Wagner et al., 2015), a preferência de espécies epífitas por determinados táxons de forófito já foi evidenciada

(Callaway et al., 2002; Francisco et al., 2018; Laube & Zotz, 2006; Quaresma et al., 2017), sugerindo que algumas espécies de árvores apresentam conjuntos de caraterísticas estruturais e microclimáticas que as torna melhores forófitos que outros (Francisco et al., 2018; Zhao et al., 2015). Nosso estudo revelou que algumas espécies de forófitos, como *Aldina heterophylla, Schoepfia clarkii, Ouratea spruceana* e *Vitex duckei,* endêmicas das WSE (Demarchi et al. 2022), contribuem significativamente na dinâmica e estruturação das comunidades de epífitas nesses ecossistemas. Características estruturais dos forófitos, tais como tamanho e traços intrínsecos da espécie, como o tipo de casca, são importantes variáveis que determinam grande parte interações entre epífitas-forófitos (Sáyago et al., 2013; Ceballos et al., 2016). Desta forma, identificar as espécies-chaves em um ecossistema tem grande importância, principalmente para medidas de conservação, uma vez que a sua retirada local pode causar uma significativa perda nas interações (Sáyago et al., 2013) e, consequentemente, na biodiversidade.

Variações nos gradientes de luz, umidade relativa e temperatura criam distintas condições microclimáticas entre os ramos externos até a base do tronco dos forófitos (Krömer et al., 2007), e são considerados os fatores ambientais que, em conjunto, constituem as principais forças motrizes que determinam a distribuição e rotatividade vertical das espécies epífitas (Johansson, 1974). Entretanto, características bióticas, como a heterogeneidade estrutural das diferentes zonas verticais dos forófitos (diâmetro, dos ramos e altura da árvore) são também fortes preditores para a estruturação das comunidades de epífitas (Woods et al., 2018). Diante disso, nossa hipótese que as epífitas vasculares não se distribuem aleatoriamente entre as zonas ecológicas dos forófitos de WSE foi confirmada. Em geral, as epífitas foram mais ricas e abundantes nas zonas da copa, que diferiram significativamente em relação às zonas do tronco. A alta riqueza de espécies na copa pode estar relacionada à maior disponibilidade de áreas para colonização, uma vez que, principalmente na zona interna da copa, os ramos são mais grossos, suportando maior abundância de indivíduos e também epífitas de maiores tamanhos, como exemplos, as grandes bromélias tanques, *Aechmea longifolia* (Rudge) L.B.Sm. & M.A.Spencer, *Aechmea setigera* Mart. ex Schult. & Schult.f. e *Mezobromelia pleiosticha* (Griseb.) Utley & H.Luther, e os grandes agrupamentos de espécies, formados majoritariamente por *Prosthecea aemula*. Além disto, os ramos projetados mais horizontalmente na copa possibilitam maior retenção de matéria orgânica e formação de tapetes de musgos, que servem como fonte de água e nutrientes para a fixação e germinação dos propágulos das epífitas, contribuindo para que comunidades mais abundantes e diversificadas consigam se estabelecer (Krömer et al., 2007; ter Steege & Cornelissen 1989; Woods et al., 2015).

Verticalmente observamos que a composição das espécies de epífitas vasculares apresentou um padrão significativo de estratificação. As análises de redes ecológicas indicaram que a distribuição das espécies no gradiente vertical apresenta uma estrutura aninhada, com baixa especialização e pouco modular. O aninhamento sugere que poucas espécies são especialistas de *habitat*, uma vez que, a maioria das espécies estão amplamente distribuídas ao longo do gradiente vertical, podem ser consideradas espécies generalistas na utilização dos recursos (Burns, 2007). Observamos uma rede vertical pouco modular composta por três módulos que foram compartilhados por 45% das espécies de epífitas. Espécies abundantes como, *Brassavola martiana, Prosthechea aemula, Maxillaria lutescens,* se distribuem amplamente no gradiente vertical, enquanto outras 34 espécies (29%) são exclusivas de um dos módulos verticais.

Neste estudo, o módulo 1, formado pelas zonas do fuste (ZI e ZII), foi ocupado por samambaias, enquanto que nos demais módulos (ZIII e ZIV), as orquídeas e bromélias prevaleceram. Padrão de estratificação taxonômica é usualmente evidenciado para epífitas vasculares (Couto et al., 2022; Hietz & Hietz-Seifert, 1995; Krömer et al., 2007; Pos & Sleegers, 2010; ter Steege & Cornelissen, 1989; Woods et al., 2018). As diferenciações ecológicas na distribuição das espécies podem ser o resultado de distintos mecanismos de utilização dos recursos e indicam potenciais preferências de nicho para cada espécie (Callaway et al., 2002; Kersten & Silva, 2002; Sáyago et al., 2013). Por exemplo, comparado com a copa, o fuste proporciona condições microclimáticas relativamente constantes, sendo mais protegido da radiação direta e dos ventos incidentes e retém maior teor de umidade (Johansson, 1974). Estas condições favorecem o desenvolvimento de epífitas mais tolerantes à sombra e umidade, como as samambaias indicadoras *Elaphoglossum discolor* e *Elaphoglossum plumosum,* as quais são predominantes na base do fuste dos forófitos, próximo ao solo (Krömer et al., 2007; ter Steege & Cornelissen, 1989). Em contrapartida, regiões da copa que estão mais expostas a luminosidade direta, recebem maior incidência de ventos e a umidade é consideravelmente reduzida, sendo o acesso a água um dos principais limitantes no dossel das florestas (Johansson, 1974). Contudo, para se adaptar ao ambiente mais seco das copas, várias espécies de epífitas desenvolveram distintas adaptações anatômicas, morfológicas e fisiológicas, que lhes possibilita o sucesso na colonização destas regiões dos forófitos (Kersten & Silva, 2002; Benzing, 1990; Hietz et al., 1999). Nas regiões mais externas da copa, o número de espécies providas de estruturas adaptadas para conservação de água, como pseudobulbos e folhas suculentas (*Cattleya wallisii, Codonanthopsis crassifolia*, *Caularthron bicornutum* e *Prosthechea aemula*, por exemplo) foi maior quando comparados às regiões do fuste. De maneira similar, as espécies indicadoras (*Brassavola martiana*, *Epidendrum strobiliferum* e *Tillandsia adpressiflora*) das regiões externas da copa (ZIV), apresentam entre as adaptações fisiológicas o Metabolismo Ácido das Crassuláceas (CAM) que lhes permite se desenvolverem e serem representativas em regiões mais expostas a altas taxas de luminosidade (Bonates & Braga, 1992; Bonates, 1993). A configuração observada dos módulos verticais sugere que algumas espécies apresentam traços funcionais que lhes permitem responder diferentemente a níveis de luminosidade e umidade como também ao tipo de substrato (Agudelo et al., 2019; Petter el al., 2015).

Em um cenário de mudanças climáticas e alterações no uso da terra, conhecer e relacionar os padrões que estruturam a composição e distribuição das comunidades de epífitas vasculares nos gradientes horizontais e verticais com variáveis ambientais, é fundamental para aumentar nossa capacidade de prever as respostas das epífitas frente às mudanças no ambiente (Pettter el al., 2021; Zotz & Bader, 2009). Nos últimos anos, pressões exploratórias sobre os WSEs têm se intensificado, o que é muito preocupante, uma vez que estes ambientes são frágeis e pobremente protegidos em unidades de conservação (Adeney et al., 2016; Demarchie et al., 2019). Desta forma, nosso estudo contribui para aumentar o entendimento dos fatores que influenciam e estruturam as interações entre epífitas-forófitos em WSEs. Nós identificamos que o DAP, a altura e a identidade taxonômica dos forófitos são os melhores preditores que determinam a riqueza, abundância de indivíduos e a composição das comunidades de epífitas vasculares nestes ambientes. Consequentemente, a retirada de grandes árvores ou de espécies-chaves que mantém grande número de interações, podem reduzir consideravelmente as populações epifíticas, ocasionar a perda de interações e levar algumas espécies à extinção local devido à perda de *habitat* e alterações microclimáticas. Verticalmente nós detectamos que diferentes regiões dos forófitos apresentam diferenças na distribuição e na composição de epífitas vasculares, o que resulta em um padrão de estratificação e de modularidade. Nós conseguimos identificar que algumas espécies de epífitas foram indicadoras de determinadas zonas ecológicas, podendo refletir um conjunto de traços adaptativos que lhes permitem ter mais sucesso e representatividade em determinadas regiões dos forófitos. Por fim, ainda são necessários estudos futuros, em especial, para identificar quais variáveis ambientais e microclimáticas influenciam a distribuição vertical das espécies ao longo do gradiente; investigar os traços funcionais que elas apresentam e suas relações com essas variações ambientais.

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LISTA DE TABELAS:

Tabela 1: Modelos lineares generalizados mistos (GLMM) com melhor valor de ajuste para explicar a distribuição da riqueza, abundância e composição das epífitas vasculares nos gradientes horizontais e verticais em cinco ecossistemas de areia branca da Amazônia central.

	Variável resposta	Modelo	Δ R2m	Δ R2c	AIC	Pr(>Chisq)
Distribuição	Riqueza de espécies	Modelo = (DAP) + (altura) + (espécie de forófito) + (1|indivíduos arbóreos) + (1|local)	0,62	0,72	2103,9	2,2e-16***
	Número de espécies	Modelo = (DAP) + (altura) + (espécie de forófito) + (1|indivíduos arbóreos) + (1|local) +	0,64	0,98	3666,9	2,2e-16 ***
	Composição de espécies	Modelo = (DAP) + (altura) + (espécie de forófito) + (1|indivíduos arbóreos)	0,30	0,99	-178,3	2,2e-16 ***
Distribuição	Riqueza de espécies	Modelo = (zonas ecológicas) + (DAP) + (altura) + (espécie de forófito) + 1| indivíduos arbóreos)	0,48	0,61	6081,8	2,2e-16 ***
	Número de espécies	Model = (zonas ecológicas) + (DAP) + (altura) + (espécie de forófito) + (1| indivíduos arbóreos)	0,67	0,96	6859,2	2,2e-16 ***
	Composição de espécies	Model = (zonas ecológicas) + (DAP) + (altura) + (espécie de forófito) + (1| indivíduos arbóreos)	0,34	0,60	-456,1	2,2e-16 ***

Tabela 2. Organização dos módulos formados através da análise da modularidade da rede de interação vertical entre espécies e zonas ecológicas. Lista com destaque em cor cinza, são as espécies exclusivas dos módulos.

Módulo	Código	Espécie
1	Acimiq	*Acianthera miqueliana*
	Actpen	*Actinostachys pennula*
	Aecbro	*Aechmea bromeliifolia*
	Aecrod	*Aechmea rodriguesiana*
	Agacya	*Aganisia cyanea*
	Aptaph	*Apteria aphylla*
	Batcol	*Batemannia colleyi*
	Biflon	*Bifrenaria longicornis*
	Bifven	*Bifrenaria venezuelana*
	Bulset	*Bulbophyllum setigerum*
	Camfas	*Campylocentrum fasciola*
	Clunem	*Clusia nemorosa*
	Clupen	*Clusia penduliflora*
	Cluspa	*Clusia spathulaefolia*
	Cocfur	*Cochlidium furcatum*
	Cocpum	*Cochlidium pumilum*
	Cocser	*Cochlidium serrulatum*
	Eladis	*Elaphoglossum discolor*
	Elagla	*Elaphoglossum glabellum*
	Elaobo	*Elaphoglossum obovatum*
	Elaplu	*Elaphoglossum plumosum*
	Enccon	*Encyclia conchaechila*
	Encmap	*Encyclia mapuerae*
	Epiapu	*Epidendrum apuahuense*
	Episcu	*Epidendrum sculptum*
	Ficmath	*Ficus mathewsii*
	Guzbra	*Guzmania brasiliensis*

	Hecpum	*Hecistopteris pumila*
	Hylpet	*Hylaeorchis petiolaris*
	Hympol	*Hymenophyllum polyanthos*
	Linlan	*Lindsaea lancea*
	Ludlanc	*Ludovia lancifolia*
	Madkerrii	*Madisonia kerrii*
	Maxdes	*Maxillaria desvauxiana*
	Mornana	*Moranopteris nana*
	Octyau	*Octomeria yauaperyensis*
	Phimel	*Philodendron melinonii*
	Procra	*Prosthechea crassilabia*
	Rodlan	*Rodriguesia lanceolata*
	Rudaur	*Rudolfiella aurantiaca*
	Sobgra	*Sobralia granítica*
	Triccris	*Trichomanes crispum*
	Tricmar	*Trichomanes martiusii*
	Tricspru	*Trichomanes spruceanum*
	Tricorb	*Trichosalpinx orbicularis*
	Vanbic	*Vanilla cf. bicolor*
2	Aechue	*Aechmea huebneri*
	Aeclon	*Aechmea longifolia*
	Aecset	*Aechmea setigera*
	Aecval	*Aechmea vallerandii*
	Antbon	*Anthurium bonplandii*
	Antemi	*Anthurium eminens*
	Antobt	*Anthurium obtusum*
	Aramic	*Araeococcus micranthus*
	Aspsp	*Asplenium sp.*
	Catwal	*Cattleya wallisii*
	Cluuca	*Clusia ucamira*
	Coddis	*Codonanthopsis dissimulata*

Codulei	*Codonanthopsis ulei*
Couasp	*Coussapoa asperifolia*
Dicpic	*Dichaea picta*
Elaray	*Elaphoglostum raywaense*
Epiphy	*Epiphyllum cf. phyllanthus*
Erisce	*Eriopsis sceptrum*
Jacglo	*Jacquiniella globosa*
Maxbra	*Maxillaria brasiliensis*
Maxkeg	*Maxillaria kegelii*
Maxlut	*Maxillaria lutescens*
Maxpar	*Maxillaria parviflora*
Maxpen	*Maxillaria pendens*
Maxsup	*Maxillaria superflua*
Maxtenui	*Maxillaria tenui*
Maxunc	*Maxillaria uncata*
Mezple	*Mezobromelia pleiosticha*
Micper	*Microgramma percursa*
Nepriv	*Nephrolepis rivularis*
Octgra	*Octomeria surinamensis*
Phipul	*Philodendron pulchrum*
Plebom	*Pleopeltis bombycina*
Plehir	*Pleopeltis hirsutissima*
Polfol	*Polystachya concreta*
Polste	*Polystachya stenophylla*
Scasic	*Scaphyglottis sickii*
Scaste	*Scaphyglottis stellata*
Scuste	*Scuticaria steelei*
Seratte	*Serpocaulon attenuatum*
Serses	*Serpocaulon sessilifolium*
Sobble	*Sobralia bletiae*
Sobses	*Sobralia sessilis*

	Spepic	*Speclinia picta*
	Tilbul	*Tillandsia bulbosa*
	Vitlin	*Vittaria lineata*
3	Aecmer	*Aechmea mertensii*
	Antgra	*Anthurium gracile*
	Bramar	*Brassavola martiana*
	Caubic	*Caularthron bicornutum*
	Cluins	*Clusia insignis*
	Codcra	*Codonanthopsis crassifolia*
	Encchl	*Encyclia chloroleuca*
	Epibah	*Epidendrum bahiense*
	Epicar	*Epidendrum carpophorum*
	Epicom	*Epidendrum compressum*
	Epimicron	*Epidendrum micronocturno*
	Epimicrop	*Epidendrum microphylum*
	Epiorc	*Epidendrum orchidiflorum*
	Epirig	*Epidendrum rigidum*
	Episch	*Epidendrum schlechterianum*
	Epistro	*Epidendrum strobiliferum*
	Macmir	*Macroclinium miralis*
	Maxobt	*Maxillaria obtusa*
	Maxsub	*Maxillaria subrepens*
	Micbal	*Microgramma baldwinii*
	Notsp.	*Notylia aromatica* Barker ex Lindl.
	Octtar	*Octomeria taracuana*
	Orlama	*Orleanesia amazonica*
	Pabyau	*Pabstiella yauaperyensis*
	Proaem	*Prosthechea aemula*
	Tiladp	*Tillandsia adpressiflora*

Lista de figuras:

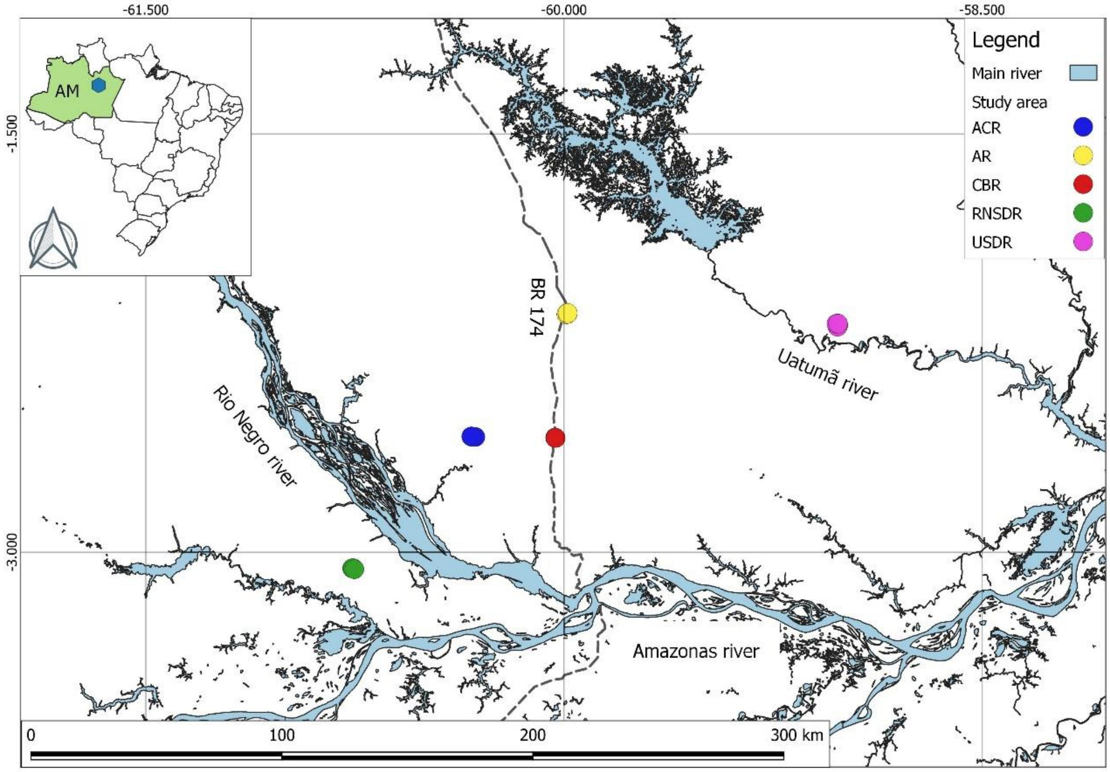

Figura 1: Localização dos sítios de estudo nos cinco ecossistemas de areia branca da Amazônia central, Brasil. Reserva Alto Cuieiras (ACR); Reserva Asframa (AR); Reserva Biológica da Campina (CBR); Reserva do Desenvolvimento Sustentável do Rio Negro (RNSDR); Reserva do Desenvolvimento Sustentável Uatumã (USDR).

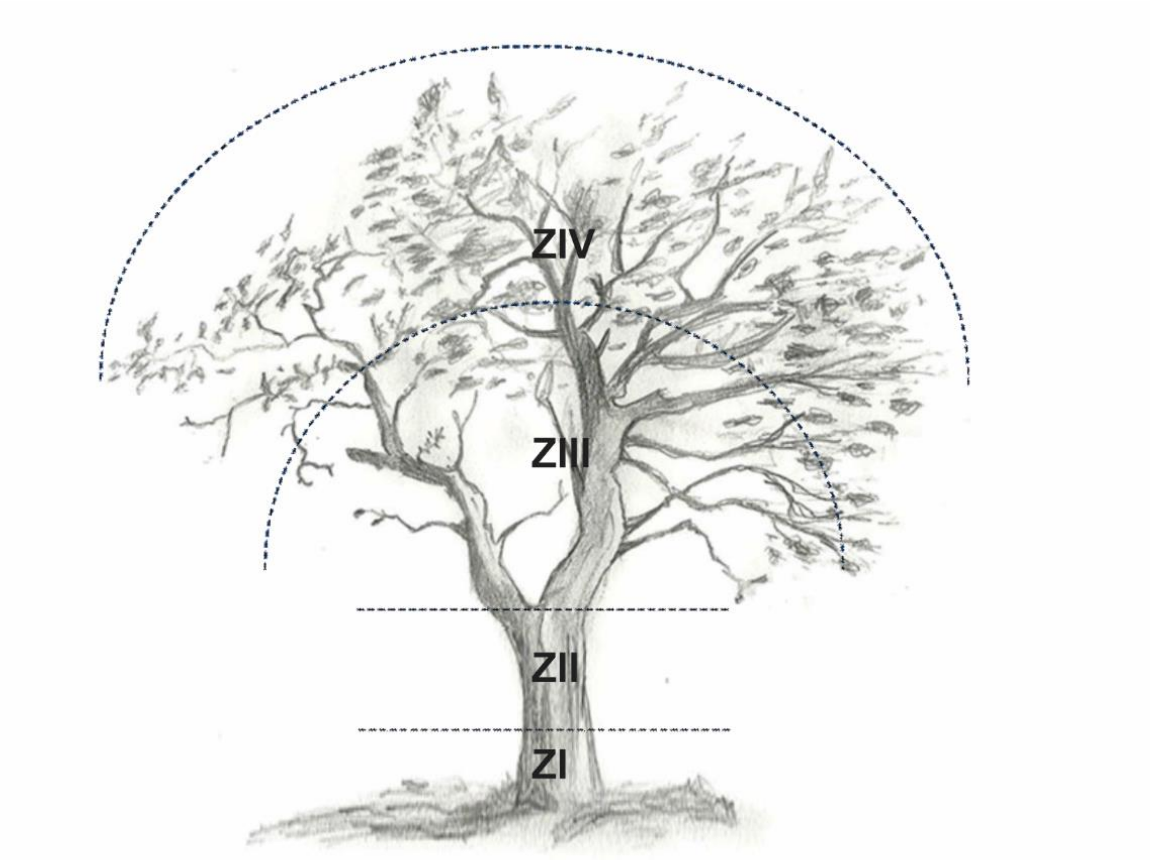

Figura 2: Representação esquemática das zonas ecológicas estabelecidas nos forófitos. ZI – base do tronco (desde o solo até 1m de altura); ZII – tronco alto (acima de 1 m de altura até a emissão das primeiras bifurcações); ZIII – copa interna (região dos ramos primários) e ZIV – copa externa (região dos ramos mais jovens e finos). Metodologia adaptada de Johansson (1974).

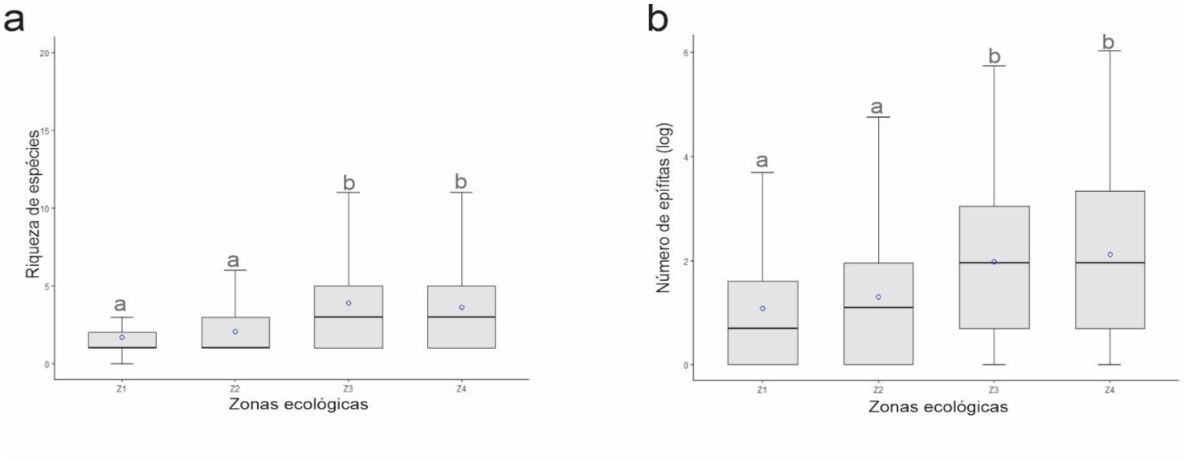

Figura 3: Distribuição vertical da riqueza (a) e do número de indivíduos de epífitas vasculares em ecossistemas de areia branca da Amazônia central. Letras indicam diferenças significativas entre as zonas ecológicas.

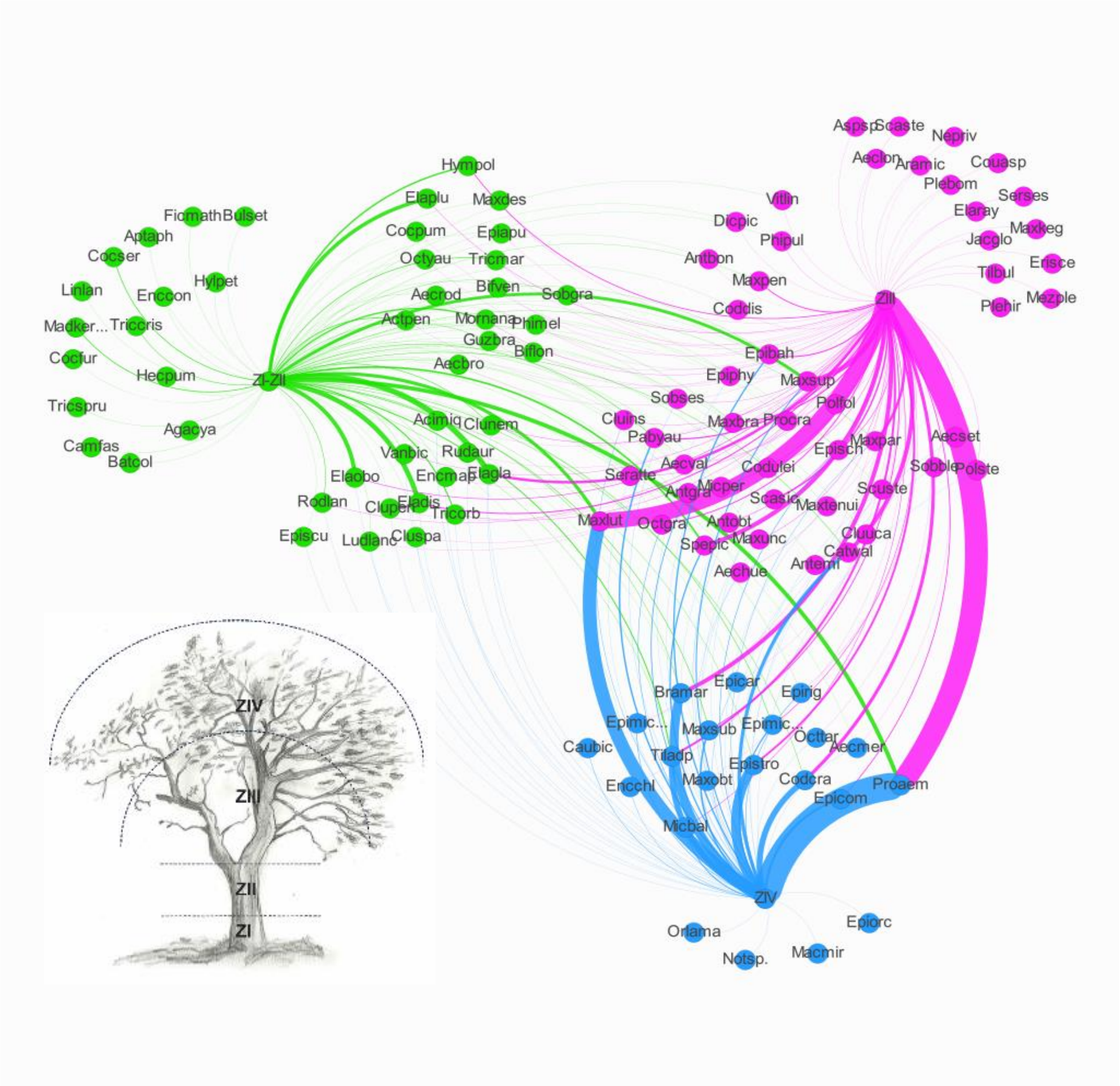

Figura 4: Representação da divisão modular da rede vertical das epífitas vasculares em relação às zonas ecológicas. A rede foi dividida em três módulos: Módulo 1 (cores em verde): formado pelas zonas ZI e ZII. Modulo 2 (cores em rosa): formado por ZIII. Modulo 3 (cores em azul): formado por ZIV. Os vértices da rede (epífitas e os módulos) são apresentados em círculos coloridos e foram codificados pois representam os módulos e as espécies associadas a eles. Espécies periféricas aos módulos, foram exclusivas. Espécies centrais são as compartilhadas entre os módulos. A espessura das linhas é proporcional à frequência das interações das espécies em cada módulo. A lista das espécies e os códigos estão na Tabela 2.

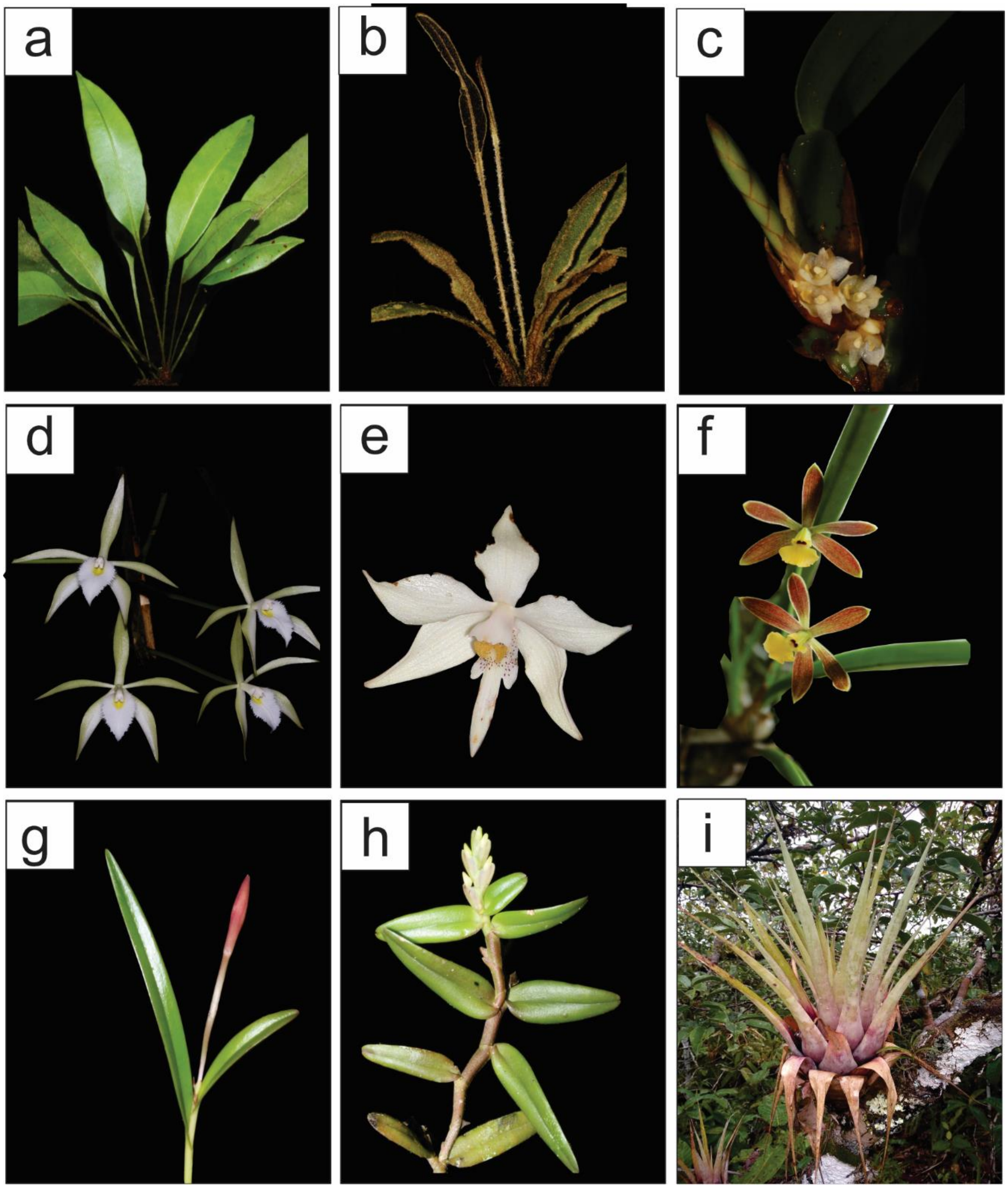

Figura 5: Espécies características das zonas ecológicas dos forófitos. Em ZI (a) *Elaphoglossum discolor* (Kuhn) C.Chr. e (b) *Elaphoglossum plumosum* (Fée) T.Moore. Em ZIII (c) *Maxillaria parviflora* (Poepp. & Endl.) Garay. Em ZIV (d) *Brassavola martiana* Lindl., (e) *Caularthron bicornutum* (Hook.) Raf., (f) *Encyclia chloroleuca* (Hook.) Neumann, (g) *Epidendrum micronocturnum* Carnevali & G.A.Romero, (h) *Eipidendrum strobiliferum* Rchb.f. e em (i) *Tillandsia adpressiflora* Mez.

Material suplementar:

Tabela S1: Valores estatísticos significativos dos modelos Modelos Generalizados Mistos (GLMM) de distribuição horizontal e vertical das epífitas vasculares em campinaranas da Amazônia central.

Horizontal distribuição

Fixed effects:	Std.	Error	z	value	Pr(>|z|)
Modelo 1: dados$species richness ~ (dados$DAP) + (dados$ tree height + (dados$ tree species) + (1 | dados$Local) + (1 \| dados$Ind_for)	dados$DAP	0.02384	0.0022	11.804	<2e-16
	dados$Altura	-0.01326	0.0102	-1.323	0.04
	dados$*Aldina heterophylla*	1.45207	0.7275	1.997	0.048
	dados$*Leptobalanus latus*	2.02985	0.8162	2.486	0.0129
	dados$*Licania canescens*	1.44276	0.7323	1.971	0.0488
	dados$*Peltogyne catingae*	1.61766	0.7688	2.104	0.0354
	dados$*Protium heptaphyllum*	1.71959	0.8079	2.13	0.0332
	dados$*Schoepfia clarkii*	1.71098	0.8351	2.047	0.0407
	dados$*Ternstroemia dentata*	1.66162	0.7358	2.259	0.0239
	dados$*Vitex duckei*	1.69533	0.851	1.99	0.0466
Modelo 2: dados$Numberepiphytes ~ (dados$DAP) + (dados$ tree height) + (dados$ tree species) + (1 | dados$Ind_for) + (1 \| dados$Local)	dados$DAP	0.04494	0.0041	9.342	<0.002
	dados$ *Aldina heterophylla*	2.76143	1.0055	2.747	0.00602
	dados$ *Leptobalanus latus*	3.70331	1.3241	2.795	0.00519
	dados$ *Licania canescens*	2.36141	1.0228	2.309	0.02092
	dados$ *Myrcia umbraticola*	2.69986	1.3153	2.052	0.04014
	dados$ *Peltogyne catingae*	2.34118	1.1271	2.077	0.03782
	dados$ *Protium heptaphyllum*	2.99858	1.3143	2.281	0.02255
	dados$ *Schoepfia clarkii*	3.47826	1.3229	2.629	0.00856
	dados$*Ternstroemia dentata*	2.28431	1.036	2.204	0.02751

Modelo 3: scores_pcoa_horizontal~ (dados$DAP) + (dados$ tree height) + (dados$ tree species) + (1 | dados$Ind_for)	epft$Altura	0.01641	0.00312	368.45422	4.955
Vertical distribuição					
Modelo 1: dados$ species richnes ~ dados$ecologicalzone + dados$Sp.for + dados$ tree height + dados$DAP + (1 \| dados$id_for) + (1 | dados$Local)	dados$ZonaZ1	1.61E+00	7.04E-01	2.29E+00	0.022
	dados$ZonaZ3	6.59E-01	4.99E-02	1.32E+01	2.00E-16
	dados$ZonaZ4	4.26E-01	5.21E-02	8.17E+00	3.16E-16
	dados$DAP	2.22E-02	2.56E-03	8.67E+00	2.00E-16
	dados$*Aldina_heterophylla*	1.53E+00	6.84E-01	2.23E+00	0.0257
	dados$ *Leptobalanus latus*	2.03E+00	8.33E-01	2.43E+00	0.015
	dados$ *Licania canescens*	1.38E+00	6.91E-01	2.00E+00	0.0459
	dados$*Myrcia umbraticola*	1.74E+00	8.18E-01	2.13E+00	0.0334
	dados$ *Peltogyne catingae*	1.66E+00	7.39E-01	2.25E+00	0.0243
	dados$ *Schoepfia clarkii*	1.76E+00	8.38E-01	2.10E+00	0.0359
	dados$*Ternstroemia dentata*	1.65E+00	6.97E-01	2.36E+00	0.0182
	dados$*Vitex_duckei*	1.84E+00	8.56E-01	2.15E+00	0.032
Modelo2: dados$Numberepiphytes ~ dados$ecological_zone + (dados$DAP) + (dados$ tree height) + (dados$ tree species) + (1 | dados$Ind_for) + (1 \| dados$Local)	dados$ZonaZ1	-2.76218	1.043544	-2.647	0.00812
	dados$ZonaZ2	0.460699	0.033285	13.841	2.00E-16
	dados$ZonaZ3	1.56576	0.028658	54.636	2.00E-16
	dados$ZonaZ4	1.580866	0.028621	55.234	2.00E-16
	dados$DAP	0.043254	0.004721	9.162	2.00E-16

	dados$*Aldina heterophylla*	2.796687	1.012695	2.762	0.00575
	dados$ *Leptobalanus latus*	3.749657	1.331245	2.817	0.00485
	dados$ *Licania canescens*	2.321444	1.030061	2.254	0.02422
	dados$*Macrolobium bifolium*	2.756526	1.351023	2.04	0.04132
	dados$*Myrcia umbraticola*	2.730077	1.320951	2.067	0.03876
	dados$ *Peltogyne catingae*	2.345688	1.134601	2.067	0.0387
	dados$*Protium heptaphyllum*	3.0113	1.320983	2.28	0.02263
	dados$*Schoepfia clarkii*	3.54608	1.328039	2.67	0.00758
	dados$*Terminalia macrophylla*	1.303449	1.127975	1.156	0.24786
	dados$*Ternstroemia dentata*	2.326476	1.043659	2.229	0.0258
	dados$*Vitex duckei*	2.693231	1.349967	1.995	0.04604
Modelo 3: scores_pcoa_vertical ~ epftv$ecological zone + (epftv$DAP) + (epftv$ tree height) + (epftv$tree species) + (1 \| epftv$id)	epftv$ZonaZ2	-1.30E-01	1.28E-02	8.17E+02	-10.166
	epftv$ZonaZ3	-2.10E-01	1.31E-02	8.38E+02	-15.991
	epftv$ZonaZ4	-2.09E-01	1.38E-02	8.38E+02	-15.09
	epftv$DAP	1.51E-03	7.36E-04	3.32E+02	2.054
	epftv$Altura	1.60E-02	2.62E-03	4.21E+02	6.092
	epftv$*Pera bicolor*	-4.83E-01	2.22E-01	4.70E+02	-2.174

CAPÍTULO 3

Viviane Pagnussat Klein, Talitha Mayumi Francisco, Adriano Costa Quaresma e Maria Teresa Fernandez Piedade. **The structure and low robustness of epiphyte-phorophyte networks show vulnerabilities in white-sand ecosystems in Amazonia.** Sob avaliação após correções na Biotropica.

RESUMO

A Amazônia é a maior floresta tropical do mundo, apresenta grande diversidade de espécies e fornece serviços ecossistêmicos essenciais. Porém, os processos exploratórios antrópicos vêm se intensificando e estão influenciando seriamente este bioma. As abordagens baseadas na teoria das redes ecológicas são uma excelente ferramenta para descrever a estrutura das comunidades, as interações entre as espécies e a estabilidade dos ecossistemas. Usando um conjunto específico de métricas de rede foi criada a primeira rede comensal epífita-forófita para os frágeis ecossistemas de areia branca (WSEs) da Amazônia central. A estrutura e organização das interações foram analisadas e descritas; também testamos a estabilidade do sistema para simular a perda de espécies no nível regional e no nível local. Um total de 725 interações entre 52 espécies de forófitos e 118 epífitas vasculares foram registradas nos WSEs. Em nível regional, a rede epífita-forófita exibiu uma estrutura aninhada, com baixo grau de especialização (H2'), conectância, modularidade e robustez. Padrão semelhante foi observado em nível local. Quando simulamos a eliminação de forófitos altamente conectados, as extinções secundárias em epífitas foram altas, o que indica baixa estabilidade do sistema à distúrbios. O forófito generalista *Aldina heterophylla* foi particularmente importante para manter a estrutura da redes. Essa espécie interage com 89% das espécies e com 75% dos indivíduos de epífitas. Nossos resultados indicam que a riqueza e abundância de epífitas vasculares em WSEs estão concentradas em algumas espécies de forófitos, especialmente em árvores de grande porte. Sendo assim, a remoção destas do sistema pode perturbar as interações, alterar a estrutura da rede e desequilibrar todo o ecossistema.

PALAVRAS-CHAVE: Campinaranas, conservação, árvore hospedeira, interações planta-planta, floresta tropical, epífitas vasculares.

ABSTRACT

The Amazon is the world’s largest tropical forest, has a great diversity of species, and provides essential ecosystem services. However, anthropic exploratory processes have intensified and are seriously influencing this biome. Approaches that are based on ecological network theory are an excellent tool for describing the structure of communities, interactions between species, and the stability of ecosystems. Using a specific set of network metrics; the first epiphyte-phorophyte commensal network for the fragile white-sand ecosystems of the central Amazon was created. The structure and organization of interactions were analyzed and described; we also tested the stability of the system to simulate species loss at the regional-level and local-levels. A total of 725 interactions between 52 phorophyte species and 118 vascular epiphytes were recorded in the white-sand ecosystem (WSE). At the regional-level, the epiphyte-phorophyte network exhibited a nested structure, with a low degree of specialization (H2’), connectance, modularity, and robustness. Similar pattern was observed at the local-level in the ecological network. When the elimination of highly connected phorophytes were simulated, secondary extinctions in epiphytes were high, which indicates low stability of the system when disturbances occur. The generalist phorophyte *Aldina heterophylla* was particularly important, interacting with 89% of the species and hosting 75% of the epiphytes. Our results indicate that the richness and abundance of vascular epiphytes in WSEs is concentrated in a few species of phorophytes, especially in large trees. As such, removing this species from the system can disrupt interactions, change the network’s structure, and unbalance the entire ecosystem.

KEYWORDS: Campinaranas, conservation, host tree, plant–plant interactions, tropical forest, vascular epiphytes.

1. INTRODUCTION

Anthropogenic actions have caused major environmental changes and are currently the main cause of species extinction (Smart et al., 2006; Morris, 2010; Caro et al., 2022). Tropical regions are recognized among the most threatened areas on the planet, mainly due to intensive exploratory processes resulting from human activities. The loss of biodiversity directly affects interspecific interactions by disrupting the links between associated species, which compromises the stability and functioning of ecosystem services (Tylianakis et al., 2007; Morris, 2010). Ecological communities are formed by different associations between species and result in complex networks of interactions (Jordano, 1987; Bascompte et al., 2003; Bascompte & Jordano, 2014). Identifying the factors that drive such interactions and the associated species is fundamental in order to understand how ecosystems function and determine actions for the conservation and recovery of biodiversity (Taylor et al., 2016; Hu et al., 2021; Francisco et al., 2018). Intense efforts are being made by researchers worldwide to understand the patterns of distribution and structure of ecological communities (e.g., Ricklefs & Schluter, 1994; Mendieta-Leiva et al., 2020). Approaches based on the theory of networks are gaining momentum as one of the most helpful tools for describing species interactions and for analyzing the structure of communities (Delmas et al., 2019; Guimarães, 2020).

The ecological network theories use a specific set of metrics (connectance, specialization, modularity, nestedness, and robustness) to represent species interactions and provide ecological inferences about the evolutionary dynamics of a system (Landi et al., 2018). Network approaches are used to understand the organization of different ecological systems, such as food webs (e.g., Keyes et al., 2021), mutualistic interactions (e.g., Mello et al., 2019), antagonistic interactions (e.g., Morris et al., 2014), and commensal interactions (e.g., Burns, 2007). Of the various properties of the ecological network, robustness is a metric that is used to assess the stability and tolerance of the natural system in regard to disturbances (Dunne et al., 2002; Memmott et al., 2004). This approach allows one to assess the fragility of the network and provides information on the structure and functioning of ecosystems that can be used to support plans for the management and conservation of biodiversity (Francisco et al., 2018; Zotarelli et al., 2019).

However, until now, this approach has been little used in studies of commensal networks, such as those existing between phorophytes and vascular epiphytes (Araújo, 2018; Francisco et al., 2018; Zotarelli et al., 2019; Couto et al., 2022). Vascular epiphytes are structurally dependent on another plant, the phorophyte. Vascular epiphytes represent about 10% of the world's vascular plant diversity (Zotz et al., 2021) and, in Neotropical forests, epiphytes can represent up to 50% of plant diversity (Kelly et al., 2004; Taylor et al., 2022). The ecological factors that drive and maintain epiphyte diversity and structure are poorly understood, yet this understanding is crucial for guiding biodiversity conservation plans.

Research describing the structure of vascular epiphyte-phorophyte networks has been conducted in different forest ecosystems around the world (Burn, 2007; Silva et al., 2010; Sáyago et al., 2013; Zhao et al., 2015; Ceballos et al., 2016; Taylor et al., 2016; Francisco et al., 2018, 2019; Naranjo et al., 2019; Zotarelli et al., 2019; Couto et al., 2022), and highlights two consistent arrangements: nested and low specialization patterns (Francisco et al., 2019; Couto et al., 2022). Low levels of specialization indicate that vascular epiphytes have low specificity in interactions with phorophyte species (Francisco et al., 2018, 2019; Couto et al., 2022), while the nested pattern indicates that phorophytes with few epiphyte interactions (specialists) are subsets of phorophytes with many interactions (generalists) (Burns, 2007; Francisco et al., 2018). Trees in initial growth stages do not have associated epiphytes, but accumulate species over time (Burns, 2007; Woods et al., 2015), indicating that distinct ecological processes, such as ecological succession, species abundance, and phorophyte characteristics, favor a nested structure in the epiphyte network (Burns, 2007; Ceballos et al., 2016; Taylor et al., 2016; Francisco et al., 2018; Zotarelli et al., 2019). Well-established patterns indicate positive relationships between epiphyte diversity and tree size (Couto et al., 2019; Zotarelli et al., 2019; Quaresma et al., 2020; Francisco et al., 2021), tree age (Zotz & Vollrath 2003; Johansson et al., 2007), and microhabitat heterogeneity (Sáyago et al., 2013; Woods et al., 2015). In other words, epiphytes are phorophyte-dependent and, because tree structural and microclimatic characteristics vary between species, some trees are expected to have attributes that make them better hosts than others (Sáyago et al., 2013).

The Amazon region is formed by a mosaic of ecosystems, among them the fragile white-sand ecosystems (WSEs), also known as ‘campinaranas’. The intensification of vegetation suppression processes that has been registered in recent years (Nobre et al., 2016) directly affects the WSEs due to its low primary productivity and low resilience to disturbance (Adeney et al., 2016). Several anthropic actions, including forest fires, sand extraction, deforestation for agricultural activities, and exploitation of wood resources (Ferreira et al., 2013; Adeney et al., 2016; Demarchi et al., 2019), are recorded for these environments, and occur mainly close to large urban centers (Capurucho et al., 2020). The intensive use of timber resources of terra firme forests has caused a drastic decline in the populations of some species of economic interest, which in turn has caused an increase in the exploitation of species of lower commercial value in adjacent environments, including in WSEs (Demarchi et al., 2019). Dominant species, such as *Aldina heterophylla* Spruce ex Benth (Fabaceae), are historically recognized as the preferred substrate for many vascular and non-vascular epiphyte communities (Spruce, 1901; Mari et al., 2016); however, this species and other potential phorophytes are among the main trees exploited in these WSEs (Demarchi et al., 2019). In this perspective, network metrics can be used as an excellent tool to analyze and describe the structural organization of epiphyte-phorophyte interactions in WSEs (Naranjo et al., 2019), as well as to identify key phorophyte species and predict the impact of their removal in epiphytic communities (Francisco et al., 2018; Zotarelli et al., 2019).

Here, we investigate in five areas WSEs of the central Amazonian, the general patterns of organization of vascular epiphyte communities, the structure and robustness of networks of epiphyte-phorophyte interactions and identify the most important phorophyte species for the networks in these environments. We tested three main hypotheses: 1) the size of the phorophytes (using the diameter as a proxy) is a good predictor of the observed interactions and positive correlations between the richness and abundance of vascular epiphytes and the diameter of the phorophytes. This is because the size of the phorophyte aggregates a set of characteristics, such as longer length of time in the environment, a larger area for colonization, and greater microclimate heterogeneity, which are closely related to the distribution of vascular epiphytes (Quaresma et al., 2020; Francisco et al., 2021); 2) we assume that the epiphyte-phorophyte network in the WSEs has a nested structure, low degree of specialization (H2'), low connectance and low modularity, which is a pattern observed for many networks of interactions involving vascular epiphytes (Francisco et al., 2019; Couto et al., 2022); 3) we predict that the network has a low degree of tolerance to the loss of key-phorophyte species and a few phorophytes maintain most of the interactions. In WSEs, previous studies have indicated that the species *Aldina heterophylla* maintains a large number of interactions with vascular epiphytes, suggesting that this phorophyte species provides a unique habitat for many epiphyte species in white-sand ecosystems (Mari et al., 2016; Klein et al., 2022). Most species of vascular epiphytes are connected to a few species of phorophytes (Francisco et al., 2018) and the removal of highly connected phorophytes from the system can change the structure of the networks and cause a series of secondary extinctions in vascular epiphytes, thus compromising the stability of the ecosystem (Francisco et al., 2018; Zottareli et al., 2018).

2. MATERIALS AND METHODS

2.1 White-sand ecosystems in the Amazon

White-sand ecosystems are irregularly distributed throughout the Amazon basin, covering approximately 5% of the domain (Adeney et al., 2016). In the upper Negro River, they cover large continuous areas; in other regions, they occur as small islands, surrounded by *terra* *firme* forests (Anderson, 1981). The vegetation of the WSE, when compared to the vegetation of areas of *terra firme*, has lower species diversity, higher number of endemic lineages, and a distinct structure ranging from open areas dominated by grasses and shrubs to stratified forests with emerging trees exceeding 20 m in height (Anderson, 1981; Fine & Kembel, 2011; García-Villacorta et al., 2016). The prevailing stressful abiotic conditions (oligotrophic soils, high temperatures, irregular water tables) result in lower basal area, and low biomass and primary productivity, which characterize these ecosystems as fragile (Adeney et al., 2016). In recent decades, the WSEs have been severely threatened by anthropogenic pressures, such as the advance of cities (Anderson, 1981), illegal sand extraction (Ferreira et al., 2013), exploratory logging (Demarchi et al., 2019), and fires (Adeney et al., 2016).

2.2 Study areas

This study was carried out in five forested areas of the WSEs located in conservation units (CUs) of the central Amazon (Figure 1; Table S1): **Asframa Reserve (AR),** located on the BR 174 highway, approximately 110 km from Manaus, Amazonas. The reserve is comprised of *terra firme* forests, riparian vegetation, and a WSE; **Alto Cuieiras Reserve (ACR)**, located in the mosaic of conservation units of the lower Negro River, approximately 80 km from Manaus, Amazonas. The reserve comprises *terra firme* forests, black-water floodplain forests, and a WSE; **Campina Biological Reserve (CBR),** located along the BR 174 highway, about 50 km from Manaus, Amazonas. The reserve is formed by *terra firme* forests and a WSE; **Rio Negro Sustainable Development Reserve (RNSDR)**, located in the mosaic of conservation units of the lower Negro River, approximately 150 km from Manaus, Amazonas. The reserve comprises extensive black-water floodplain forests, *terra firme* forests, and a WSE; **Uatumã Sustainable Development Reserve (USDR),** located approximately 200 km from Manaus, Amazonas. The reserve contains black-water floodplain forests, *terra firme* forests, and a WSE.

Considering the difficult access to the Amazonian regions in our study, our sites were selected based on: 1) the accessibility of the place; 2) similarities in environmental characteristics, mainly soil type and vegetation structure; 3) number of previous studies on the tree component (Ferreira, 1997; Targhetta et al., 2015; Farroñay et al., 2019; Demarchi et al., 2022). The study areas are, on average, 100 km away from each other, and cover a total area of approximately 4,500 km^2 (Figure 1). The annual average rainfall in the region is approximately 2,800 mm with a pronounced dry season (July to November); the average annual temperature is around 26.7 ºC (Fisch 1990). In the central Amazon, the vegetation of the WSEs has similar structural characteristics, such as a high density of trees (average of 630 individuals/ha), most of these with a diameter of ≥ 20 cm, and the dominance of certain species (Vicentini, 2004; Targhetta et al., 2015; Demarchi et al., 2018). Vascular epiphytes are abundant and diverse in all the studied WSEs (Braga, 1977; Mari et al., 2016; Klein & Piedade, 2019).

2.3 Data collection and floristic survey

We sampled the communities of vascular epiphytes present in a total area of 1.25 ha considering the five WSEs surveyed. In each area, we randomly marked four plots of 25 x 25 m (0.25 ha/area), totaling 20 plots of WSE sampled. All trees with a diameter at breast height (DBH) of greater than 10 cm were registered, botanically identified, and measured for total height and DBH. For each phorophyte, we recorded the presence and abundance of all individuals of holoepiphytes and hemiepiphytes (sensu Zotz et al., 2021). An individual was considered as any plant or cluster of plants geographically distinguishable from each other (Sanford 1968). For the observation of canopy species, binoculars (Bushnell H2O), a camera with close-up lenses, and climbing techniques were used (Perry, 1978). These methods allowed us to accurately identify and quantify all the epiphytes present in the crown of the phorophyte.

For species identification, consultation of the literature (Mez, 1891, 1892, 1894; Hoehne, 1949; Pabst & Dungs, 1975, 1977; Croat, 1988; Zuquim et al., 2007) and consultation with specialists were used. Collected specimens were deposited in the Herbarium of the National Institute for Amazonian Research in Manaus, AM. The nomenclature of the angiosperms follows the Angiosperm Phylogeny Group (APG IV, 2016) and, for lycophytes and monilophytes, we followed the classification of the Pteridophyte Phylogeny Group (PPG I, 2016).

2.4 Analyses of data

The sample sufficiency was verified through species rarefaction curves using EstimateS 9.1 (Colwell, 2013) and employed three non-parametric richness estimators (Bootstrap, Chao 1, and Jack1; 1,000 random resamplings). Spearman’s linear correlations were used to analyze the relationship between the richness and abundance of vascular epiphytes with the DBH of the phorophyte (a proxy for phorophyte size). All statistical analyses were performed using the R with the 'vegan' package (Oksanen et al., 2016; R Development Core Team, 2020).

Epiphyte-phorophyte interactions were analyzed at the general regional-level and at the local-level (Forman, 1995). To describe the epiphyte-phorophyte interaction, a matrix for each studied site (network at the local level) and a general matrix with data from the five study areas were built to verify the general patterns that structure the interaction networks in the WSEs (network at the regional level). In the weighted matrixes, cell values indicate the abundance of epiphytes on the phorophytes. In the binary matrixes, cell values represent the presence or absence of the interaction. Network-level metrics were used to describe the structure of these interactions at the network level and species level.

2.4.1 Network-level metrics

The following descriptors were used to characterize the structure of the networks: connectance, complementary specialization index, nestedness, modularity, and robustness. Connectance (*C*) represents the percentage of observed interactions divided by the possible number of interactions (Jordano, 1987). The complementary specialization index (H_2') was used to evaluate the network specialization and Patefield null model (1,000 randomizations) was used to test the significance of H_2' (Blüthgen et al., 2006).

For nestedness, the *NODF* was used, which is a metric based on the overlap and decreasing fill, and *WNODF*, a weighted nestedness metric based on the overlap and decreasing fill (Almeida-Neto et al., 2008). In a nested network, specialist species (with a low number of interactions) interact with a proper subset of the partners that interact with generalist species (species with many interactions) (Bascompte et al., 2003). The significance of the *NODF* index was estimated using a null model 2 (*CE*) proposed by Bascompte et al., (2003), and *WNODF* was measured using a null model proposed by Almeida-Neto and Ulrich (2011), with 1,000 randomizations. The modularity index indicates the degree of niche specialization in the community. The modularity (*Q*) was estimated using the *QuaBiMo* algorithm (Dormann & Strauss, 2014) and tested the significance of *Q* using null models with 1,000 randomizations (Patefield, 1981). Values of *Q* close to zero indicate the absence of a modular structure in the network. Conversely, high values may indicate that species are structured in groups (modules) of similar preference (Newman, 2006; Dormann & Strauss, 2014).

To assess the robustness and network tolerance to species extinctions (Memmott et al., 2004), the proportion of secondary extinctions of epiphytes was considered in relation to primary extinctions of species of phorophytes. Robustness was measured in two scenarios: (a) the random deletion of species was used, with all phorophytes species having the same probability of primary extinction. This algorithm randomly removes a phorophyte species and estimates the susceptibility of the interacting epiphytes to extinction with the extinct phorophyte; (b) the extinction of phorophyte species was simulated according to the degree of connection. The most connected (generalist) phorophyte to the least connected (specialists) phorophyte was sequentially removed. The simulated loss of species was obtained through the extinction curves using the function *second.extinct* (1,000 randomizations). All network analyses were conducted using R with the 'bipartite' package (Dormann et al., 2008; Development Core Team, 2020).

2.4.2 Species-level metrics

To assess the importance of the phorophyte species in the network, basic centrality metrics were used: degree of species (number of links that affect species); normalized degree (proportion of connections made by the species in relation to the total number of potential connections); species strength (a metric related to the degree of interactions that considers the sum of dependencies for each species and, interaction push/pull (which estimates the asymmetric direction of interactions, a metric based on dependence) (Bascompte et al., 2006; Vazquez et al., 2007). The analyses were performed using R with the function 'species level' from the 'bipartite' package (R Development Core Team, 2020).

3. RESULTS

In the five areas of the WSEs, 52 species, 486 individuals, and 29 families of phorophytes were sampled. The vascular epiphytes totaled 17,808 individuals, 118 species, and 18 families (Table S2), of these, 108 are holoepiphytes and 10 are hemiepiphytes. The sampling sufficiency was 91% via the Bootstrap estimator, 87% via the Chao 1 estimator, and 82% via the Jackknife 1 estimator, with the species accumulation curves tending to stabilize (Figure

S1). The DBH was positively correlated with the richness (r^2 = 0.53, $P < 0.0001$) and abundance of epiphytes (r^2 = 0.46, $P < 0.0001$). A small proportion of vascular epiphytes, 46 species (38%) and 661 individuals (3.7%) occur in phorophytes with small diameter classes (10 – 11 cm of DBH). In contrast, in large phorophytes (≥ 30 cm of DBH), a greater number of epiphytes was recorded; 99 species (84%) and 11,208 individuals (63%). A small proportion of vascular epiphytes was found in small phorophytes, while large phorophytes concentrate a greater number of species and epiphytic individuals (Figure 2).

3.1 Network structure

Regional-level structure – In the general network, 725 epiphytes-phorophytes interactions were recorded, which equates to only 11% of all possible interactions (Figure 3a; Table 1). The network presented a highly nested structure (*NODF* = 57.82; *WNOF* = 42.00; $P \leq 0.005$), low specialization (H_2'= 0.21), and low modularity (Q= 0.13; $P \leq 0.002$). The robustness of the network showed differences between the evaluated scenarios. First, when phorophytes were randomly eliminated, the high robustness of the system to the secondary extinction of epiphytes (R = 0.74) was observed. However, when the phorophytes with most interactions were removed, the network exhibited low robustness (R = 0.36). This is evident when the most generalist phorophyte (*Aldina heterophylla)* was removed, which showed a fast reduction in the slope of the curve, and reflected a secondary extinction of approximately 30% of epiphyte species (Figure 4).

Local-level structure – There was little variation in the structure of the epiphyte-phorophyte network between the WSE sites. All areas showed a nested structure, low connectance, low specialization, low modularity, and low robustness (Table 1), thus following the general pattern observed at the regional level. However, the networks of the CBR (R = 0.26) and the AR (R = 0.27) were more sensitive to system disturbance when compared to the other sites (Figure 4; Table 1). The removal of the generalist phorophyte *A. heterophylla* promoted a rapid reduction in the slope of the curve and resulted in the loss of more than 40% of epiphytic species in both areas. In contrast, the ACR showed greater robustness *(R*= 0.44); even so, the removal of *A. heterophylla* caused a secondary extinction of approximately 25% of the vascular epiphytes (Figure 4).

3.2 Organization of interactions

Regional-level interaction – The 725 links involved 118 vascular epiphyte species and 52 phorophyte species (Figure 3). The degree of interactions for the phorophyte species varied from one to 105, revealing highly asymmetric interactions (Table 2). *Pradosia schomburgkiana* was the most abundant tree species (122 individuals); however, only 56% of the individuals interacted with the epiphytes. The second most abundant tree species, *Aldina heterophylla* (109 individuals), was the phorophyte with the highest number of connections, and interacted with species of 105 epiphytes (Figure 3; Table 2), 26 of which had exclusive occurrence. Also important were *Licania canescens* and *Neea obovata Spruce* ex Heimerl, which interacted with 38 (32%) and 35 (29%) species of epiphytes, respectively, and maintained one exclusive interaction each. These last three species are responsible for 30% of all interactions in the WSEs and host about 83% of the epiphytes.

Local-level interaction – The network with the greatest number of interactions was ACR, with 376 links between 71 epiphyte species and 27 phorophyte species (Figure 3b; Table 1). Six phorophyte species are responsible for 51% of all epiphyte interactions: *A. heterophylla, Aspidosperma verruculosum, L. canescens, N. obovata, Peltogyne campestris* Huber ex Ducke and *Ternstroemia dentata* (Aubl.) Sw. (Table S3). The greatest abundance of epiphytes occurs in *A. heterophylla* (61%) and *L. canescens* (9%), which together hosted 70% of the epiphyte communities in the habitat. The most abundant epiphytes were *Prosthechea aemula* (846 individuals), *Specklinia picta* (Lindl.) Pridgeon & M.W. Chase (421 individuals) and *Maxillaria lutescens* (278 individuals).

The second-largest network was the AR, with 166 links between 66 epiphyte species and 15 phorophyte species (Figure 3c). The phorophytes most connected with the species of epiphytes are *A. heterophylla, P. schomburgkiana*, and *T. dentata*; together, they interact with 61% of species (Table S3) and host 89% of the epiphytes. *Codonanthopsis crassifolia* (435 individuals), *Tillandsia adpressiflora* Mez (333 individuals), and *M. lutescens* (278 individuals) are the most abundant epiphytes. The network in the RNSDR was composed of 166 interactions between 58 species of epiphytes and 16 species of phorophytes (Figure 3d). *A. heterophylla, Cybianthus fulvopulverulentus* (Mez) G.Agostini and *Manilkara bidentata* maintain 54% of observed interactions (Table S3) and host 84% of the epiphytes. *P. aemula*

(1515 individuals), *Epidendrum strobiliferum* Rchb.f. (368 individuals) and *M. lutescens* (360 individuals) were the most abundant species of epiphytes.

The network in the USDR shows 133 links between 42 epiphyte species and 16 phorophyte species (Figure 3e). The phorophytes *A. heterophylla, C. fulvopulverulentus, Emmotum orbiculatum* (Benth.) Miers and *M. bidentata* are responsible for 55% of the interactions (Table S3) and are host 78% of the epiphytes. The most representative epiphytes were *P. aemula* (336 individuals), *Elaphoglossum obovatum Mickel* Mickel (148 individuals), and *T. adpressiflora* (131 individuals). Finally, the smallest network was found in the CBR, with only 117 links registered. A small number of phorophyte species (9 spp.) interact with 56 epiphyte species (Figure 3d). *A. heterophylla* and *Ormosia trifoliolata* Huber maintain 60% of observed interactions (Table S3) and are host 90% of the epiphytes. *P. aemula* (1,422 individuals), *Brassavola martiana* Lindl. (461 individuals) and *Elaphoglossum glabellum* J.Sm. (379 individuals) are the most representative epiphytes in the area.

4. DISCUSSION

This study is the first to present regional and local-level ecological network approaches in order to describe the structure and complexity of epiphyte-phorophyte interactions in WSEs and, as far as we know, in an Amazonian forest. At the regional-level and local-level, the epiphyte-phorophyte networks followed a similar structural pattern since both were poorly connected, with low complementary specialization, low modularity, and low robustness, though with high nestedness, which is a pattern that is commonly found for epiphyte-phorophyte networks in other forest ecosystems (Burns, 2007; Sáyago et al., 2013; Zhao et al., 2015; Ceballos et al., 2016; Taylor et al., 2016; Araújo, 2018; Francisco et al., 2018, 2019; Araújo, 2018; Naranjo et al., 2019; Zotarelli et al., 2019; Saiz et al., 2021; Couto et al., 2022). Large phorophytes play an important role in the structure of the studied networks. *Aldina heterophylla* is an important generalist phorophyte that maintains the network structure and robustness in all habitats, and sustains unique interactions; its removal from the network via simulation models results in the secondary extinction of approximately 30% of vascular epiphytes.

Our results support the hypothesis that tree size influences patterns of richness and abundance of vascular epiphytes in the studied WSEs. Positive relationships between the DBH of phorophytes and epiphytes were evidenced in other Amazonian environments (Benavides et al., 2011; Quaresma et al., 2018, 2020). Epiphytes structurally depend on phorophytes for colonization; therefore, it is expected that tree characteristics influence their distribution patterns (Benzing, 1990; Zotz, 2016). As trees grow, structural and microclimatic complexity increases, new habitats are formed and a larger surface area becomes available for colonization and establishment of epiphytes (Woods et al., 2015; Sanger & Kirkpatrick 2016). Large trees, in addition to providing important ecosystem services in forests (Lindenmayer et al., 2014), also play a key role in the structure of epiphyte-phorophyte interactions in WSEs.

4.1 Network structure

Epiphyte-phorophyte networks at the regional and local level exhibited low connectance, low complementary specialization, and low modularity. These results are consistent with other studies of commensal networks (Sáyago et al., 2013; Ceballos et al., 2016; Francisco et al., 2018; Zotarelli et al., 2019). High connectance can promote the persistence and resilience of antagonistic networks (Dunne et al., 2002) and mutualistic networks (Thébault & Fontaine, 2010). However, low connectance has important implications for the conservation of epiphyte species, since many interactions are restricted to a few species, even though there are many potential species of phorophytes (Francisco et al., 2018; Zotarelli et al., 2019). Commensal interactions between epiphytes and phorophytes are generally less specialized than mutualistic and antagonistic interactions (Piazzon et al., 2011), thus reflecting the epiphytes' low degree of specialization in their use of phorophyte species (Silva et al., 2010; Sáyago et al., 2013). Although specificity is not expected in structurally dependent plants, the distribution of epiphytes is not random (Burns, 2007; Wagner et al., 2015). In WSEs, the distribution of species was highly asymmetric, and most phorophytes (77%) interacted with less than 20% of the vascular epiphyte. In contrast, *A. heterophylla* interacted with almost 100% of the species of epiphytes. Structural characteristics and microclimatic conditions vary with tree size and age (Taylor & Burns 2015), which suggests that some individuals have traits that make them better phorophytes than others (Sáyago et al., 2013). The epiphyte-phorophyte network also showed low modularity, indicating that epiphytes in WSEs are generalists in the use of resources (Genini et al., 2012). A similar pattern of low modularity was also evidenced in studies that evaluated the horizontal (Hu et al., 2021) and vertical distribution of epiphytes and their respective phorophytes (Francisco et al., 2019; Couto et al., 2022). On the other hand, horizontal distribution networks between lichens and phorophytes showed segregated distribution, suggesting that, for certain groups of epiphytes, habitat specialization is a determinant factor in structuring the network (Saiz et al., 2021).

In the studied WSEs, the epiphyte-phorophyte network has a nested structure (*NODF* = 57.82), which reflects a consistent distribution pattern for epiphyte communities (Burns, 2007; Piazzon et al., 2011). Structural characteristics of phorophytes and the sequential colonization of epiphytes can be decisive factors for the structure of the network (Burns, 2007; Ceballos et al., 2016). The size of phorophytes is related to the complexity of ecological characteristics, which change over time and contribute to the nested colonization of species (Silva et al., 2010; Zhao et al., 2015; Francisco et al., 2018; Zotarelli et al., 2019). Additionally, the epiphyte communities found on small phorophytes are subsets of the communities found on large phorophytes, which suggests that the colonization of species can occur sequentially, in which a set of generalists colonizing species provide favorable conditions for the late establishment of other species (Woods et al., 2015). Generalist species, such as *Brassavola martiana*, *Prosthechea aemula*, and *Maxillaria lutescens*, are abundant and widely distributed in all diametric classes of phorophytes; however, approximately 20% of the epiphyte species (22 spp.) only occurred on phorophytes with DBHs of greater than 30 cm. In large phorophytes, *P. aemula* and *M. lutescens* form huge clusters of individuals, with organic matter retained between the stem and root. Some species, such as *Apteria aphylla*, *Elaphoglossum raywaense, Maxillaria pendens,* and *Vittaria lineata*, were observed only in these clusters, which indicates that specific environmental conditions are provided for the establishment of certain species and these contribute to the nested distribution pattern (Wagner et al., 2015; Zhao et al., 2015).

The low robustness of the commensal epiphyte-phorophyte network in WSEs highlights the sensitivity of this interaction to environmental disturbances, and these results are evidenced for different environments of the Atlantic Forest (Francisco et al., 2018;

Zotarelli et al., 2019; Couto et al., 2022). This result is worrying for the conservation of epiphytes in these environments, since logging has been increasing (Demarchi et al., 2019). The removal of generalist phorophytes, such as *A. heterophylla,* in WSEs scan cause a series of secondary extinctions, and can reduce species richness by up to 30% and cause a loss of 75% of the abundance of epiphyte individuals in the regional-level network. In heterogeneous environments, such as tropical forests, phorophyte species contribute in different ways to maintain the stability and persistence of networks (Memmott et al., 2004). The removal of generalist phorophytes causes a greater imbalance in the structure of the network when compared to the loss of poorly connected specialist species (Dunne et al., 2002; Francisco et al., 2018; Couto et al., 2022). Although most of the epiphytic flora is not habitat-specialist (Klein et al., 2022), species such as *Aechmea setigera, Cattleya wallisii, Elaphoglossum discolor, Maxillaria lutescens, Prosthechea aemula,* and *Tillandsia adpressiflora* are very abundant in these environments and provide essential ecosystem services such as carbon fixation, nutrient cycling, and habitat for fauna (Ferreira et al., 2019; Klein et al., 2022). Removal of endemic phorophytes, such as *A. heterophylla, Aspidosperma verruculosum, Byrsonima laevis,* and *Pagamea coriacea*, can cause changes in the composition and structure of vegetation in WSEs, which causes disruption of important links between epiphytes and phorophytes, changes the organization of the interactions and promotes various disturbances in the system (Obermüller et al., 2012; Francisco et al., 2018).

4.2 Organization of interactions

Although similar patterns were recorded for all the WSEs studied, the number of interactions varied considerably among the species of phorophytes. *Pradosia schomburgkiana* was the most abundant tree species, but showed few interactions with the epiphytes (30 links). Abundant species are more likely to be colonized; however, they may have characteristics that limit germination and establishment of epiphytes (Zotarelli et al., 2019). In *P. schomburgkiana,* characteristics of the bark, such as the partial detachment of the rhytidome, can inhibit germination and the establishment of epiphytes; some authors (Callaway et al., 2002; Wagner et al., 2015) also discuss the effect of secondary compounds; however, specific studies are needed. In contrast, *A. heterophylla* is the most important phorophyte in epiphyte-phorophyte interactions in the WSEs. The species interacted with many species (105 spp.), hosted large numbers of epiphytes (13,378 individuals) and had several unique interactions (26 species). In one single individual of *A. heterophylla*, we recorded 29 species and 752 individuals of epiphytes. In the WSEs, *A. heterophylla* is one of the emerging and dominant tree species with large individuals (Targhetta et al., 2015; Vicentini, 2004), which harbor a greater quantity and richness of vascular epiphytes than any other tree species in these environments (Braga, 1978; Mari et al., 2016). Certain structural characteristics of this species, such as a large basal and canopy area, horizontal arrangement of branches and a great heterogeneity of microhabitats, are ecological factors that positively influence colonization by epiphytic communities (Woods et al., 2015; Wagner & Zotz 2020). As already suggested in study with *A. heterophylla* in WSEs of the central Amazon (Mari et al., 2016), this species is shown to be a preferred phorophyte, a hypothesis that was corroborated by our analyses regarding network centrality. Other phorophytes, such as *Licania canescens, Manilkara bidentata,* and *Neaa obovata* also host a considerable portion of epiphyte biodiversity (62 species and 1,374 individuals); however, these phorophytes maintain only two exclusive interactions, with *Batemannia colleyi* and *Encyclia conchaechila*.

The overexploitation of species causes loss of biodiversity, local extinctions, and changes in the structure of communities and ecosystems (Morris, 2010; Caro et al., 2022). The intensive use of species of trees with a high timber value is causing a decline in populations in *terra firme* forests, and has generated a demand for species with a lower timber value in other Amazonian environments, including WSEs (Daly et al., 2016). In the WSEs of the central Amazon, few species reach large diameters; however, among the species sought for selective exploitation are *A. heterophylla* and *Manilkara bidentata* (Demarchi et al., 2019), which are species with a high degree of connections with vascular epiphytes. Historically, WSEs have not been considered a high priority for preservation and are poorly protected in CUs (Adeney et al., 2016). Their conservation value should not be underestimated, as many species and lineages are endemic and adapted to the limited conditions of the WSEs (Capurucho et al., 2020). Environmental characteristics and evolutionary and ecological processes make these ecosystems unique in the Amazonian context.

5. CONCLUSIONS

It is possible to conclude that in relation to the five studied WSEs in the central Amazon: a) the richness and abundance of vascular epiphytes are expressive; b) The epiphyte-phorophyte network has a nested structure and low specificity in the use of resources; c) The robustness of the epiphyte-phorophyte network is low and the removal of generalist phorophytes can change the structure of the network; d) The preservation of large phorophytes, especially *A. heterophylla*, is essential in order to maintain the richness and robustness of the networks at the regional level and local level. Finally, conservation policies and biodiversity management plans must consider the maintenance of tree communities and all diversity associated with the WSEs.

TABLES

Table 1. General values of interactions and values of network metrics between vascular epiphytes and phorophytes at regional level and local level in the five white-sand ecosystems (WSE) of the central Amazon. AR – Asframa Reserve, ACR – Alto Cuieiras Reserve, CBR – Campina Biological Reserve, RNSDR – Rio Negro Sustainable Development Reserve, USDR – Uatumã Sustainable Development Reserve.

	Regional Level	Local Level				
General Values		AR	ACR	CBR	RNSDR	USDR
Tree species	52	15	27	9	16	16
Tree individual	486	122	146	94	100	145
Epiphyte species	118	66	71	56	58	42
Epiphyte abundance	17,808	3,314	5,615	3,891	3,814	1,174
Number of links (degree)	725	178	376	117	166	133
Network Metrics						
Connectance	0.11	0.17	0.19	0.23	0.17	0.19
H'2	0.21 ($P \leq 0.01$)	0.30	0.21	0.18	0.27	0.33
NODF	57.82 ($P \leq 0.05$)	64.50	54.38	62.68	54.24	54.02
WNODF	42.00	41.39	37.47	45.69	40.62	34.21
Robustness (degree)	0.36 ($P \leq 0.01$)	0.25	0.44	0.26	0.31	0.33
Modularity (*Q*)	0.13 ($P \leq 0.02$)	0.14	0.18	0.08	0.15	0.27

Table 2. Basic network centrality values at regional level in the five white-sand ecosystems of the central Amazon. Species of phorophytes organized by the degree of interactions with vascular epiphytes. For the description of the metrics, see the Methods section.

Botanical family	Phorophyte species	Species code	Degree	Normalized Degree	Species Strength	Interaction Push/Pull
Fabaceae	*Aldina heterophylla* Spruce ex Benth.	Alhet	105	0.88	759.84	0.71
Chrysobalanaceae	*Licania canescens* Benoist	Lican	38	0.32	55.50	0.11
Sapotaceae	*Manilkara bidentata* (A.DC.) A.Chev.	Mabid	36	0.30	33.35	0.06
Pentaphylacaceae	*Ternstroemia dentata* (Aubl.) Sw.	Teden	36	33.89	0.06	0.30
Nyctaginaceae	*Neea obovata* Spruce ex Heimerl	Neobo	35	0.29	29.01	0.05
Primulaceae	*Cybianthus fulvopulverulentus* (Mez) G.Agostini	Cyful	33	0.27	29.46	0.05
Sapotaceae	*Pradosia schomburgkiana* (A.DC.) Cronquist	Prsch	30	23.36	0.04	0.25
Fabaceae	*Peltogyne campestres* Huber ex Ducke	Pecam	29	22.35	0.04	0.24
Metteniusaceae	*Emmotum orbiculatum* (Benth.) Miers	Emorb	28	0.23	28.34	0.06
Apocynaceae	*Aspidosperma verruculosum* Müll.Arg.	Asver	27	0.22	15.93	0.02
Fabaceae	*Swartzia recurva* Poepp.	Swrec	25	18.96	0.03	0.23
Malpighiaceae	*Byrsonima laevis* Nied.	Bylae	20	0.20	17.21	0.03
Simaroubaceae	*Simaba guianensis* Aubl.	Sigui	20	0.79	-0.01	0.16
Rubiaceae	*Pagamea coriacea* Spruce ex Benth.	Pacor	17	10.75	0.004	0.14
Fabaceae	*Ormosia trifoliolata* Huber	Ortri	16	0.13	0.52	-0.02
Fabaceae	*Parkia igneiflora* Ducke	Paign	16	0.86	-0.08	0.13
Myrtaceae	*Myrcia citrifolia* (Aubl.) D. Legrand	Mycit	14	0.11	0.02	-0.05
Fabaceae	*Macrolobium arenarium* Ducke	Maare	13	0.11	0.91	-0.006
Malvaceae	*Pachira minor* (Sims) Hemsl.	Pamin	13	0.21	-0.06	0.11
Fabaceae	*Peltogyne catingae* Ducke	Pecat	12	11.85	0.01	0.10
Sapotaceae	*Elaeoluma schomburgkiana* (Miq.) Baill.	Elsch	11	0.09	0.17	-0.07

Chrysobalanaceae	*Licania hypoleuca* Benth.	Lihyp	11	0.09	0.18	-0.07
Combretaceae	*Terminalia macrophylla* (Spruce ex Eichler) Gere & Boatwr.	Temac	11	0.33	-0.06	0.09
Moraceae	*Ficus mathewsii* (Miq.) Miq.	Fimat	10	0.08	0.16	-0.08
Fabaceae	*Ormosia* sp. Jacks.	Ormsp	10	0.05	0.14	-0.14
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand	Prhep	10	0.11	-0.08	0.08
Clusiaceae	*Clusia nemorosa* G.Mey.	Clnem	9	0.07	0.25	-0.08
Chrysobalanaceae	*Leptobalanus latus* (J.F.Macbr.) Sothers & Prance	Lelat	9	0.07	0.41	-0.06
Ochnaceae	*Ouratea spruceana* Engl.	Ouspr	9	0.82	0.07	0.07
Chrysobalanaceae	*Leptobalanus longistylus* (Hook.f.) Sothers & Prance	Lelon	8	0.06	0.66	-0.04
Myrtaceae	*Myrcia umbraticola* (Kunth) E.Lucas & C.E.Wilson	Myumb	7	0.05	0.35	-0.09
Schoepfiaceae	*Schoepfia clarkii* Steyerm.	Sccla	7	0.06	-0.13	0.05
Melastomataceae	*Macairea theresiae* Cogn.	Mathe	6	0.05	0.11	-0.14
Lamiaceae	*Vitex duckei* Huber	Viduc	6	0.49	-0.09	0.05
Chrysobalanaceae	*Couepi*a Aubl.	Cousp	4	0.03	11.13	0.02
Fabaceae	*Macrolobium bifolium* (Aubl.) Pers.	Mabif	4	0.03	0.09	-0.22
Myristicaceae	*Iryanthera laevis* Markgr.	Irlae	3	0.02	0.05	-0.31
Chrysobalanaceae	*Licania apetala* (E.Mey.) Fritsch	Liape	3	0.02	0.07	-0.30
Myrtaceae	*Myrcia multiflora* (Lam.) DC.	Mymul	3	0.02	0.05	-0.31
Euphorbiaceae	*Alchornea discolor* Poepp.	Aldis	2	0.01	0.13	-0.43
Fabaceae	*Dimorphandra mollis* Benth.	Dimol	2	0.01	0.06	-0.46
Fabaceae	*Dimorphandra vernicosa* Spreng. ex Benth.	Diver	2	0.01	0.01	-0.49
Myrtaceae	*Myrcia clusiifolia* (Kunth) DC.	Myclu	2	0.01	0.005	-0.49
Peraceae	*Pera schomburgkiana* (Benth.) Müll.Arg.	Pescho	2	0.002	-0.49	0.01
Fabaceae	*Swartzia tessmannii* Harms	Swtes	2	0.059	-0.47	0.01
Bignoniaceae	*Tabebuia barbata* (E.Mey.) Sandwith	Tabar	2	0.16	-0.49	0.01
Annonaceae	*Xylopia spruceana* Benth. ex Spruce	Xyspr	2	0.02	-0.48	0.01

Clusiaceae	*Clusia* L.	Clusp1	1	0.008	0.001	-0.99
Rubiaceae	*Ferdinandusa chlorantha*	Fechl	1	0.008	0.01	-0.98
Humiriaceae	*Humiria balsamifera* (Aubl.) A.St.-Hil.	Hubal	1	0.008	0.001	-0.99
Peraceae	*Pera bicolor* (Klotzsch) Müll.Arg.	Pebic	1	0.007	-0.99	0.008
Humiriaceae	*Sacoglottis guianensis* Benth.	Sagui	1	0.001	-0.99	0.008

FIGURES

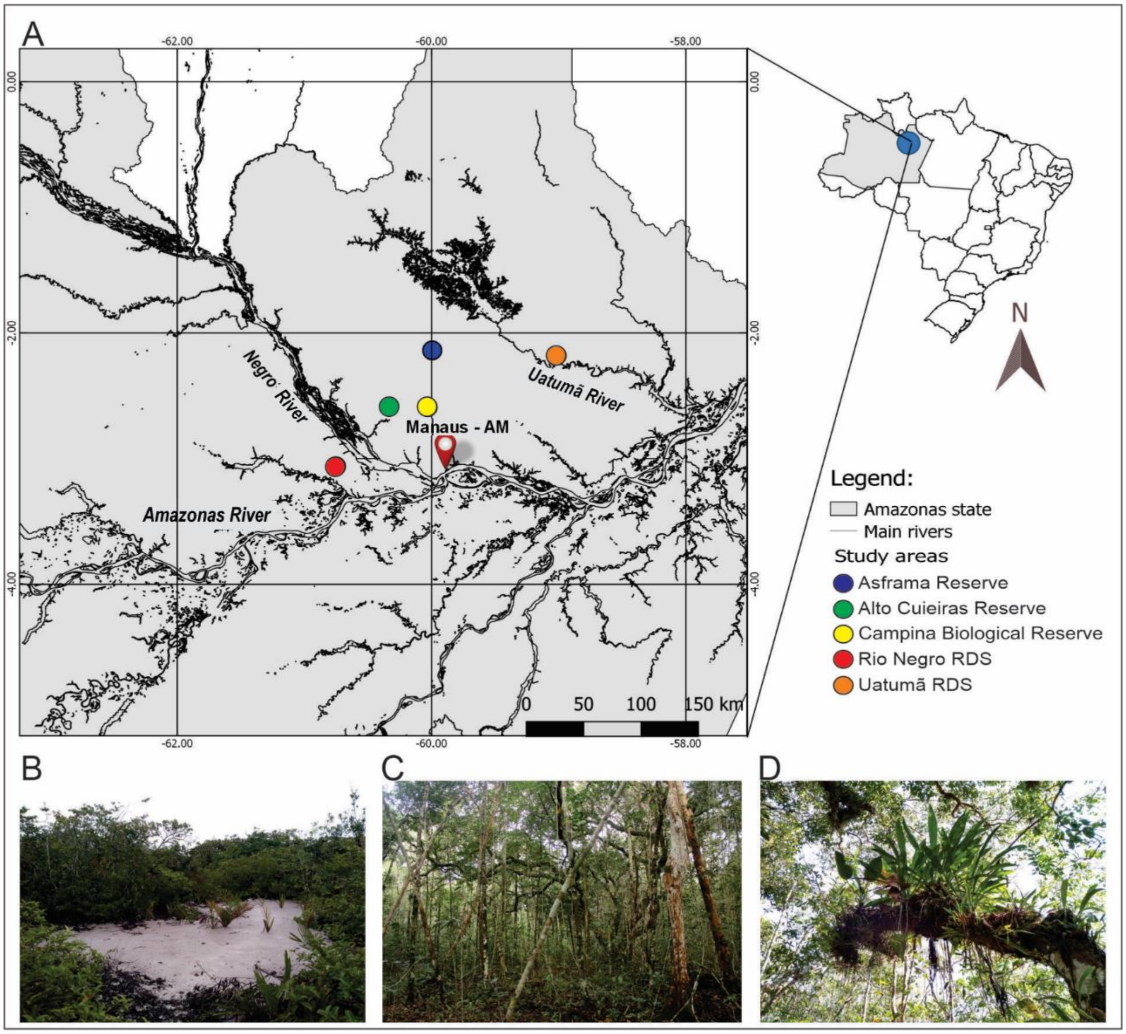

Figure 1. (a) Localization of the study sites in the five white-sand ecosystems of the central Amazon, Brazil. (b-c) The general aspect of the arboreal vegetation and (d) details of the vascular epiphyte flora present in the studied areas.

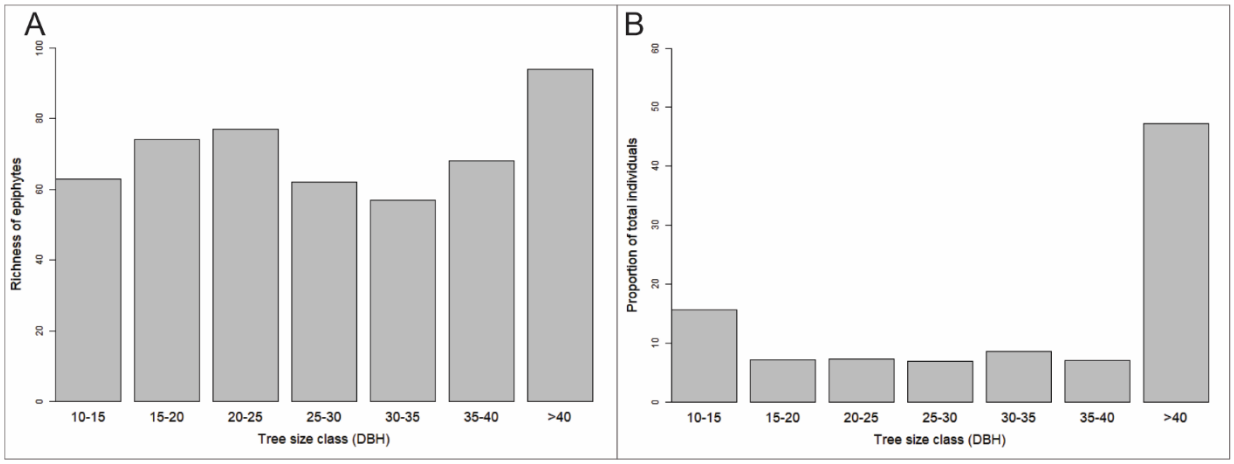

Figure 2: Richness of species (A) and proportion individuals (B) of vascular epiphytes by phorophyte class size (DBH) in the five white-sand ecosystems of the central Amazon.

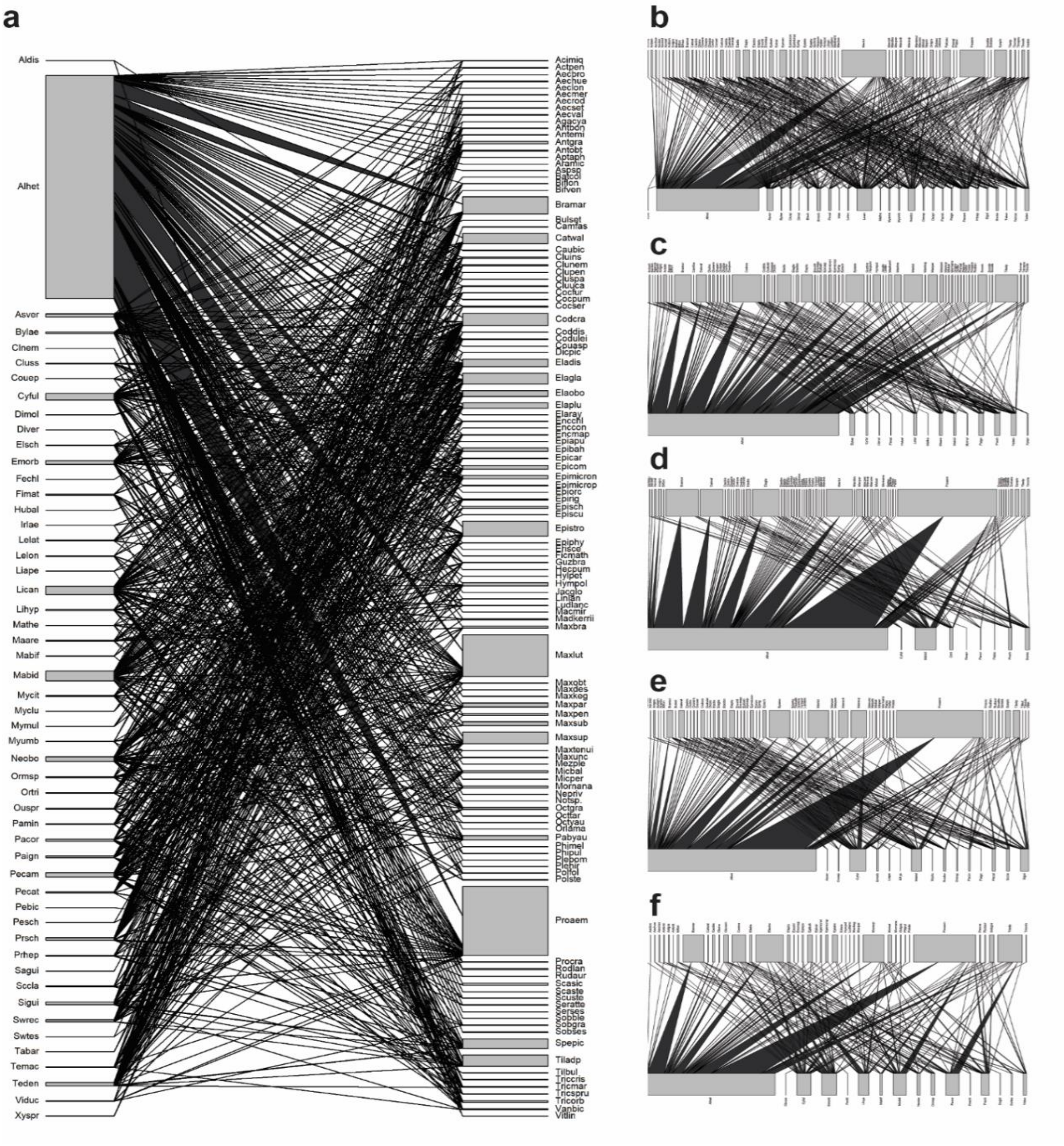

Figure 3. Network representation of the interactions between species of phorophytes (left bars) and species of vascular epiphytes (right bars) in the five white-sand ecosystems (WSEs) of the Central Amazon. The thickness of the line indicates the number of interactions between the pairs (a thicker line shows greater interaction strength). The abbreviations used for each species are given in Table S2 (vascular epiphytes) and Table S3 (phorophytes). Figures: a= Regional level network for the WSEs; local level: b= Network in the Alto Cuieiras Reserve

(ACR); c= Network in the Asframa Reserve (AR); d= Network in the Campina Biological Reserve (CBR); e= Network in the Rio Negro Sustainable Development Reserve (RNSDR); f= Network in the Uatumã Sustainable Development Reserve (USDR).

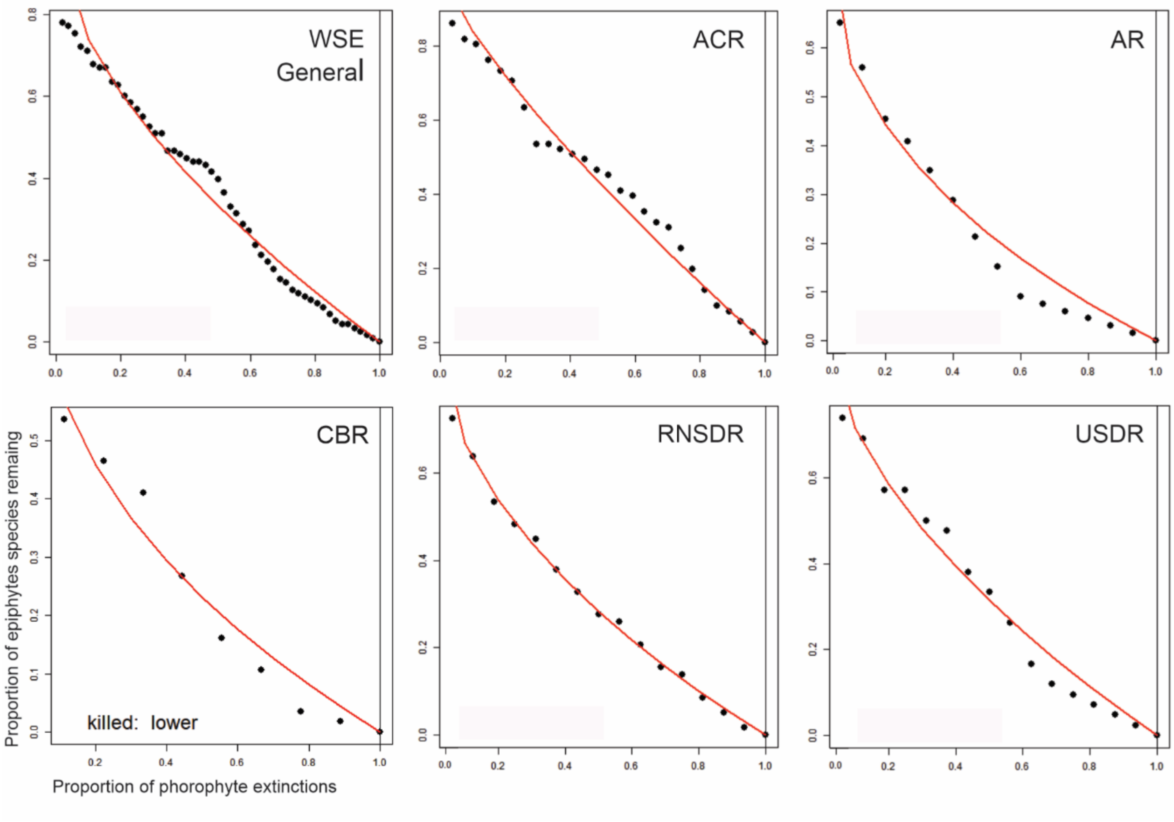

Figure 4. Simulation of secondary extinction in the removal scenario by degree of interaction. Curves generated from the sequential removal of more connected to less connected phorophyte species (extinction by degree) in the five white-sand ecosystems of the central Amazon. Plot WSE general = Regional-level extinction curve for the WSEs; Local level: ACR= Extinction curve in the Alto Cuieiras Reserve; AR= Extinction curve in the Asframa Reserve; CBR= Extinction curve in the Campina Biological Reserve; RNSDR= Extinction curve in the Rio Negro Sustainable Development Reserve); USDR= Extinction curve in the Uatumã Sustainable Development Reserve.

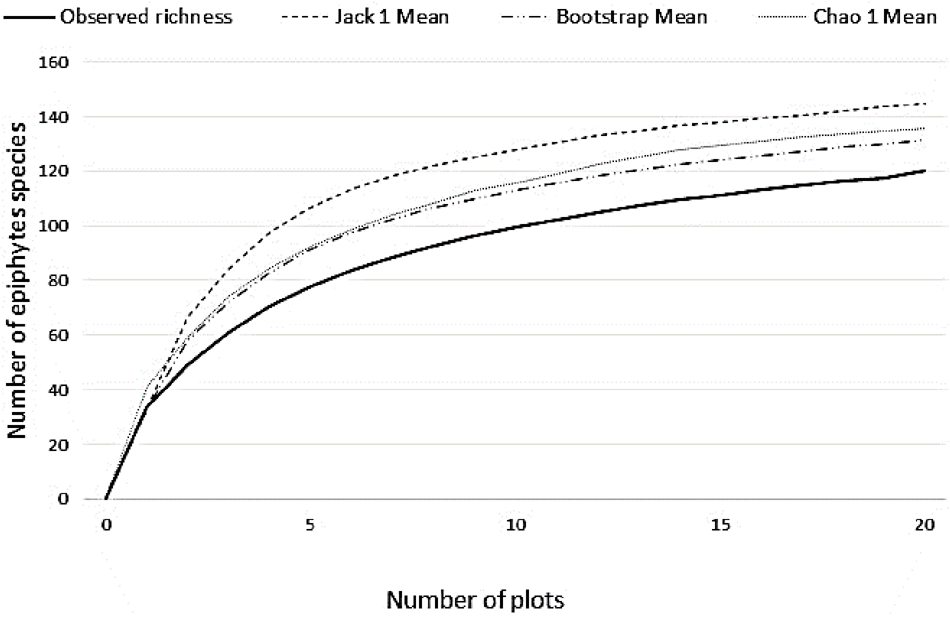

Figure S1: Rarefaction curves and richness estimates for sampling of vascular epiphytes in the five white-sand ecosystems in the central Amazon. Solid black line indicates the number of species observed and dotted lines indicate the number of species estimated using the three richness estimators: Chao 1, Bootstrap and Jackknife

AUTHOR CONTRIBUTIONS

All authors participated in the elaboration and writing of the manuscript. V.P.K, A.C.Q, and M.T.F.P designed the survey. V.P.K and A.C.Q carried out the field collections. V.P.K and T.M.F organized and performed the statistical analyses. All authors reviewed the manuscript before submission.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

Our study is part of a larger project called PELD (Long-Term Ecological Research Program) financed by government agencies, all collections are deposited in the herbarium of the

Instituto Nacional de Pesquisas da Amazônia and the occurrence data of the species has been deposited on the SiBBr (Sistema de Informação sobre a Biodiversidade Brasileira) platform, which is interactive with GBIF (Global Biodiversity Information Facility). To view the data deposited by the PELD MAUA project, access: https://specieslist.sibbr.gov.br/public/speciesLists

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SUPPLEMENTARY INFORMATION

Table S1. General information regarding the five areas of white-sand ecosystem in the central Amazon.

Sites	Geographical coordinates	Distance from Manaus, AM	Types of vegetation	Average altitude (a.s.l.)	Average canopy height
Asframa reserve (AR)	2°08’22”S 59°59’44”W	110 km	Riparian vegetation; *Terra firme* forest; WSE	68 m	13 m
Alto Cuieiras Reserve (ACR)	2°35’06”S 60°20’04”W	80 km	Black-water floodplain forest; *Terra firme* forest; WSE	52 m	12 m
Campina Biological Reserve (CBR)	2°35’27”S 60°01’55”W	50 km	*Terra firme* forest; WSE	75 m	10 m
Rio Negro Sustainable Development Reserve (RNSDR)	3°03’43”S 60°45’07”W	150 km	Black-water floodplain forest; *Terra firme* forest; WSE	61m	9 m
Uatumã Sustainable Development Reserve (USDR)	2°11’23”S 59°01’06”W	200 km	Black-water floodplain forest; *Terra firme* forest; WSE	58 m	10 m

Table S2. Vascular epiphytes species present in the studied white-sand ecosystems of the central Amazon. Gray shading represents the sites of occurrence of the species, and the values represent the degree of interaction of the species in each studied area. (AR) Asframa Reserve, (ACR) Alto Cuieiras Reserve, (CBR) Campina Biological Reserve, (RNSDR) Rio Negro Sustainable Development Reserve; (USDR) Uatumã Sustainable Development Reserve.

Group	Botanical Family	Vascular Epiphytes Species	Code	AR	ACR	CBR	RNSDR	USDR
FERNS	Aspleniaceae	*Asplenium* sp.	Aspsp	1				
	Dryopteridaceae	*Elaphoglossum discolor* (Kuhn) C.Chr.	Eladis	12	16	4	6	5
		Elaphoglossum glabellum J.Sm.	Elagla	1	17	6	7	
		Elaphoglossum obovatum Mickel	Elaobo	1	9	3	5	10
		Elaphoglossum plumosum (Fée) T.Moore	Elaplu	5	7	2	8	5
		Elaphoglossum raywaense (Jenman) Alston	Elaray			1		
	Hymenophyllaceae	*Hymenophyllum polyanthos* (Sw.) Sw.	Hympol	3	5	3	1	1
		Trichomanes crispum L.	Triccris			1		1
		Trichomanes martiusii C.Presl	Tricmar	2	7			
		Trichomanes spruceanum Hook.	Tricspru	4	3			
	Lindsaeaceae	*Lindsaea lancea* (L.) Bedd.	Linlan	2	1			
	Nephrolepidaceae	*Nephrolepis rivularis* (Vahl) Mett. ex Krug	Nepriv		1			
	Polypodiaceae	*Cochlidium furcatum* (Hook. & Grev.) C.Chr.	Cocfur	2	1	2		
		Cochlidium pumilum C.Chr.	Cocpum	1				
		Cochlidium serrulatum (Sw.) L.E.Bishop	Cocser		4		3	
		Microgramma baldwinii Brade	Micbal	3	6	3	2	4
		Microgramma percussa (Cav.) de la Sota	Micper				1	
		Moranopteris nana (Fée) R.Y. Hirai & J. Prado	Mornana	2		3	2	2
		Pleopeltis bombycina (Maxon) A.R.Sm	Plebom	2				
		Pleopeltis hirsutissima (Raddi) de la Sota	Plehir			1	1	

		Serpocaulon attenuatum (Humb. & Bonpl. ex Willd.) A.R. Sm.	Seratte		2	1	2	
		Serpocaulon sessilifolium (Desv.) A.R.Sm.	Serses				1	
	Pteridaceae	*Hecistopteris pumila* (Spreng.) J.Sm.	Hecpum	1	1			
		Vittaria lineata (L.) Sm.	Vitlin				2	
	Schizaeaceae	*Actinostachys pennula* (Sw.) Hook.	Actpen	1	2	1		1
ANGIOSPERMS	Araceae	*Anthurium bonplandii* Bunting	Antbon		8			
		Anthurium eminens Schott	Antemi	3				3
		Anthurium gracile (Rudge) Lindl.	Antgra	4	7	2	4	2
		Anthurium obtusum (Engl.) Grayum	Antobt	9				1
		Philodendron melinonii Brongn. ex Regel	Phimel	1	2			
		Philodendron pulchrum G.M.Barroso	Phipul		1	1		1
	Bromeliaceae	*Aechmea bromeliifolia* (Rudge) Baker	Aecbro	1				1
		Aechmea huebneri Harms	Aechue		2		1	2
		Aechmea longifolia (Rudge) L.B.Sm. & M.A.Spencer	Aeclon		1			
		Aechmea mertensii (G.Mey.) Schult. & Schult.f.	Aecmer			2	1	1
		Aechmea rodriguesiana (L.B.Sm.) L.B.Sm.	Aecrod		4			
		Aechmea setigera Mart. ex Schult. & Schult.f.	Aecset		2	2		
		Aechmea vallerandii (Carrière) Erhardt, Götz & Seybold	Aecval			2		
		Araeococcus micranthus Brongn.	Aramic				1	
		Guzmania brasiliensis Ulle	Guzbra	4	6		1	
		Mezobromelia pleiosticha (Griseb.) Utley & H.Luther	Mezple				1	
		Tillandsia adpressiflora Mez	Tiladp	5	7	3	8	8
		Tillandsia bulbosa Hook.f.	Tilbul				1	
	Burmanniaceae	*Apteria aphylla* (Nutt.) Barnhart ex Small	Aptaph				1	

Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	Epiphy		4	1	1	
Clusiaceae	*Clusia insignis* Mart.	Cluins	4	2	4	4	1
	Clusia nemorosa G.Mey.	Clunem	2	1	1	3	8
	Clusia penduliflora Engl.	Clupen	2				
	Clusia spathulaefolia Engl.	Cluspa	1	3			
	Clusia ucamira J.E. Nascim. & Bittrich	Cluuca	3	3			
Cyclanthaceae	*Ludovia lancifolia* Brongn.	Ludlanc		4	1	1	1
Gesneriaceae	*Codonanthopsis crassifolia* H. Focke) Chautems & Mat. Perret	Codcra	12	15	4	8	10
	Codonanthopsis dissimulata (H.E.Moore) Wiehler	Coddis	2	1	2		
	Codonanthopsis ulei Mansf.	Codulei	7	2	2	1	
Moraceae	*Ficus mathewsii* (Miq.) Miq.	Ficmath				1	
Orchidaceae	*Acianthera miqueliana* (H.Focke) Pridgeon & M.W.Chase	Acimiq	4	1			
	Aganisia cyanea (Schltr.) Rchb.f.	Agacya	2				
	Batemannia colleyi Lindl.	Batcol		1			
	Bifrenaria longicornis Lindl.	Biflon	2	2	1	1	5
	Bifrenaria venezuelana C.Schweinf.	Bifven		1			
	Brassavola martiana Lindl.	Bramar	8	11	5	8	6
	Bulbophyllum setigerum Lindl.	Bulset				1	
	Campylocentrum fasciola (Lindl.) Cogn.	Camfas	1				
	Cattleya wallisii (Linden) Linden ex Rchb.f.	Catwal	5	9	6	7	1
	Caularthron bicornutum (Hook.) Raf.	Caubic		1	1	1	1
	Dichaea picta Rchb.f.	Dicpic	2			1	
	Encyclia chloroleuca (Hook.) Neumann	Encchl	2	6	1	2	
	Encyclia conchaechila (Barb.Rodr.) Porto & Brade	Enccon					1
	Encyclia mapuerae (Huber) Brade & Pabst	Encmap	1	1	3	4	1
	Epidendrum apuahuense Mansf.	Epiapu					2

	Epidendrum bahiense Rchb.f.	Epibah	3	10	1	4	5
	Epidendrum carpophorum Barb.Rodr.	Epicar	6	1		1	1
	Epidendrum compressum Griseb.	Epicom		11	1		
	Epidendrum micronocturnum Carnevali & G.A.Romero	Epimicron	4	11	2	7	2
	Epidendrum microphyllum Lindl.	Epimicrop	1	1			2
	Epidendrum orchidiflorum (Salzm.) Lindl.	Epiorc				1	
	Epidendrum rigidum Jacq.	Epirig	1	10	1	1	
	Epidendrum schlechterianum Ames	Episch	2		1	4	
	Epidendrum sculptum Rchb.f.	Episcu			2		
	Epidendrum strobiliferum Rchb.f.	Epistro	4	11	3	6	3
	Eriopsis sceptrum Rchb.f. & Warsz.	Erisce					1
	Hylaeorchis petiolaris (Schltr.) Carnevali & G.A.Romero	Hylpet		2			
	Jacquiniella globosa (Jacq.) Schltr.	Jacglo	1				
	Macroclinium mirabile (C.Schweinf.) Dodson	Macmir			1		
	Madisonia kerrii (Braga) Luer	Madkerri	3	1			
	Maxillaria brasiliensis Brieger & Illg	Maxbra	3	2	2		
	Maxillaria desvauxiana Rchb.f.	Maxdes		2	1		
	Maxillaria obtusa (Lindl.) Molinari	Maxobt		5			
	Maxillaria kegelii Rchb.f.	Maxkeg	1				1
	Maxillaria lutescens Scheidw.	Maxlut	1	24	1	5	
	Maxillaria parviflora (Poepp. & Endl.) Garay	Maxpar	2		5	3	2
	Maxillaria pendens Pabst	Maxpen	1	3	2	1	
	Maxillaria subrepens (Rolfe) Schuit. & M.W.Chase	Maxsub		4		1	
	Maxillaria superflua Rchb.f.	Maxsup	1	7	3	2	7
	Maxillaria tenui Lindl.	Maxten		3			

	Maxillaria uncata Lindl.	Maxunc		4	1	1	
	Notylia aromatica Barker ex Lindl.	Notsp.			1		
	Octomeria grandiflora Lindl.	Octgra	1	8			3
	Octomeria taracuana Schltr.	Octtar	1				
	Octomeria yauaperyensis Barb.Rodr.	Octyau		2			
	Orleanesia amazonica Barb.Rodr.	Orlama		1	1		
	Pabstiella yauaperyensis (Barb.Rodr.) F.Barros	Pabyau		11			
	Polystachya concreta (Jacq.) Garay & Sweet	Polfol	1			5	
	Polystachya stenophylla Schltr.	Polste	2			2	1
	Prosthechea aemula (Lindl.) W.E.Higgins	Proaem	1	18	6	10	8
	Prosthechea crassilabia (Poepp. & Endl.) Carnevali & I.Ramírez	Procra			1	1	4
	Rodriguezia lanceolata Ruiz & Pav.	Rodlan	1		1	2	
	Rudolfiella aurantiaca (Lindl.) Hoehne	Rudaur				1	3
	Scaphyglottis sickii Pabst	Scasic	2				
	Scaphyglottis stellata Lodd. ex Lindl.	Scaste	1				
	Scuticaria steelei (Hook.) Lindl.	Scuste	2		2		
	Sobralia bletiae Rchb.f.	Sobble			1		
	Sobralia granitica G.A.Romero & Carnevali	Sobgra					5
	Sobralia sessilis Lindl.	Sobses		1	1		
	Specklinia picta (Lindl.) Pridgeon & M.W.Chase	Spepic		14	1	3	
	Trichosalpinx orbicularis (Lindl.) Luer	Tricorb	1	7		1	
	Vanilla bicolor Lindl.	Vanbic		11			
Urticaceae	*Coussapoa asperifolia* Trécul	Couasp	1	1			

Table S3**.** Network degree values per studied area in the five white-sand ecosystems of the central Amazon. In gray, the degree of interactions between vascular epiphytes and phorophyte species. AR) Asframa Reserve, (ACR) Alto Cuieiras Reserve, (CBR) Campina Biological Reserve, (RNSDR) Rio Negro Sustainable Development Reserve; (USDR) Uatumã Sustainable Development Reserve.

Botanical Family	Phorophyte Species	Code	AR	ACR	CBR	RNSDR	USDR
Annonaceae	*Xylopia spruceana* Benth. ex Spruce	Xyspr	2				
Apocynaceae	*Aspidosperma verruculosum* Müll.Arg.	Asver		27		3	
Bignoniaceae	*Tabebuia barbata* (E.Mey.) Sandwith	Tabar		2			
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand	Prhep		10			
Chrysobalanaceae	*Couep*ia Aubl.	Couepia				4	
	Leptobalanus latus (J.F.Macbr.) Sothers & Prance	Lelat	9				
	Leptobalanus longistylus (Hook.f.) Sothers & Prance	Lelon		8			
	Licania apetala (E.Mey.) Fritsch	Liape				3	
	Licania canescens Benoist	Lican		38			
	Licania hypoleuca Benth.	Lihyp				1	10
Clusiaceae	*Clusia* L.	Clusp1		9			
	Clusia nemorosa G.Mey.	Clnem					1
Combretaceae	*Terminalia macrophylla* (Spruce ex Eichler) Gere & Boatwr.	Temac		11			
Euphorbiaceae	*Alchornea discolor* Poepp.	Aldis		2			
Fabaceae	*Aldina heterophylla* Spruce ex Benth.	Alhet	61	49	54	45	32
	Dimorphandra mollis Benth.	Dimol	2				
	Dimorphandra vernicosa Spreng. ex Benth.	Diver		2			
	Macrolobium arenarium Ducke	Maare	13				
	Macrolobium bifolium (Aubl.) Pers.	Mabif					4
	Ormosia sp. Jacks.	Ormsp		7		3	3
	Ormosia trifoliolata Huber	Ortri			16		
	Parkia igneiflora Ducke	Paign	7	10		2	

	Peltogyne campestres Huber ex Ducke	Pecam		29			
	Peltogyne catingae Ducke	Pecat				12	
	Swartzia recurva Poepp.	Swrec		17	13		
	Swartzia tessmannii Harms	Swtes					2
Humiriaceae	*Sacoglottis guianensis* Benth.	Sagui					1
	Humiria balsamifera (Aubl.) A.St.-Hil.	Hubal	1				
Lamiaceae	*Vitex duckei* Huber	Viduc					6
Malpighiaceae	*Byrsonima laevis* Nied.	Bylae	13	9			
Malvaceae	*Pachira minor* (Sims) Hemsl.	Pamin		13			
Melastomataceae	*Macairea theresiae* Cogn.	Mathe	1	5			
Metteniusaceae	*Emmotum orbiculatum* (Benth.) Miers	Emorb		18		7	14
Moraceae	*Ficus mathewsii* (Miq.) Miq.	Fimat	2	8			
Myristicaceae	*Iryanthera laevis* Markgr.	Irlae		3			
Myrtaceae	*Myrcia citrifolia* (Aubl.) D. Legrand	Mycit		14			
	Myrcia clusiifolia (Kunth) DC.	Myclu				2	
	Myrcia multiflora (Lam.) DC.	Mymul	3				
	Myrcia umbraticola (Kunth) E.Lucas & C.E.Wilson	Myumb		7			
Nyctaginaceae	*Neea obovata* Spruce ex Heimerl	Neobo		27		11	7
Ochnaceae	*Ouratea spruceana* Engl.	Ouspr		8	1		
Pentaphylacaceae	*Ternstroemia dentata* (Aubl.) Sw.	Teden	24	21			
Peraceae	*Pera schomburgkiana* (Benth.) Müll.Arg.	Pescho					2
	Pera bicolor (Klotzsch) Müll.Arg.	Pebic			1		
Primulaceae	*Cybianthus fulvopulverulentus* (Mez) G.Agostini	Cyful	10		4	23	16
Rubiaceae	*Ferdinandusa chlorantha* (Wedd.) Standl.	Fechl					1
	Pagamea coriácea Spruce ex Benth.	Pacor			5	8	10
Sapotaceae	*Elaeoluma schomburgkiana* (Miq.) Baill.	Elsch		11			
	Manilkara bidentata (A.DC.) A.Chev.	Mabid	10		14	22	12
	Pradosia schomburgkiana (A.DC.) Cronquist	Prsch	20		9		12

Schoepfiaceae	*Schoepfia clarkii* Steyerm.	Sccla			7	
Simaroubaceae	*Simaba guianensis* Aubl.	Sigui	11		13	

CAPÍTULO 4

Viviane Pagnussat Klein, Layon Oreste Demarchi, Adriano Costa Quaresma, Jefferson da Cruz e Maria Teresa Fernandez Piedade. **The vascular epiphyte flora in a white-sand ecosystem of the Uatumã Sustainable Development Reserve, Central Amazon**. *Check List* 18(1): 157–186 (2022). https://doi.org/10.15560/18.1.157.

Resumo

Os ecossistemas amazônicos têm sofrido perdas constantes devido aos processos de fragmentação, o que coloca em risco a biodiversidade associada. Embora as epífitas vasculares constituam um componente representativo das florestas tropicais, ainda são pouco estudadas em ecossistemas de areia branca. Apresentamos uma descrição e checklist das epífitas vasculares presentes em ecossistemas de areia branca (campinaranas) da Amazônia Central. Também analisamos a estrutura e determinamos o valor de importância epifítica (VEI) para cada uma das espécies de epífitas. Um total de 112 espécies, 58 gêneros e 16 famílias de epífitas vasculares foram registradas. A maior riqueza (95 spp.) foi observada nas fitofisionomias florestadas. Orchidaceae (66 spp.), Bromeliaceae (12 spp.) e Araceae (9 spp.) foram as famílias mais ricas. *Prosthechea aemula* W.E.Higgins (Orchidaceae) apresentou o maior VEI e representou cerca de 28% da abundância de indivíduos. Dentre as espécies, 36,6% possuem distribuição restrita à região amazônica, o que ressalta a importância da conservação desses ambientes.

Palavras-chave

Floresta Amazônica, campinaranas, valor de importância epifítico, distribuição vertical

Abstract

Amazon ecosystems have suffered constant losses due to fragmentation processes, which as a result puts associated biodiversity at risk. Although vascular epiphytes constitute a representative component of tropical forests, they are still poorly studied in white-sand ecosystems. We present a description and checklist of the vascular epiphytes present in white-sand ecosystems (campinaranas) in the Central Amazon. We also analyzed the structure and determined of the value of epiphytic importance (VEI) for the species. We recorded 112 species, 58 genera, and 16 families of vascular epiphytes. The greatest richness (95 spp.) was observed in forested phytophysiognomies. Orchidaceae (66 spp.), Bromeliaceae (12 spp.), and Araceae (9 spp.) were the richest families. *Prosthechea aemula* W.E.Higgins (Orchidaceae) had the highest VEI and accounted for about 28% of an abundance of individuals. Among the species, 36.6% have a distribution restricted to the Amazon region, which emphasizes the importance of the conservation of these environments.

Keywords

Amazon rainforest, campinaranas, epiphytic importance value, vertical occurrence.

Introduction

The Amazon occupies 40% of the territory of South America and possesses in its different ecosystems the greatest plant biodiversity on the planet (Mayer and Pimm 1997). It is estimated that 50,000 species of vascular plants occur in the Amazon, of which between 12,000 and 16,000 are tree species (Hubbell et al. 2008; ter Steege et al. 2013). For some groups of plants, such as vascular epiphytes, the diversity of species is still little known due to the incipient number of studies carried out in the region (Quaresma et al. 2017), although they constitute some of the most diverse and expressive groups of plants of the world and represent about 10% of the richness of known species (Zotz 2013).

The vegetation that develops on white-sand soils is known in Brazil as campinaranas, which are distributed over approximately 335,000 km2 and cover about 5% of the Amazon region (Adeney et al. 2016). The general characteristics of the campinaranas include sandy, acidic, nutrient-poor soils (podzols) and water saturation or even exposure of the water table during rainy periods, but with a water deficit in dry periods (Rossetti et al. 2019; Capurucho et al. 2020). These combined characteristics act as environmental filters (Fine and Kembel 2011; Costa et al. 2020) which select plants with morphological, anatomical, and/or physiological adaptations, and, thus, there is a high number of endemic lineages and species (Fine et al. 2010; Fine and Baraloto 2016; Guevara et al. 2016; Capurucho et al. 2020). In recent decades, significant efforts have been made to determine the distribution patterns of the arboreal communities of the Amazonian campinaranas (Vicentini 2004; Fine and Kembel 2011; García-Villacorta et al. 2016). However, there is still a great lack of studies on the structure and, especially, on the underlying ecological patterns and processes that allow us to understand the distribution of epiphytic flora in these oligotrophic ecosystems (Zotz 2016).

Local studies in different regions of the Amazon have shown a low number of species of vascular epiphytes in the campinarana forests (ter Steege and Cornelissen 1989; Gottsberger and Morawetz 1993; Coomes and Grubb 1996; Mari et al. 2016). However, Braga (1982), who considered only the Orchidaceae, reported that 78% of the species (about 122 spp.) described for Amazonian campinaranas have an epiphytic habit, and if we consider the other epiphytic families, this number will certainly double. Considering the low representativeness of published studies on vascular epiphytes in these environments and the constant anthropic disturbance of campinaranas (Ferreira et al. 2013; Adeney et al. 2016; Demarchi et al. 2019), there is an urgent need to expand on floristic and ecological knowledge of epiphytic communities. Increased knowledge will help develop strategies for the conservation of the biodiversity of these ecosystems.

We describe the epiphytic flora and present a checklist of the species of vascular epiphytes that occur in the various phytophysiognomies of the campinaranas found in the Uatumã Sustainable Development Reserve (Uatumã SDR) in the state of Amazonas, Brazil. In addition, we quantitatively analyze the structure of the epiphytic assemblies and calculate the value of epiphytic importance (VEI) of the species for two local phytophysiognomies. A brief taxonomic description, ecological comments, and information on the geographical and local distribution of the species with the highest VEI are also presented and discussed.

Study Area

The Uatumã SDR is located in the Central Amazon, in northeastern Amazonas state, between the municipalities of Itapiranga and São Sebastião do Uatumã, approximately 150 km from Manaus (Fig. 1A). This conservation unit covers an area of 4,244 km2. It was established by State Decree no. 24.295 on 26 June 2004 in order to ensure the sustainable exploitation and conservation of renewable natural resources used by local traditional and riverine populations. In addition to the campinaranas, the ecosystems of Blackwater Flooded Forest (igapó) and Dense Ombrophilous Forest (terra firme) are also found in Uatumã SDR (Idesam 2009).

The climate in region is equatorial pluvial (Radam Brasil 1978), with an average annual precipitation of 2,077 mm. The rainy period extends from December to May, with a peak in March and April (monthly average 298.4 and 278.7 mm, respectively) (Carneiro and Trancoso 2007). The dry season lasts from June to October, with August and September driest (monthly average 72 mm). The annual average temperature is 27 °C (Carneiro and Trancoso 2007).

The studied areas are located between the coordinates −02.1991° to −02.1872° and −059.0137° to −059.0125° (Fig. 1) and are part of the research and permanent monitoring sites established within the framework of the Long-Term Ecological Program (PELD-MAUA; https://peld-maua.inpa.gov.br/). The campinaranas are located in areas adjacent to the terra firme forests (Fig. 1B). They are distributed within an area of approximately 400 ha and are physiognomically different in their vegetation structure. These physiognomies range from open formations, dominated mainly by shrubs and small trees to forested formations, composed of large trees with a height of over 20 meters (Klein and Piedade 2019).

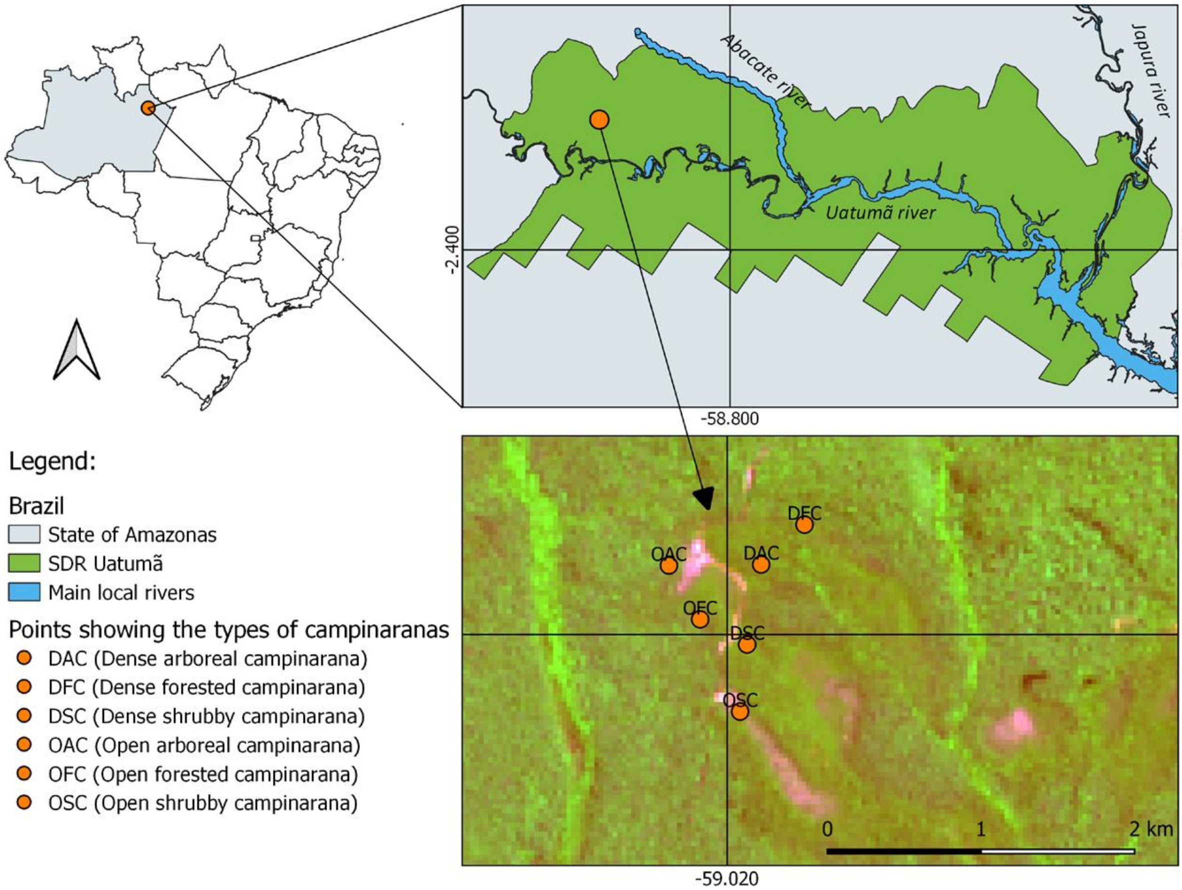

Figure 1. Map of the study area. In (a), the limits of the Uatumã Sustainable Development Reserve (Uatumã SDR) and main local rivers. In (b), the white sand ecosystems, with the points marking the different phytophysiognomies of campinaranas present in the area (Band composition source: Landsat-8, U.S. Geological Survey).

Methods

Description of epiphytic communities in the phytophysiognomies of the campinaranas. Considering the proposed classifications for the Amazonian campinaranas (Veloso et al. 1991; IBGE 2012) and the local conditions, such as the exposure level to the water table and the structure and composition of the arboreal vegetation, the campinaranas of the Uatumã SDR were classified into six phytophysiognomies: open shrubby campinarana, dense shrubby campinarana, open arboreal campinarana, dense arboreal campinarana, open forested campinarana, and dense forested campinarana (see Demarchi et al. in press). Based on these classifications, we schematically represented (Figs. 2–4) the structure of the vascular epiphyte communities and highlighted the distribution patterns of the most frequently species for each of the phytophysiognomies present in the campinaranas of the Uatumã SDR.

Floristic survey – To verify the richness of vascular epiphytes in the campinaranas of Uatumã SDR, we carried out free rambles throughout the area (Filgueiras et al. 1994) from August 2016 to March 2020. For the observation of canopy species, binoculars (Bushnell, H2O waterproof, straight barrel, 10×42, FOV 305FT), a photographic camera with close-up lenses, and manual climbing of the phorophytes were used. With regard to life form, the vascular epiphytes were classified in holoepiphytes (never connecting to the ground), facultative (for those plants that can grow as either epiphytes or terrestrial), accidental (for plants usually terrestrial, but can casually grow as epiphytes), and hemiepiphytes (connection to the ground during part of their life cycle) following Benzing (1990). All species were recorded, together with their position in the vertical gradient of the phorophytes.

To assess the occurrence of species in vertical gradients, we use the method of dividing the phorophytes into zones, adapted from Johansson (1974). Where: ZI (exposed roots and phorophytes region close to the ground, height ≤ 50 cm); ZII (trunk region above the base to the first bifurcation); ZIII (first branches, region formed by older and thicker branches); ZIV (more external region, formed by newer and thinner branches, where most of the leaves are arranged). The evaluation of species occurrences in the vertical gradient of the phorophytes was used for the descriptive characterization of the epiphyte communities in the different phytophysiognomies of campinaranas.

The samples were collected, herborized and later deposited in the Herbarium of the National Institute of Amazonian Research (INPA Herbarium; acronyms according to Thiers 2021), Manaus, Amazonas. For the identification of the species, we used literature indicated for the botanical families and genera (Mez 1891, 1892, 1894, 1896; Hoehne 1949; Harling 1958; Pabst and Dungs 1975, 1977; Croat 1988; Soares 1996; Kessler 2000; Zuquim et al. 2007), comparison with material deposited in the main herbariums of Brazil and the rest of the world (http://www.splink.org.br/), and consultation with the specialists in the given groups. The taxonomic classification for angiosperms follow the hierarchical system proposed by the Angiosperm Phylogeny Group (APG IV 2016) and to lycophytes and monilophytes (grouped as ferns), we follow the classification of Pteridophyte Phylogeny Group (PPG I 2016).

Structure of the epiphytic communities – Four plots of 25 × 25 m were marked, totaling 0.25 ha in phytophysiognomies of open arboreal campinarana and open forested campinarana. The canopy between the plots ranged from 12 to 22 m in height. All trees, with diameter at breast height (DBH) ≥10 cm inside the demarcated plots were examined and the epiphytes were identified and quantified. We considered an epiphytic individual to be any plant or cluster of plants geographically distinguishable from each other (Sanford 1968). We recorded all epiphytic individuals occurring in the phorophytes (juveniles and adults). Small individuals, less than 5 cm, were only included in the sample if found fertile (e.g. Epidendrum apuahuense Mansf.).

The value of epiphytic importance (VEI) was calculated considering the relative frequency values of the epiphytic species on the phorophyte (FfR) and the relative abundance of the species at the site (AbR), according to equations as proposed by Waechter (1998):

$$\text{AbR} = 100\ (\text{AbA} / \Sigma\text{AbA})$$

$$\text{FfR} = 100\ (\text{FfA} / \Sigma\text{FfA})$$

$$\text{FfA} = 100\ (\text{Nfe} / \text{Ntf})$$

$$\text{VEI} = (\text{AbR}+\text{FfR}) / 2$$

where, AbR = relative abundance of epiphytes, FfR = relative frequency of epiphytes on phorophytes, AbA = absolute abundance of epiphytes, FfA = absolute frequency of epiphytes on phorophytes, Nfe = number of phorophytes that were home to the epiphytic species, and Ntf = total number of phorophytes.

We provide herein a synopsis for the 25% of the species of vascular epiphytes with the highest VEI values for the sampled plots. Descriptions of morphological characteristics were based on material collected during the current study, on exsicates deposited in the INPA Herbarium, and on digitized material in the NY Herbarium collected from white-sand ecosystems near the study site. Ecological and phenological information on the species were obtained through observations and field notes, and from material deposited in herbariums. Geographical distribution data were obtained from the information available from Flora do Brasil 2020, from the SpeciesLink integrated network of herbariums, in the databases of the Royal Botanic Gardens of Kew, and in the Missouri Botanical Garden (Flora do Brasil 2020; Govaerts et al. 2020; Tropicos 2020). For the geographical distribution patterns of the taxa, we classify the species in the categories: (a) Pantropical (PAN) for widely distributed species in tropical regions of the world, (b) Neotropical (NEO) for species restricted to tropical and/or subtropical regions of the Americas, (c) Amazon basin (AB) for species with a distribution restricted to the Amazon basin, (d) endemic (EN) for species restricted to Brazil, and (e) South America (SA) for species distributed in the Amazon and also in other biomes of Brazil and South America. For local distribution, we recorded the habitat that the species occupy locally, utilizing the proposed classification for the phytophysiognomies of the campinaranas of the Uatumã SDR (Demarchi et al. in press).

Results

Description of epiphytic flora in the phytophysiognomies of campinarana. The vascular epiphyte communities present different patterns of distribution and floristic composition among the phytophysiognomies of the campinaranas of the Uatumã SDR (Figs. 2–4; Appendix Table A1). The areas of open forest campinarana (95 spp.) and open arboreal campinarana (53 spp.) were the richest in species. Only four species (*Brassavola martiana* Lindl. (Orchidaceae), *Microgramma baldwinii* Brade (Polypodiaceae), *Prosthechea aemula* W.E. Higgins (Orchidaceae), and *Tillandsia adpressiflora* Mez (Bromeliaceae) occurred in all phytophysiognomies, while 49 (43.7%) of the species occurred only in a single type of local phytophysiognomy (Appendix Table A1). A detailed description of the main characteristics of the phytophysiognomies and local distribution patterns for the most common vascular epiphyte species is presented below.

Open shrubby campinarana (OSC) – Figure 2A

In this phytophysiognomy, vascular epiphytes are commonly found on the phorophytes of the species *Aldina heterophylla* Spruce ex Benth. (Fabaceae) and *Cybianthus fulvopulverulentus* (Mez) G. Agostini (Primulaceae). In this area, the trees have low structural variation, due to their reduced heights (<5 m) and few horizontal branches, which are characteristics that reduce the formation of microhabitats as well as the area available for colonization by epiphytes. These characteristics related to the structure of the phorophytes may be one of the reasons why we have observed a low number of species and individuals in this phytophysiognomy. *Tillandsia adpressiflora* is the most common epiphyte in the area, and it forms large clusters of rosettes, mainly in the ZIII of the phorophytes. *Brassavola martiana* and *Prosthechea aemula* also occur in ZIII but are not frequent; *Encyclia mapuerae* (Huber) Brade & Pabst and *Sobralia granitica* G.A. Romero & Carnevalie occur mainly in terrestrial form in the area, but it is common to find individuals occurring as facultative epiphytes in the ZI of the phorophyte.

Dense shrubby campinarana (DSC) – Figure 2B

This phytophysiognomy is dominated by riparian shrubs. Vascular epiphytes are uncommon and tend to occur on Aldina heterophylla or near the ground in the small bushes of *Remijia morilloi* Steyerm (Rubiaceae). Among the characteristic species, we can highlight *Encyclia conchaechila* Barb.Rodr.) Porto & Brade which only occurs in this type of environment. *Hymenophyllum polyanthos* (Sw.) Sw. and *Tillandsia adpressiflora* are the most common species in this area. Some individuals of *Brassavola martiana* and *Microgramma baldwinii* were also observed in the ZIV of the phorophytes.

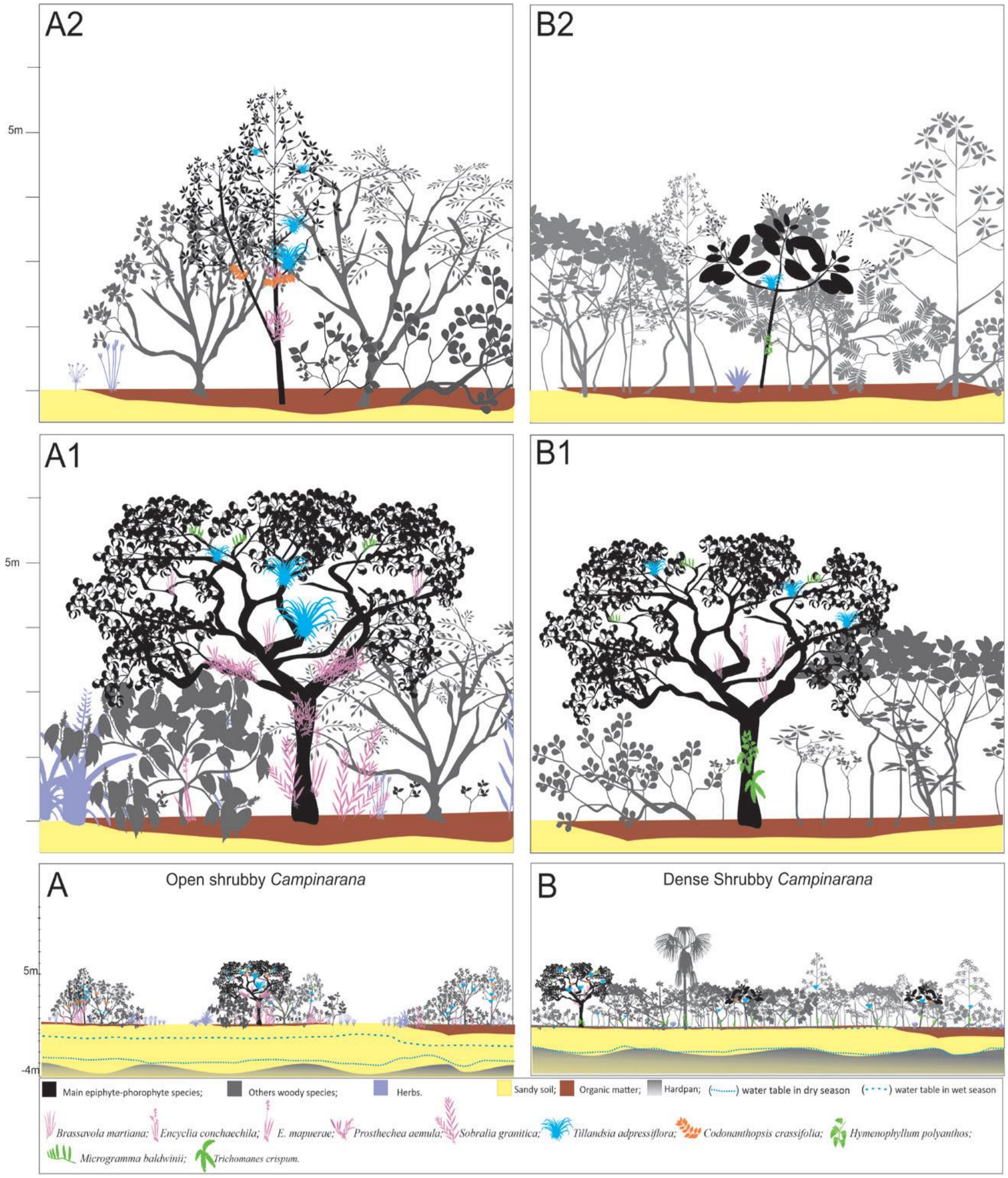

Figure 2. Schematic representation of the distribution patterns of vascular epiphytes for the phytophysiognomies. **A.** Open shrubby campinarana (OSC). **B.** Dense shrubby campinarana (DSC) in white sand ecosystems of the Uatumã Sustainable Development Reserve. Details for the distribution of vascular epiphytes in the most important phorophytes in each type of phytophysiognomy; *Aldina heterophylla* (**A1, B1**), *Cybianthus fulvopulverulentus* (**A2**), and *Remijia morilloi* (**B2**).

Open arboreal campinarana (OAC) – Figure 3A

In this phytophysiognomy, the trees possess greater heights, reaching up to 12 m, and have many horizontal branches, which increase the surface area for colonization of epiphytes. In these campinaranas, the highest density of epiphytic individuals is observed, especially on *Aldina heterophylla*, *Cybianthus fulvopulverulentus*, and *Emmotum orbiculatum* (Benth.) Miers (Metteniusaceae). *Prosthechea aemula* is the most common epiphyte, which when associated with other species, such as Anthurium gracile (Rudge) Lindl., *Brassavola martiana*, *Codonanthopsis crassifolia* (H. Focke) Chautems & Mat. Perret, *Microgramma baldwinii*, *Philodendron pulchrum* G.M. Barroso, and *Serpocaulon attenuatum* (C. Presl) A.R. Sm., forms large groups of individuals that almost fully cover the **ZIII** of the phorophytes. In **ZIV**, it is common to observe isolated individuals of *Catasetum ciliatum* Rchb.f., *Caularthron bicornutum* (Hook.) Raf., and juvenile of *Tillandsia adpressiflora*.

Dense arboreal campinarana (DAC) – Figure 3C

In this phytophysionomy, seasonal flooding occurs. The trees have a high density of individuals, usually thin, tall, and with narrow canopies. The main species of phorophytes are *Aldina heterophylla*, *Emmotum orbiculatum*, and *Pagamea coriacea* Spruce ex Benth (Rubiaceae). The epiphytes have low diversity and abundance, and the ferns, especially *Elaphoglossum plumosum* (Fée) T. Moore and *Hymenophyllum polyanthos*, are frequent and develop mainly in the **ZI** and **ZII** regions of the phorophytes. Some orchid species, such as *Acianthera discophylla* Luer, *Bulbophyllum setigerum* Lindl., and *Octomeria yauaperyensis* Barb.Rodr., were observed only in this phytophysiognomy.

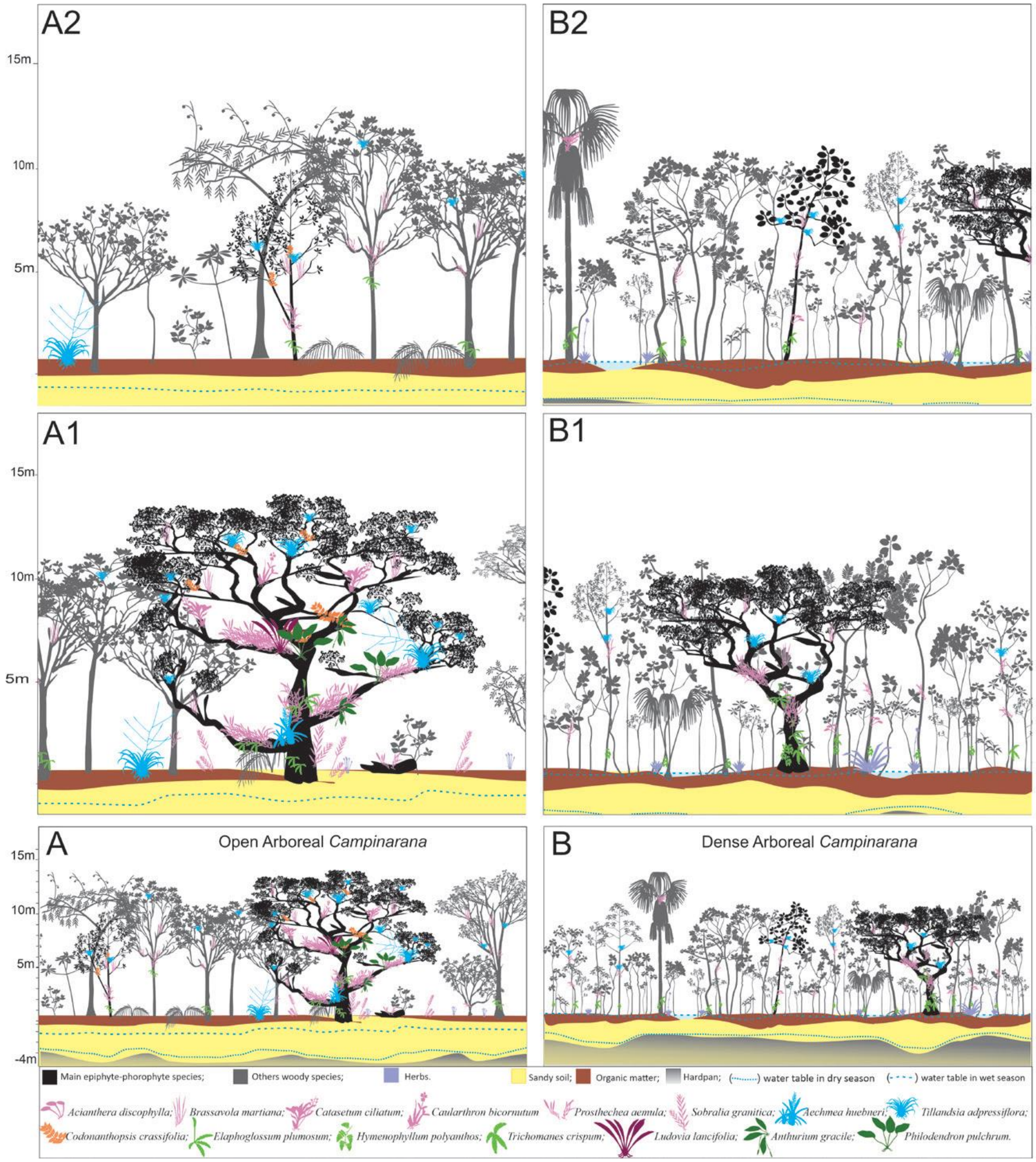

Figure 3. Schematic representation of the distribution patterns of vascular epiphytes for the phytophysiognomies. **A.** Open arboreal campinarana (OAC). **B.** Dense arboreal campinarana (DAC) in white sand ecosystems of the Uatumã Sustainable Development Reserve. Details for the distribution of vascular epiphytes in the most important phorophytes in each type of phytophysiognomy; *Aldina heterophylla* (**A1, B1**), *Cybianthus fulvopulverulentus* (**A2**), and *Emmotum orbiculatum* (**B2**).

Open forested campinarana (OFC) – Figure 4A

The main species of phorophytes are *Aldina heterophylla, Manilkara bidentata* (A. DC.) A. Chev. (Sapotaceae) and *Ternstroemia dentata* (Aubl.) Sw. (Pentaphylacaceae). In this phytophysiognomy, we found the greatest richness of vascular epiphytes (95 spp.), although the density of individuals is lower when compared with the areas of open forested campinarana. The distribution of epiphytes presents a clear, vertical stratification, with different groups colonizing different regions of the phorophytes. In the **ZI** and **ZII** regions, closer to the ground, it is common to find species of ferns such as *Elaphoglossum obovatum* Mickel, *Hymenophyllum polyanthos*, and *Trichomanes humboldtii* (Bosch). Near the first bifurcations (end portion of **ZII** and beginning of **ZIII**), species of *Maxillaria* (*M. camaridii* Rchb.f., *M. parviflora* Garay and *M. superflua* Rchb.f) are frequent. Near the crowns of the phorophytes (**ZIII** and **ZIV**), a great diversity of species is found, and *Brassavola martiana*, *Codonanthopsis crassifolia*, *Epidendrum bahiense* Rchb.f., *Prosthechea aemula*, and *Tillandsia adpressiflora* are the most common. In these forested areas, we also find the epiphytic individuals with larger sizes, such as the tank bromeliads *Aechmea beeriana* L.B. Sm. & M.A. Spencer and *Aechmea huebneri* Harms, large orchids such as *Cattleya wallisii* (Linden) Linden ex Rchb.f., *Eriopsis sprucei* Rchb.f and *Maxillaria violaceopunctata* Rchb.f, and the Araceae *Anthurium eminens* Schott and *Philodendron billietiae* Croat.

Dense forested campinarana (DFC) – Figure 4B

This phytophysiognomy is dominated by the palm trees, *Euterpe catinga* Wallace, *Mauritia carana* Wallace, and *Mauritiella armata* (Mart.) Burret (all Arecaceae). The richness of epiphytes is low in the area; however, it is often possible to find *Hymenophyllum polyanthos*, *Hylaeorchis petiolaris* (Schltr.) Carnevali & G.A. Romero, and *Trichomanes humboldtii* settling in the **ZI** and **ZII** regions of the phorophytes, while *Brassavola martiana*, *Catasetum ciliatum*, and *Prosthechea aemula* colonize the **ZIV**. In this environment, it is common to find hemiepiphyte species and nomadic vines (*Clusia insignis* Mart., *Clusia nemorosa* G. Mey., *Philodendron megalophyllum* Schott, and *Vanilla bicolor* Lindl.) developing among the leaf sheaths of *Mauritia carana*.

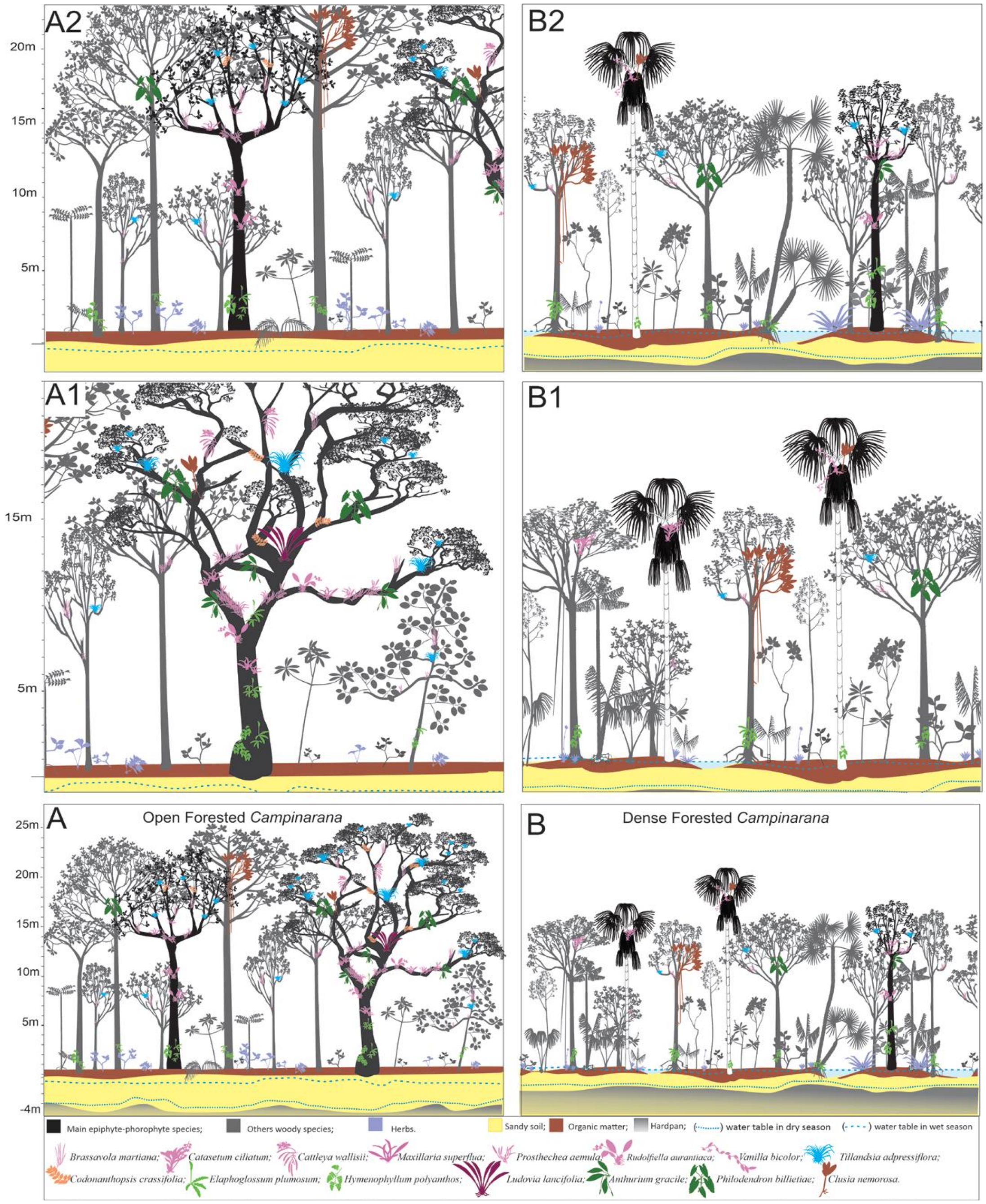

Figure 4. Schematic representation of the distribution patterns of vascular epiphytes for the phytophysiognomies. **A.** Open forested campinarana (OFC). **B.** Dense forested campinarana (DFC) in white sand ecosystems of the Uatumã Sustainable Development Reserve. Details for the distribution of vascular epiphytes in the most important phorophytes in each type of phytophysiognomy; *Aldina heterophylla* (**A1**), *Manilkara bidentata* (**A2, B2**), and *Mauritia carana* (**B1**).

Floristic composition of vascular epiphytes – A total of 112 species, 58 genera, and 16 families of vascular epiphytes were recorded in the campinaranas of the Uatumã SDR (Appendix Table A1). Angiosperms represented 86.6% of the species richness (97 spp.) and the remaining species (13.4%; 15 spp.) are ferns. Monocotyledons were the most diverse group (89 spp.). The largest contribution to species richness was found for Orchidaceae (66 spp.), Bromeliaceae (13 spp.), and Araceae (9 ssp.). Similarly, the genera *Epidendrum* L. (10 spp.), *Maxillaria* Ruiz & Pav. (9 spp.), and *Aechmea* Brongn. (7 spp.) were the richest in numbers of species.

Of the life forms, holoepiphytes (91 spp.) were dominant, representing 81% of the species, with orchids and ferns the most representative. The hemiepiphytes (11 spp.) accounted for 10% of the species richness, with a predominance of the family Araceae (Table 1). The other life forms, facultative (6 spp.) and accidental (4 spp.), represented 5% and 4% of the total species, respectively. Most of the species are Neotropical (57 spp.; 50.9%) or have a distribution that is restricted to the Amazon basin (42 spp.; 37.5%). Only six species (5.3%) are endemic to the Brazilian flora. Four species (3.6%) occur in the Amazon and other Brazilian phytogeographic domains, and only three species (2.7%) have a pantropical distribution. The species of Orchidaceae (32 spp.) are mainly restricted to the Amazon basin, while most of the taxa of Bromeliaceae (7 spp.) and Araceae (5 spp.) present a Neotropical distribution.

Structure of the epiphytic community – Vascular epiphytes occurred on 96 phorophytes (66% of the total trees sampled). A total of 62 species and 1,175 epiphytes (mean of 12.2 per phorophyte) were quantified in the sampled plots. The most species-rich families were Orchidaceae (32 spp.), Bromeliaceae (9 spp.), Araceae (6 spp.), and Dryopteridaceae (3 spp.). The species that presented the highest value of importance (Table 1) were *Prosthechea aemula* (VEI = 18.35), *Elaphoglossum obovatum* (VEI = 11.32), *Brassavola martiana* (VEI = 10.26), *Tillandsia adpressiflora* (VEI = 10.01), and *Codonanthopsis crassifolia* (VEI = 8.36). Together these five species were responsible for 58.3% of the VEI obtained in the plots and are the most frequent species in environments of campinarana that were studied.

In the open arborel campinarana plots, we recorded 38 species and 496 individuals of vascular epiphytes distributed on 38 phorophytes. *Prosthechea aemula* (137 ind.), *Maxillaria superflua* (53 ind.), and *Codonanthopsis crassifolia* (52 ind.) were the most abundant species in this phytophysiognomy. In open forested campinarana plots, 46 species and 679 individuals were recorded. The most abundant species in this phytophysiognomy were *P. aemula* (199 ind.), *E. obovatum* (101 ind.), and *T. adpressiflora* (78 ind.). Below we present the material examined for all vascular epiphytes recorded in the white-sand ecosystems of the Uatumã SDR. For the 25 % of the species with the highest VEI (Table 1), we also provide a brief description of taxonomic, information on ecology, phenology, and geographical distribution.

Table 1. Structural parameters of the 28 main species of vascular epiphytes in campinarana phytophysiognomies of the Uatumã Sustainable Development Reserve, Central Amazonia. Nfe = number of phorophytes that house the epiphyte species; AbA= absolute abundance of epiphyte; AbR = relative abundance of epiphyte; FfA = absolute frequency of epiphyte species on individual phorophytes; FfR = relative frequency of epiphyte species on individual phorophytes; VEI = value of epiphytic importance.

Species of vascular epiphytes	Nfe	AbA	AbR	FfA	FfR	VEI
Prosthechea aemula	21	336	28.60	21.88	8.11	18.35
Elaphoglossum obovatum	26	148	12.60	27.08	10.04	11.32
Brassavola martiana	28	114	9.70	29.17	10.81	10.26
Tillandsia adpressiflora	23	131	11.15	23.96	8.88	10.01
Codonanthopsis crassifolia	27	74	6.30	28.13	10.42	8.36
Maxillaria superflua	13	113	9.62	13.54	5.02	7.32
Clusia nemorosa	15	24	2.04	15.63	5.79	3.92
Epidendrum bahiense	13	27	2.30	13.54	5.02	3.66
Sobralia granitica	11	24	2.04	11.46	4.25	3.14
Elaphoglossum plumosum	9	15	1.28	9.38	3.47	2.38
Epidendrum strobiliferum	6	28	2.38	6.25	2.32	2.35
Elaphoglossum discolor	7	11	0.94	7.29	2.70	1.82
Microgramma baldwinii	5	20	1.70	5.21	1.93	1.82
Bifrenaria longicornis	6	8	0.68	6.25	2.32	1.50
Prosthechea vespa	5	6	0.51	5.21	1.93	1.22
Epidendrum microphylum	2	15	1.28	2.08	0.77	1.02
Caularthron bicornutum	2	13	1.11	2.08	0.77	0.94
Epidendrum micronocturnum	3	6	0.51	3.13	1.16	0.83

Aechmea mertensii	3	4	0.34	3.13	1.16	0.75
Aechmea huebneri	3	4	0.34	3.13	1.16	0.75
Octomeria surinamensis	3	4	0.34	3.13	1.16	0.75
Rudolfiella aurantiaca	3	4	0.34	3.13	1.16	0.75
Anthurium obtusum	3	3	0.26	3.13	1.16	0.71
Anthurium gracile	2	6	0.51	2.08	0.77	0.64
Epidendrum apuahuense	2	6	0.51	2.08	0.77	0.64
Moranopteris nana	2	5	0.43	2.08	0.77	0.60
Maxillaria parviflora	2	4	0.34	2.08	0.77	0.56
Hymenophyllum polyanthos	2	4	0.34	2.08	0.77	0.56

Araceae Juss.

***Anthurium bonplandii* Bunting**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1849, −059.0217; 40 m; 25 Mar. 2019; V. Klein 293 leg.; INPA 286939 • ibid; V. Klein 292 leg; INPA 286940.

***Anthurium eminens* Schott**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1150, −059.0081; 40 m; 21 Apr. 2019; L.O. Demarchi 840 leg.; INPA 277951.

***Anthurium gracile* (Rudge) Lindl.**

Figure 5A

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1831, −059.0226; 40 m; 26 Mar. 2019; V. Klein 323 leg.; INPA 286963 • ibid; 1 Nov. 2019; V. Klein 372 leg.; INPA 286983.

Identification. Holoepiphyte. Herb erect, 20–50 cm long. Cataphylls and prophylls brown, persistent and fibrous. Leaves 4–12, elliptical to lanceolate, 5.0–14.4 × 3.8–5.8 cm, acute apex, entire margin. Inflorescence shorter than leaves (5.8–12.5 cm long); spathe reflex, 0.5–2.1 × 0.7–1.4 cm, lanceolate, greenish; spadix erect to subpendent, 1.2–5.0 × 0.4–0.6 cm, sessile, yellowish to greenish. Infructescence 3.5–6.6 × 0.8–1.4 cm, globose berries, 3–8 mm in diameter, reddish purple.

Geographic distribution. Neotropical. Widely distributed in the Central and South America. In Brazil this species occurs in the North, Northeast and Central-West regions (Flora do Brasil 2020; Tropicos 2021).

Ecological and phenological information. The species is common in OSC and OAC. Usually occurring in ZIII region, associated with *Prosthechea aemula* forming large clusters over the phorophytes. Observed with flowers and fruits between March and November.

Anthurium obtusum **(Engl.) Grayum**

Figure 5B

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1843, −059.0230; alt. 40 m; 23 Apr. 2017; V. Klein 125 leg.; INPA 286912.

Identification. Holoepiphyte. Herb erect, 15–30 cm long. Cataphylls and prophylls brown, persistent. Leaves 3–7, ovate to elliptic, 7.0–12.0 × 3.8–5.23 cm, apiculate apex, entire margin. Inflorescence shorter than the leaves (3.8–4.5 cm long); spathe erect 1.7–21 × 0.7–1.1 cm, lanceolate, greenish; spadix erect, 2.2–4.0 × 0.4–0.8 cm, sessile, greenish white to pinkish. Infructescence 3.8–7.0 × 0.8–1.4 cm, globose berries, 5–7 mm in diameter, white or sometimes pale lavender.

Geographic distribution. Neotropical. Widely distributed in the Central and South America. In Brazil the species occurs in the North Region (Flora do Brasil 2020; Tropicos 2020).

Ecological and phenological information. The species occurs in OFC and DFC. Usually grows in ZII region of the phorophytes. Observed with flowers and fruits between April and August.

Philodendron billietiae **Croat**

Material examined. BRAZIL • Amazonas, Manaus, Reserva Florestal Adolpho Ducke; −02.9301, −059.9803; alt. 50 m; 23 Aug. 2011; L.L. Oliveira 40 leg.; INPA 241196.

Philodendron distantilobum **K.Krause**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, REBIO Uatumã; −01.8083, −059.2729; alt. 40 m; 10 Jul. 2008; J.F. Stanck 466 leg.; INPA 225245.

***Philodendron megalophyllum* Schott**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, REBIO Uatumã; −01.8054, −059.2719; alt. 40 m; 21 Jul. 2015; M.M. Pombo 647 leg.; INPA 278623.

***Philodendron pulchrum* G.M.Barroso**

Material examined. BRAZIL • Amazonas, Manuas, Br. 174, Reserva da Campina; −02.595, −060.2505; alt. 52 m; 19 Jun. 1996; M.A. Nadruz 1234 leg.; INPA 192925.

***Thaumatophyllum spruceanum* Schott**

Material examined. BRAZIL • Amazonas, Manuas, Br. 174, Reserva da Campina; −02.595, −060.2505; alt. 52 m; 19 Jun. 1996; M.A. Nadruz 1233 leg.; INPA 192924.

Aspleniaceae Newman

***Asplenium serratum* L.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1862, −059.0231; alt. 40 m; 10 Jul. 2017; L.O. Demarchi 840 leg.; INPA 277951 • ibid; 11 May 2019; V. Klein 306 leg.; INPA 286951.

Bromeliaceae A. Juss.

***Aechmea beeriana* L.B.Sm. & M.A.Spencer**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1752, −059.0451; alt. 40 m; 7 Nov. 2018; L.O. Demarchi 1419 leg.; INPA 288546 • ibid; 1 Dec. 2006; J.G. Carvalho-Sobrinho, 1331 leg.; INPA 2225313.

***Aechmea bromeliifolia* (Rudge) Baker**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Rio Uatumã; −02.0833, −059.201; alt. 40 m; 13 Aug. 1979; C.A.C. Ferreira 259 leg.; INPA 87295.

***Aechmea huebneri* Harms**

Figure 5C

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1859, −059.0241; alt. 40 m; 6 Jun. 2018; L.O. Demarchi 1223 leg.; INPA 288387.

Identification. Facultative epiphytes. Tubular rosette herb, forming tank developed. Leaves 6–12, lanceolate, 35–120 × 5.8–10.4 cm, acuminate apex, serrated margin. Floral scape and inflorescence longer than leaves (30–100 cm long); escape bracts 1.5–4.2 × 1.5–3.5 cm, lanceolate, greenish pink, pungent apex; floral bracts 0.3–0.8 × 0.3–0.5 cm, ovoid, pink, pungent apex, shorter than the sepals. Flowers attractive, sessile; sepals 0.15–0.3 × 0.15–0.2 cm, asymmetric, reddish, acute apex; petals 0.2–0.7 × 0.2–0.4 cm, spatulate, purple, acuminate apex. Fruits not observed.

Geographic distribution. Amazon basin and Atlantic Forest. Occurs in South America (Brazil and Colombia). In Brazil the species occurs in the North and Northeast regions (Flora do Brasil 2020; Tropicos 2021).

Ecological and phenological information. The species is common in OAC. Grows in the ZIII region of the phorophytes. Observed with flowers between June and October.

Aechmea longifolia (Rudge) L.B.Sm. & M.A.Spencer

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1823, −059.0011; alt. 40 m; 20 May 2021; V. Klein 433 leg.; INPA 289249.

Aechmea mertensii (G.Mey.) Schult. & Schult.f.

Figure 5D

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1759, −059.0105; alt. 40 m; 2 Oct. 2016; L.O. Demarchi 2018 leg.; INPA 288500.

Identification. Holoepiphyte. Tubular rosette herb. Leaves 5–9, ovate to elliptical, 12.8–34.0 × 1.2–4.3 cm, attenuate apex, serrated margin and retrospinous spines. Floral scape and inflorescence longer than leaves (12–35 cm long); escape bracts 2–7.25 × 0.3–2.6 cm, elliptical or lanceolate, red, pungent apex; floral bracts 0.2–2.9 × 0.2–2.5 cm, ovoid, greenish yellow, mucronate apex, shorter than the sepals. Flowers attractive, sessile, greenish yellow; sepals 0.2–0.5 × 0.15–0.3 cm, asymmetric, yellow, mucronate apex; petals 0.4–0.8 × 0.2–0.4 cm, ligulates, yellowish, mucronate apex. Fruits not observed.

Geographic distribution. Neotropical. Occurs in South America (Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, Suriname, and Venezuela). In Brazil the species occurs in the North, Northeast, and Central-West regions (Flora do Brasil 2020; Tropicos 2021).

Ecological and phenological information. The species is common in OAC. Growing preferably in the ZIV region of the phorophytes. Usually associated with ant gardens. Observed with flowers between October and November.

***Aechmea rodriguesiana* (L.B.Sm.) L.B.Sm.**

Material examined. BRAZIL • Amazonas, Manaus, Reserva Florestal Adolpho Ducke; −02.9301, −059.9803; alt. 50 m; 23 Aug. 2011; J.E.L. Ribeiro 1272 leg.; INPA 178866.

***Aechmea setigera* Mart. ex Schult. & Schult.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Rio Uatumã, Ramal da Morena; −02.9790, −060.0543; alt. 40 m; 13 Aug. 1979; D.A.C. Ferreira 346 leg.; INPA 87712.

***Araeococcus micranthus* Brongn.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1919, −059.2103; alt. 40 m; 3 Oct. 2018; L.O. Demarchi 1386 leg.; INPA 288516 • ibid; −02.1907, −059.1423; 23 Mar. 2007; J.G. Carvalho-Sobrinho, 1498 leg.; INPA 225300.

***Billbergia violacea* Bee**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Rio Uatumã; −02.0833, −059.201; alt. 40 m; 29 Apr. 1985; C.A.C. Ferreira 5874 leg.; INPA 127339.

***Bromelia grandiflora* Mez**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1776, −059.0223; alt. 40 m; 25 Feb. 2020; V. Klein 447 leg.; INPA 289259.

***Neoregelia eleutheropetala* (Ule) L.B.Sm.**

Material examined. BRAZIL • Amazonas, Manuas, Br. 174, Reserva da Campina; −02.5921, −060.2425; alt. 52 m; 2 Dec. 2000; G.M. Souza 453 leg.; INPA 207064.

***Tillandsia adpressiflora* Mez**

Figure 5E

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1766, −059.0103; alt. 40 m; 8 Feb. 2015; L.O. Demarchi 18 leg.; INPA 287405.

Identification. Facultative epiphytes. Tubular rosette herb. Leaves 8–14, lanceolate to triangular, 20–80 × 8.0–16.4 cm, acuminate apex, entire margin. Floral scape and inflorescence longer than leaves (40–120 cm long); escape bracts 4.5–7.2 × 1.5–3.5 cm, closely lanceolate, reddish, acute apex; floral bracts 3.2–6.1 × 1.2–2.8 cm, closely lanceolate, reddish yellow, acute apex, bigger than sepals. Flowers attractive, sessile; sepals 2.5–3.8 × 1.0–1.8 cm, lanceolate, reddish, acute apex; petals 5.4–7.2 × 0.8–1.3 cm, elliptical, purple, acute apex. Fruits elliptical 4.2–5.1 cm long.

Geographic distribution. Restricted to the Amazon basin. Occurs in Bolivia, Brazil, Colombia, Ecuador, French Guiana, and Peru. In Brazil the species occurs in the North Region (Flora do Brasil 2020; Tropicos 2021).

Ecological and phenological information. This species occurs in all local campinarana phytophysiognomies, but it is abundant in OSC and OAC. Occurs usually in ZIII and ZIV regions of the phorophytes, forming large tanks. Observed with flowers and fruits between September and January.

***Tillandsia bulbosa* Hook.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1768, −059.0253; alt. 40 m; 9 May 2017; L.O. Demarchi 926 leg.; INPA 278025 • ibid; −02. 1919, −059.1833; 10 Nov. 2019; L.O. Demarchi 1615 leg.; INPA 288695.

Cactaceae Juss.

***Epiphyllum phyllanthus* (L.) Haw.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1801, −059.0177; alt. 40 m; 16 Aug. 2019; L.O.A. Teixeira 1982 leg.; INPA 87667.

Clusiaceae Lindl.

Clusia insignis **Mart.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1833, −059.0223; alt. 40 m; 1 Sep. 2015; L.O. Demarchi 651 leg.; INPA 274278.

Clusia nemorosa **G. Mey.**

Figure 5F

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1833, −059.02407; alt. 40 m; 11 Jan. 2019; L.O. Demarchi 1465 leg.; INPA 288591 • ibid; −02.1855, −059.0177; 11 Aug. 2019; L.O. Demarchi 1560 leg.; INPA 288647 • ibid; −02.1759, −059.0105; 10 Feb. 2021; L.O. Demarchi 1665 leg.; INPA 288734.

Identification. Hemiepiphyte. Dioecious plant. Shrub erect, up to 7 meters tall. Cylindrical stem, exudate white to orange; Leaves obovate, 8.8–14.2 × 4.2–5.8 cm, opposite disposition, coriaceous texture, rounded apex. Inflorescence terminal 1.3–2.2 cm, cymose. Flowers 1–3, attractives; sepals 4–5, free, orbicularis, 0.5–0.8 × 0.3–0.6 cm, greenish color; petals 5–7, free, elliptical, 1.8–4.0 × 0.8–2.18 cm, white with macule reddish to pink internally; staminate flowers composed by numerous free stamens with the upper surface covered by a mixture of resin and pollen during anthesis. Pistillate flowers composed by 6–10-locular ovary, terminal stigmas, staminodes resinous forming a ring around the ovary. Fruits orbicular, globose, 2–5 × 1.4–3.5 cm, whitish when immature, green to vinaceous when ripe, dehiscent by 6–10 longitudinal slits.

Geographic distribution. Neotropical. Occurs in South America (Brazil, French Guiana, Guyana, Suriname and Venezuela). In Brazil this species occurs in all regions, except in the South Region (Flora do Brasil 2020; Tropicos 2020).

Ecological and phenological information. The species is common in DFC. Usually presents the hemiepiphyte habit, germinating on the phorophytes and subsequently reaching contact with the soil. Observed with flowers and fruits between August and February.

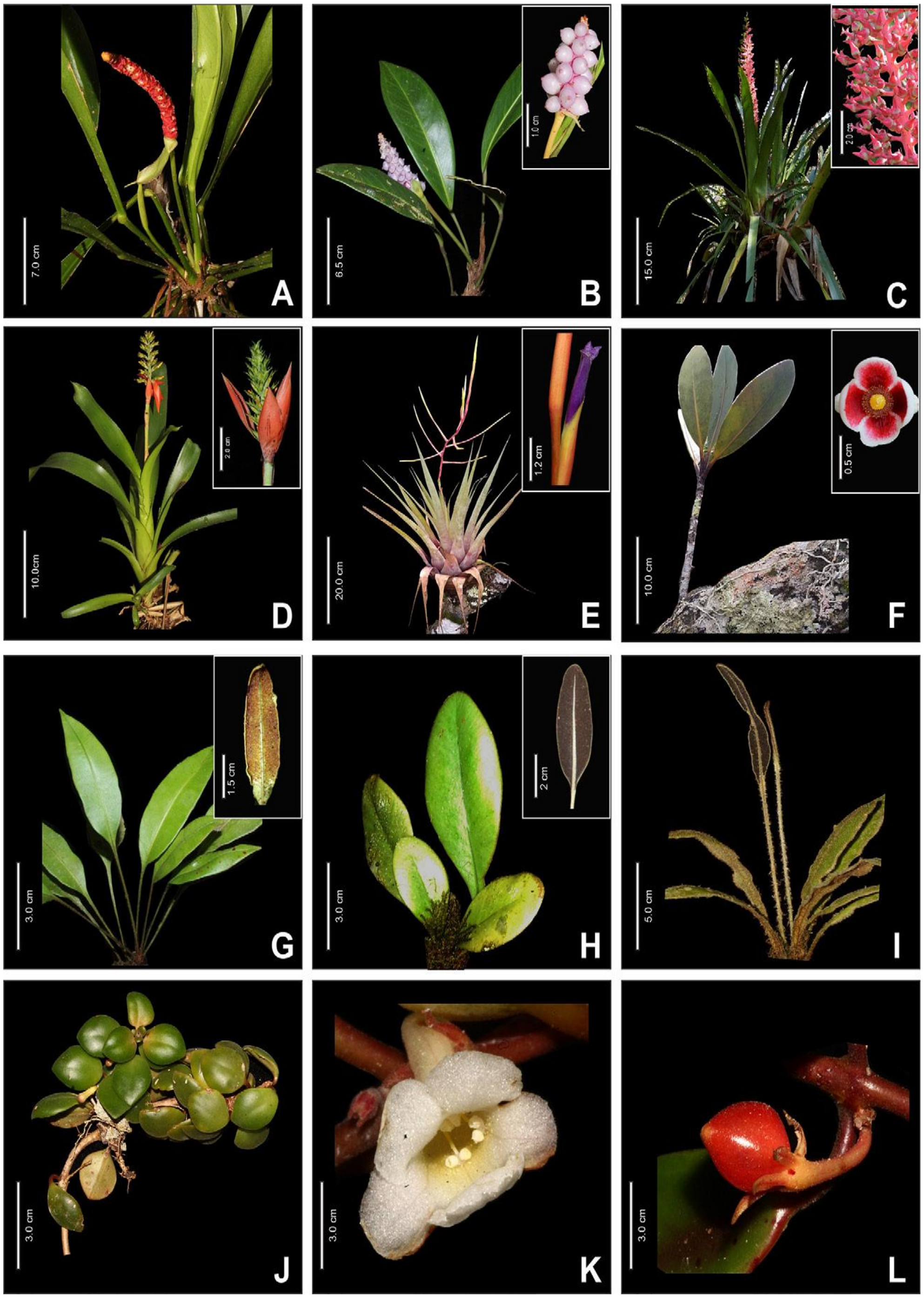

Figure 5. Species of vascular epiphytes with greater value of epiphytic importance (VEI) for the white-sand ecosystems of the Uatumã Sustainable Development Reserve. **A.** *Anthurium gracile*. **B.** *Anthurium obtusum*. **C.** *Aechmea huebneri*. **D.** *Aechmea mertensii*. **E.** *Tillandsia adpressiflora*. **F.** *Clusia nemorosa*. **G.** *Elaphoglossum discolor*. **H.** *Elaphoglossum obovatum*. I. *Elaphoglossum plumosum*. **J–L.** *Codonanthopsis crassifolia*.

Cyclanthaceae Poit. ex A.Rich.

***Ludovia lancifolia* Brongn.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1877, −059.0201; alt. 40 m; 10 Oct. 2019; L.O. Demarchi 1603 leg.; INPA 288684.

Dryopteridaceae Herter

***Elaphoglossum discolor* (Kuhn) C.Chr.**

Figure 5G

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1875, −059.0198; alt. 40 m; 23 Apr. 2017; V. Klein 126 leg.; INPA 286913.

Identification. Holoepiphyte. Herb erect. Stem cylindrical, 3.8.0–7.9 × 0.2–0.4 cm, covered by brown scale. Leaves 3–9, entire; sterile leaves, petiole (2–5.6 cm long), leaf blade 3.4–8.7 × 3.5–5.4 cm, triangular to lanceolate, acuminate apex, orange reddish scales in the underside of the leaf; fertile leaves longer petiole (4.6–7.3 cm long), leaf blade 3.2–5.6 × 1.8–3.5 cm, narrow-elliptical, acute apex. Sori light brown, throughout the entire underside of the leaf.

Geographic distribution. Amazon basin and Atlantic Forest. Occurs in South America (Brazil, Colombia, Ecuador, Peru and Venezuela). In Brazil the species occurs in the North, Northeast, and Central-West regions (Flora do Brasil 2020; Tropicos 2021).

Ecological and phenological information. This species is common in areas with high moisture, occurring mainly in DAC, DFC, and OFC. Usually growing in ZI and ZII regions of the phorophytes. Observed in fertile stage between April and May.

***Elaphoglossum glabellum* J.Sm.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1832, −059.02304; alt. 40 m; 11 Jun. 2019; V. Klein 313 leg.; INPA 286956 • ibid; −02.1827, −059.02303; 11 Jun. 2019; V. Klein 314 leg.; INPA 286957.

***Elaphoglossum obovatum* Mickel**

Figure 5H

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1871, −059.0183; alt. 40 m; 23 Apr. 2017; V. Klein 126 leg.; INPA 286913.

Identification. Holoepiphyte. Herb erect. Stem cylindrical, 4.2–8.0 × 0.2–0.4 cm, covered by brown scale. Leaves 2–9, entire; sterile leaves, short petiole (1–2 cm long), leaf blade 5.0–9.4 × 4.5–5.4 cm, obovate, rounded apex, light chestnut scales in the underside of the leaf; fertile leaves, longer petiole (3–5 cm long), leaf blade 4.0–6.6 × 1.8–2.8 cm, narrow-elliptical, rounded apex. Sori black, hroughout the entire underside of the leaf.

Geographic distribution. Neotropical. Widely distributed in American continent, occurring from Mexico to Brazil. In Brazil the species occurs in the North region (Flora do Brasil 2020; Tropicos 2021).

Ecological and phenological information. The species is common in areas with high moisture, occurring mainly in DAC and DFC. Occurs usually growing in the lower parts of the trunk (ZI and ZII). Observed in fertile stage between February and April.

***Elaphoglossum plumosum* (Fée) T.Moore**

Figure 5I

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1832, −059.02304; alt. 40 m; 16 Jun. 2017; V. Klein 181 leg.; INPA 286915 • ibid; −02.1812, −059.0202; 11 May 2019; V. Klein 299, 300 leg.; INPA 286944, 286945.

Identification. Holoepiphyte. Herb erect. Stem cylindrical, 3.2–6.6 × 0.2–0.5 cm, covered by brown scale. Leaves 3–8, entire; sterile leaves, short petiole (2.0 cm long), leaf blade 8.0–19.6 × 2.8–4.2 cm, lanceolate, acute to acuminate apex, abundance of light-brown and golden scales in leaf; fertile leaves, longer petiole (10.0 cm long), leaf blade 5.2–7.5 × 1.3–2.6 cm, narrow-lanceolate, rounded to acute apex. Sori dark, throughout the entire underside of the leaf.

Geographic distribution. Amazon basin and Atlantic Forest. Occurs in South America (Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela). In Brazil the species occurs in the North, Northeast, and Southeast regions. (Flora do Brasil 2020; Tropicos 2020).

Ecological and phenological information. The species is common in areas with high moisture, occurring mainly in DAC, OFC, and DFC. Usually growing in ZI and ZII region of the phorophytes. Observed in fertile stage between May and August.

Gesneriaceae Rich. & Juss. ex DC.

***Codonanthopsis crassifolia* (H. Focke) Chautems & Mat. Perret**

Figure 5J–L

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1811, −059.0246; alt. 40 m; 28 Oct. 2019; V. Klein 371 leg.; INPA 286982.

Identification. Holoepiphyte. Herb pendant. Stem cylindrical 40–175.0 × 0.10–0.20 cm, long-creeping stem. Leaves 12–27, distichous along the stem, elliptical, 2.2–5.3 × 1.8–3.9 cm, acute apex. Inflorescence 1.2–2.3 cm long, lateral, cymose. Flowers 1–3, attractive; sepal 5, linear narrow, 0.6–1.2 × 0.10–0.25 cm, white flowers, internally with yellow spots. Fruits, ovoid berries, 10–20 mm in diameter, pink to red.

Geographic distribution. Neotropical. The species is widely distributed in Central and South America. In Brazil the species occurs in the North and Central-West regions (Flora do Brasil 2020; Tropicos 2020).

Ecological and phenological information. The species is common in OAC and OFC. Grows preferably in the ZIV region of the phorophytes, usually associated with ant gardens. Observed with flowers and fruits between October and January.

***Codonanthopsis ulei* Mansf.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1812, −059.0202; alt. 40 m; 20 Apr. 2017; L.O. Demarchi 277 leg.; INPA 277928.

Hymenophyllaceae Gaudich.

***Hymenophyllum polyanthos* (Sw.) Sw.**

Figure 6A

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1801, −059.0256; alt. 40 m; 11 May 2019; V. Klein 305 leg.; INPA 286950 • ibid; −02.1810, −059.0211; 7 Sep. 2019; V. Klein 336 leg.; INPA 286970.

Identification. Holoepiphyte. Herb subpendent. Stem cylindrical, 15–20 × 0.05–0.10 cm, creeping stem, rust colored. Leaves 9–14, distichous along the stem, 3-pinnate, 6.6–13.8 × 2.0–3.6 cm, very thin and delicate. Sori formed by two flat valves, localized in the margin of leaves, at the ends of the veins.

Geographic distribution. Pantropical. In America is widely distributed in tropical forests from Mexico to Paraguay. Also, in eastern Asia and Africa. In Brazil, this species occurs in the North and Southeast regions. (Flora do Brasil 2020; Tropicos 2020).

Ecological and phenological information. This species is common in areas with high moisture, occurring mainly in DAC and DFC. Usually growing in ZI and ZII region of the phorophytes. Observed in fertile stage between May and September.

***Trichomanes crispum* L.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1811, −059.0246; alt. 40 m; 11 May. 2019; V. Klein 301 leg.; INPA 286946.

***Trichomanes humboldtii* (Bosch) Lellinger**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1811, −059.0246; alt. 40 m; 11 May. 2019; V. Klein 302 leg.; INPA 286947 • ibid; −02.1810, −059.0211; 22 May 2021; V. Klein 432 leg.; INPA 289248.

Moraceae Gaudich.

***Ficus mathewsii* (Miq.) Miq.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, REBIO Uatumã; −1.8083, −059.2729; alt. 40 m; 18 May 2015; D.P. Saraiva 606 leg.; INPA 272956.

Orchidaceae Juss.

***Acianthera discophylla* Luer & Carneval**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1714, −059.0240; alt. 40 m; 17 Jun. 2017; V. Klein 167 leg.; INPA 280994.

***Acianthera fockei* (Lindl.) Pridgeon & M.W.Chase**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1712, −059.0314; alt. 40 m; 7 Nov. 2016; V. Klein 69 leg.; INPA 280908 • ibid; −02.1712, −059.0211; alt. 40 m; 26 Mar. 2019; V. Klein 289 leg.; INPA 286938.

***Acianthera miqueliana* (H.Focke) Pridgeon & M.W.Chase**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1727, −059.0140; alt. 40 m; 13 Jun.. 2019; V. Klein 320 leg.; INPA 286962 • ibid; −02.1802, −059.0001; 1 Jul. 2019; V. Klein 373 leg.; INPA 286984.

***Aganisia fimbriata* Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1842, −059.0130; alt. 40 m; 20 May 2018; V. Klein 251 leg.; INPA 286917.

***Batemannia colleyi* Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1921, −059.0220; alt. 40 m; 12 Jun. 2019; V. Klein 318 leg.; INPA 286960.

***Bifrenaria longicornis* Lindl.**

Figure 6B, C

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1731, −059.01240; alt. 40 m; 28 Feb. 2017; V. Klein 108 leg.; INPA 280944 • ibid; −02.1810, −059.0201; 17 Jun. 2017; V. Klein 150 leg.; INPA 280981 • ibid; −02.1831, −059.0240; Apr.2018; L.O. Demarchi 1155 leg.; INPA 284814.

Identification. Holoepiphyte. Herb erect. Pseudobulb elliptical tetragonal 4.8–6.0 × 1.8–2.0 cm. Leaves 1, elliptical, 15.0–21.0 × 4.0–6.5 cm, acute apex. Inflorescence 8.0–14.0 cm long, lateral, in a raceme. Flowers 6–12, attractive, pale-yellow with brown spots; dorsal sepal 1.0–1.2 × 0.3–

0.5 cm, oblong, acute apex; lateral sepals 1.2–2.2 × 0.3–0.5 cm, connate at the base forming a spur, oblong, acute apex; petals 0.8–1.2 × 0.2–0.4 cm, oblong, acuminate apex; lip 1.2–1.7 × 0.9–1.3 cm, trilobed, white with purple veins. Fruits elliptical, 2.0–3.0 × 0.8–1.0 cm.

Geographic distribution. Amazon basin. Occurs in Bolivia, Brazil, Colombia, Guyana, French Guiana, Peru, Suriname, and Venezuela. In Brazil the species occurs in the North region (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. Occurs in OAC and OFC. Usually growing in ZII region of the phorophytes. Observed with flowers and fruits between February and June.

***Brassavola martiana* Lindl.**

Figure 6D

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1831, −059.0240; alt. 40 m; 5 Nov. 2016; V. Klein 58 leg.; INPA 280901 • ibid; −02.1906, −059.0190 Jan. 2017; V. Klein 94 leg.; INPA 280932 • ibid; −02.1833, −059.2407; 20 Aug. 2017; V. Klein 207 leg.; INPA 281023.

Identification. Holoepiphyte. Herb subpendant. Stem cylindrical, 5.2–13.0 × 0.2–0.4 cm. Leaves 1, cylindrical, 11.0–22.0 × 0.3–0.6 cm, acute apex. Inflorescence 3.8–6.1 cm long, terminal, in a raceme. Flowers 6–14, attractive, yellowish; dorsal sepal 2.0–2.5 × 0.4–0.6 cm, elliptical to lanceolate, acute apex; lateral sepals 2.2–2.5× 0.4–0.6 cm, elliptical-falcate, acute apex; petals 2.0–2.4 × 0.2–0.5 cm, elliptical-falcate, acute apex; lip 1.4–2.2 × 1.0–1.2 cm, ovate, white with yellow spot on disc. Fruits elliptical, 8.0–10.2 × 1.4–1.8 cm.

Geographic distribution. Restricted to the Amazon basin. Occurs in Bolivia, Brazil, Colombia, Guyana, French Guiana, Peru, Suriname, and Venezuela. In Brazil this species occurs in the North and Central-West regions (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. The species is abundant and common in all local campinarana phytophysiognomies. Occurs mainly in the ZIII and ZIV region of the phorophytes. Observed with flowers and fruits between June and December.

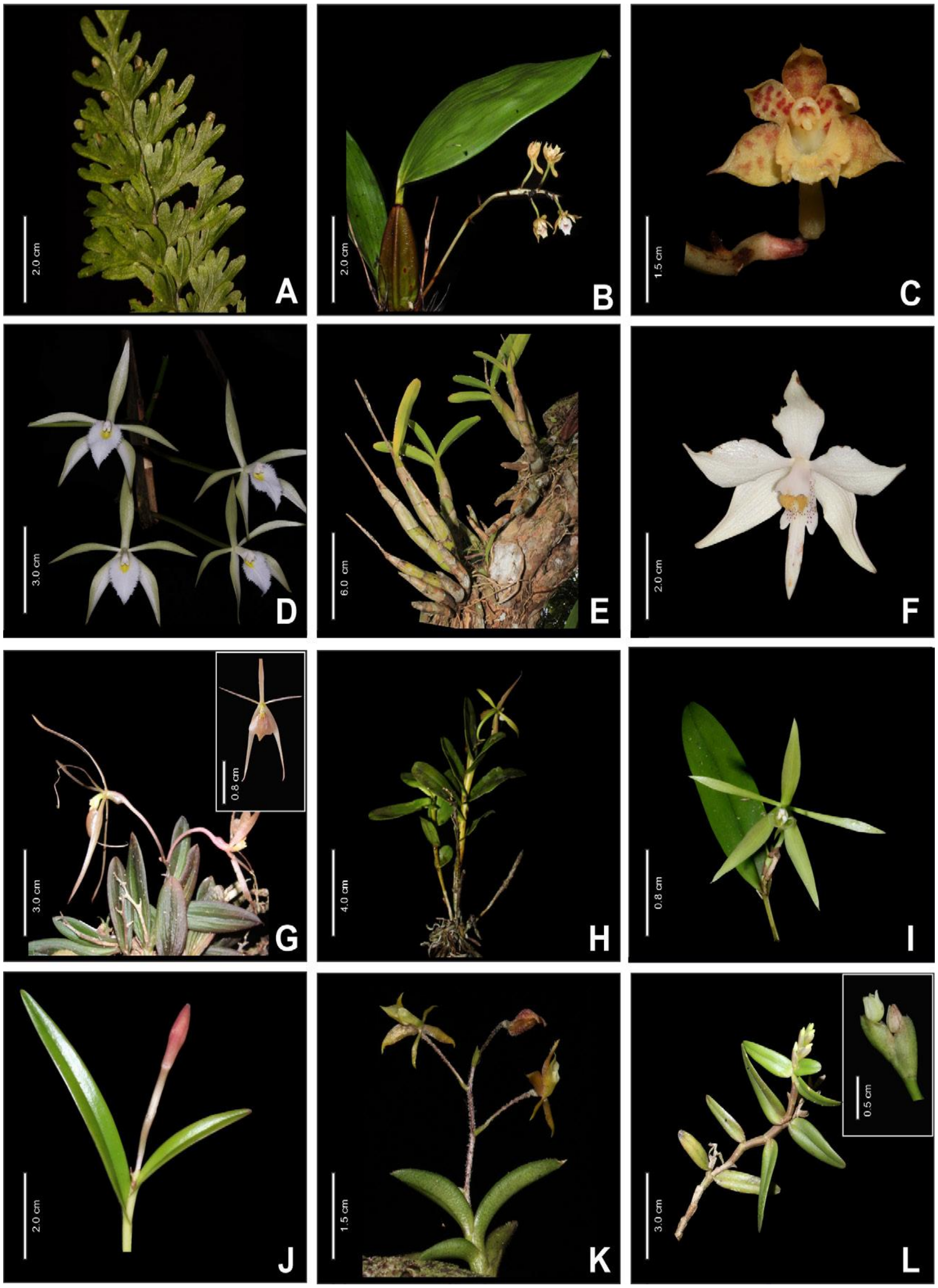

Figure 6. Species of vascular epiphytes with greater value of epiphytic importance (VEI) for the white-sand ecosystems of the Uatumã Sustainable Development Reserve. **A.** *Hymenophyllum polyanthos.* **B, C.** *Bifrenaria longicornis.* **D.** *Brassavola martiana.* **E, F.** *Caularthron bicornutum.* **G.** *Epidendrum apuahuense.* **H, I.** *Epidendrum bahiense.* **J.** *Epidendrum micronocturnum.* **K.** *Epidendrum microphyllum.* **L.** *Epidendrum strobiliferum.*

***Bulbophyllum setigerum* Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1921, −059.0423; alt. 40 m; 15 Jun. 2017; V. Klein 154 leg.; INPA 280985.

***Campylocentrum fasciola* (Lindl.) Cogn.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1944, −059.0354; alt. 40 m; 5 Aug. 2018; V. Klein 353 leg.; INPA 286980.

***Catasetum discolor* (Lindl.) Lindl**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1931, −059.0233; alt. 40 m; 20 Mar. 2017; V. Klein 112 leg.; INPA 280947 • ibid; −02.1813, −059.0211; 29 Apr. 2017; V. Klein 134 leg.; INPA 280965.

***Catasetum rivularium* Barb.Rodr.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1855, −059.0177; alt. 40 m; 10 Fev. 2018; L.O. Demarchi 1118 leg.; INPA 284797.

***Catasetum tigrinum* Rchb.f.**

Material examined. BRAZIL • Amazonas, Manaus, Reserva Florestal Adolpho Ducke; −02.9301, −059.9803; alt. 50 m; 19 Nov. 1996; J.E. Ribeiro 1861 leg.; INPA 195192.

***Cattleya wallisii* (Linden) Linden ex Rchb.f**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1912, −059.01334; alt. 40 m; 5 Nov. 2016; V. Klein 68 leg.; INPA 280907 • ibid; −02.5981, −060.0305; 28 Jun. 2018; D.R.P. Krahl 41 leg.; INPA 285412.

***Caularthron bicornutum* (Hook.) Raf.**

Figure 6E, F

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1903, −059.0234; alt. 40 m; 8 Aug. 2016; V. Klein 53 leg.; INPA 280896 • ibid; −02.1906, −059.0190; 19 Sep. 2017; A.C. Quaresma 44 leg.; INPA 280285.

Identification. Holoepiphyte. Herb erect. Pseudobulb oblong, 8.0–14.0 × 2.0–2.3 cm. Leaves 5–7 per pseudobulb, oblong, 9.0–12.2 × 0.8–1.2 cm, emarginate apex. Inflorescence 40.0–56.0 cm long, terminal, in a raceme. Flowers 3–9, attractive, white; dorsal sepal 2.5–3.0 × 0.9–1.2 cm, obovate to elliptical, acute apex; lateral sepals 2.2–3.0 × 0.9–1.2 cm, obovate, cuneate apex; petals 2.5–3.0 × 1.2–1.5 cm, elliptical, acute apex; lip 2.3–2.7 × 1.0–1.3 cm, trilobed, white with purple spots 2.0–2.5 × 0.4–0.6 cm. Fruits not observed.

Geographic distribution. Neotropical. Occurs in Central and South America (Brazil, Colombia, Guyana, Trinidad and Tobago, and Venezuela). In Brazil the species occurs in the North and Central-West regions (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. This species is common in OAC. Usually growing on *Aldina heterophylla* in ZIII and ZIV regions. Observed with flower in August.

***Dichaea anchoraelabia* C.Schweinf.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1847, −059.0345; alt. 40 m; 12 Apr. 2017; V. Klein 116 leg.; INPA 280951.

***Dichaea picta* Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1921, −059.0124; alt. 40 m; 20 Feb. 2017; V. Klein 111 leg.; INPA 280846 • ibid; −02.1806, −059.0220; 19 Fev. 2018; V. Klein 260 leg.; INPA 281063.

***Encyclia chloroleuca* (Hook.) Neumann**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1801 −059.0301; alt. 40 m; 5 May 2018; V. Klein 236 leg.; INPA 281046.

***Encyclia conchaechila* Barb.Rodr.) Porto & Brade**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1811, −059.0314; alt. 40 m; 5 Nov. 2016; V. Klein 71 leg.; INPA 280910 • ibid; −02.1826, −059.0242; 20 Aug. 2017; V. Klein 204 leg.; INPA 281021.

***Encyclia mapuerae* (Huber) Brade & Pabst**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1812, −059.0101; alt. 40 m; 5 Nov. 2016; V. Klein 60 leg.; INPA 280903 • ibid; −02.1722, −059.0423; 20 Aug. 2017; V. Klein 203 leg.; INPA 281022.

***Epidendrum apuahuense* Mansf.**

Figure 6G

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1855, −059.0177; alt. 40 m; 11 May 2017; L.O. Demarchi 912 leg.; INPA 278517 • ibid; −02.1907, −059.0193; 15 Jun. 2017, V. Klein 156 leg.; INPA 278519.

Identification. Holoepiphyte. Herb erect. Pseudobulb ovoid, 0.2–0.5 × 0.2–0.30 cm. Leaves 2–3 per pseudobulb, elliptical to oblong, 1.2–3.9 × 2.8–1.3 cm, acute apex. Inflorescence 0.9–3.3 cm long, terminal, in a raceme. Flowers 2–4, attractive, ochre; dorsal sepal 2.0–3.8 × 0.2–0.4 cm, narrowly elliptical, acuminate apex; lateral sepals 2.0–3.4 × 0.2–0.4 cm, narrowly lanceolate, acuminate apex; petals 2.2–4.0 × 0.1–0.2 cm, linear, acuminate apex; lip 1.5–2.5 × 1.0–1.5 cm, entire, ovate to distinctly 3-lobed trilobed, light pink with reddish veins. Fruits not observed.

Geographic distribution. Amazon basin. Occurs in South America (Brazil and Venezuela). In Brazil this species occurs in the North Region (Flora do Brasil 2020)

Ecological and phenological information. Rare species, recently recollected for the Brazilian Amazon. Occurs in DAC and OFC. Usually growing in ZII region of the phorophytes. Observed with flowers between May and August.

***Epidendrum bahiense* Rchb.f.**

Figure 6H, I

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1803, −059.0227; alt. 40 m; 8 Aug. 2016; V. Klein 46 leg.; INPA 280889 • ibid; −02.1845, −059.0171; 21 Apr. 2017; V. Klein 117 leg.; INPA 280952 • ibid; −02.1906, −059.0190; 1 Sep. 2015; L.O. Demarchi 654 leg.; INPA 274281 • ibid; −02.1833, −059.2407; 24 Sep. 2017; V. Klein 177 leg.; INPA 271000.

Identification. Holoepiphyte. Herb erect. Stem cylindrical, 14.0–24.0 × 0.3–0.4 cm. Leaves 4–6 distichous along the stem, elliptical, 5.5–9.8 × 0.5–1.7 cm, retuse apex. Inflorescence 1.6–2.1 cm long, terminal, in a raceme. Flowers 1–3, attractive, yellow-greenish; dorsal sepal 1.9–2.8 × 0.2–0.4 cm, elliptical, acuminate apex; lateral sepals 2.2–3.0 × 0.3–0.5 cm, elliptical-falcate, acuminate apex; petals 1.9–2.8 × 0.15–0.2 cm, narrow-elliptical, acuminate apex; lip 1.3–2.1 × 1.1–1.6 cm, trilobed-clawed, greenish-white. Fruits fusiform, 5.6–6.8 × 0.8–1.3 cm.

Geographic distribution. Neotropical. This species is widely distributed in Central and South America. In Brazil this species occurs in all regions, except the South Region (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. The species is common in OSC, OAC, and OFC. Occurs mainly in the ZII region of the phorophytes. Observed with flowers and fruits between June and November.

Epidendrum carpophorum Barb.Rodr.

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1822, −059.0123; alt. 40 m; 21 Apr. 2017; V. Klein 117 leg.; INPA 280952 • ibid; −02.1832, −059.02304; 15 May 2018; V. Klein 138 leg.; INPA 280969.

Epidendrum compressum Griseb.

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1819, −059.0103; alt. 40 m; 11 Oct. 2017; V. Klein 245 leg.; INPA 280951 • ibid; −02.1821, −059.0234; 6 Feb. 2018; V. Klein 255; INPA 281059.

Epidendrum micronocturnum Carnevali & G.A.Romero

Figure 6J

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1829, −059.0221; alt. 40 m; 21 Apr. 2017; V. Klein 122 leg.; INPA 280957 • ibid; −02.1832, −059.0204; 5 Jun. 2017; V. Klein 160 leg.; INPA 280987.

Identification. Holoepiphyte. Herb erect. Stem cylindrical, 3.8–5.0 × 0.15–0.25 cm. Leaves 2–5 distichous along the stem, narrow-linear, 4.0–8.1 × 0.4–0.6 cm, retuse apex. Inflorescence 0.8–1.2

cm long, terminal, in a raceme. Flowers 1–2, attractive, greenish-pink; dorsal sepal 1.7–1.9 × 0.2–0.3 cm, narrow elliptical, acuminate apex; lateral sepals 1.5–1.65 × 0.4–0.5 cm, elliptical, acuminate apex; petals 1.8–2.0 × 0.1–0.2 cm, linear-falcate, acuminate apex; lip 1.0–1.5 × 1.2–1.2 cm, trilobed, white. Fruits fusiform, 2.8–3.0 × 0.6–1.1 cm.

Geographic distribution. Amazon basin. Occurs in South America (Brazil, Colombia, Ecuador, Guyana, Peru, and Venezuela). In Brazil this species occurs in the North and Central-West regions (Govaerts et al. 2021; Flora do Brasil 2020).

Ecological and phenological information. The species occurs in DSC, OAC, and DAC. Usually grows in ZIII region of the phorophytes. Observed with flowers and fruits between April and June.

Epidendrum microphyllum **Lindl.**

Figure 6K

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1782, −059.0180; alt. 40 m; 11 Feb. 2017; V. Klein 105 leg.; INPA 280942 • ibid; −02.1803, −059.2207; 6 Feb. 2018; V. Klein 273 leg.; INPA 286921 • ibid; −02.1906, −059.0190; 28 April 2018; L.O. Demarchi 678 leg.; INPA 284734.

Identification. Holoepiphyte. Herb reptant. Stem cylindrical 3.8–4.2 × 0.15–0.3 cm. Leaves 4–6 distichous along the stem, linear, 2.0–2.5 × 0.5–0.7cm, acute apex. Inflorescence 4.2–6.3 cm long, terminal, in a raceme. Flowers 3–7, discreet, greenish; dorsal sepal 0.4–0.6 × 0.2–0.3 cm, elliptical, acute apex; lateral sepals 0.4–0.5 × 0.2–0.3 cm, elliptical-falcate, attenuate apex; petals 0.4–0.5 × 0.1–0.2 cm, linear, acute apex; lip 0.4–0.6 × 0.2–0.4 cm, ovoid, greenish. Fruits not observed.

Geographic distribution. Neotropical. Occurs in Central and South America (Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Panama, Peru, Suriname, and Venezuela). In Brazil this species occurs in the North region (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. Occurs in OAC and OFC. Usually grows in ZII region, forming clusters of small individuals on the phorophytes, Observed with flowers between February and April.

Epidendrum orchidiflorum **(Salzm.) Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1723, −059.0210; alt. 40 m; 8 Nov. 2016; V. Klein 74 leg.; INPA 280912.

***Epidendrum rigidum* Jacq.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1814, −059.0237; alt. 40 m; 21 Apr. 2017; V. Klein 115 leg.; INPA 280950 • ibid; −02.1803, −059.0234; 21 Apr. 2017; V. Klein 118 leg.; INPA 280953.

***Epidendrum sculptum* Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1812, −059.0131; alt. 40 m; 3 May 2017; V. Klein 135 leg.; INPA 280966 • ibid; −02.1803, −059.0234; 8 May 2018; V. Klein 238 leg.; INPA 281048.

***Epidendrum strobiliferum* Rchb.f.**

Figure 6L

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1831, −059.0240; alt. 40 m; 16 Aug. 2016, V. Klein 52 leg.; INPA280895 • ibid; −02.1833, −059.2407; 16 Jun. 2017; V. Klein 140 leg.; INPA 280971 • ibid; −02.1903, −059.0122 29 Apr. 2018; L.O. Demarchi 1159 leg.; INPA 284817.

Identification. Holoepiphyte. Herb pendant to subpendant. Stem cylindrical 5.5–9.4 × 0.3–0.5 cm. Leaves 4–9 distichous along the stem, oblong, 1.2–3.6 × 0.4–0.7 cm, emarginate apex. Inflorescence 0.8–2.5 cm long, terminal, in a raceme. Flowers 2–6, inconspicuous, whitish; dorsal sepal 0.3–0.6 × 0.15–0.2 cm, elliptical, cuneate apex; lateral sepals 0.3–0.6 × 0.15–0.2 cm, elliptical, acute apex; petals 0.2–0.5 × 0.05–0.1 cm, linear-falcate, rounded apex; lip clawed 0.3–0.4 × 0.15–0.25 cm, cordate, whitish. Fruits elliptical, 0.6–1.0 × 0.3–0.6 cm.

Geographic distribution. Neotropical. Widely distributed in the American continent. In Brazil the species occurs in all regions. (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. This species is common in OAC. Usually growing in ZIV region of the phorophytes. Observed with flowers and fruits between February and November.

Eriopsis sceptrum **Rchb.f. & Warsz.**

Material examined. BRAZIL • Amazonas, Manaus, Rio Cuieiras; −02.6000, −060.3330; alt. 50 m; 9 Apr. 1974; D.G. Campelli 21975 leg.; INPA 459153.

Jacquiniella globosa **Schltr.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1912, −059.0170; alt. 40 m; 21 Apr. 2017; V. Klein 123 leg.; INPA 280858.

Hylaeorchis petiolaris **(Schltr.) Carnevali & G.A.Romero**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1722, −059.0210; alt. 40 m; 8 Aug. 2016; V. Klein 106 leg.; INPA 280843 • ibid; −02.1823, −059.0243; 17 Jul. 2017, V. Klein 165 leg.; INPA 280992.

Madisonia kerrii **Luer**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1923, −059.0120; alt. 40 m; 15 Jun. 2017; V. Klein 146 leg.; INPA 280977.

Maxillaria brasiliensis **Brieger & Illg**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1820, −059.0422; alt. 40 m; 25 Apr. 2017; V. Klein 230 leg.; INPA 280961.

Maxillaria camaridii **Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.17893, −059.0112; alt. 40 m; 16 Feb. 2017; V. Klein 102 leg.; INPA 280939.

Maxillaria crassifolia **(Lindl.) Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1702, −059.0345; alt. 40 m; 16 Fev. 2017; V. Klein 103 leg.; INPA 280940.

Maxillaria desvauxiana **Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1848, −059.0268; alt. 40 m; 9 Nov. 2016; V. Klein 79 leg.; INPA 280817 • ibid; −02.1731, −059.0223; 14 Jun. 2017, V. Klein 143 leg.; INPA 280974.

***Maxillaria kegelii* Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1822, −059.0355; alt. 40 m; 29 Mar. 2017; V. Klein 114 leg.; INPA 280949 • ibid; −02.1831, −059.0244; 28 Oct. 2018, V. Klein 253 leg.; INPA 281057.

***Maxillaria parviflora* (Poepp. & Endl.) Garay**

Figure 7A

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1875, −059.0198; alt. 40 m; 8 Aug. 2016; V. Klein 50 leg.; INPA 280893 • ibid; −02.1831, −059.0240; 7 Aug. 2017, V. Klein 202 leg.; INPA 281020.

Identification. Holoepiphyte. Herb pendant. Pseudobulb ovate, laterally flattened 1.4–2.1 × 0.3–0.5 cm. Leaves 1 per pseudobulb, lanceolate, 8.0–12.0 × 0.9–1.2 cm, acute apex. Inflorescence 0.2–0.3 cm long, lateral, single-flower. Flowers 1, inconspicuous, whitish; dorsal sepal 0.4–0.6 × 0.2–0.3 cm, elliptical, cuneate apex; lateral sepals 0.3–0.5 × 0.2–0.3cm, oblong, cuspidate apex; petals 0.2–0.5 × 0.1–0.2 cm, elliptical, cuspidate apex; lip 0.5–0.6 × 0.2–0.3 cm, lightly trilobed, white. Fruits not observed.

Geographic distribution. Neotropical. Widely distributed in the Central and South America. In Brazil the species occurs in all regions (Flora do Brasil 2020; Tropicos 2021).

Ecological and phenological information. Occurs mainly in OFC and DFC. Usually grows in ZII region of the phorophytes. Observed with flowers in August.

***Maxillaria superflua* Rchb.f.**

Figure 7B

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1935, −059.1882; alt. 40 m; 9 Nov. 2016; V. Klein 78 leg.; INPA 280916 • ibid; −02.1847, −059.0215; 3 Apr. 2017; V. Klein 132 leg.; INPA 280963 • ibid; −02.1774, −059.0213; 4 May 2018; L.O.

Demarchi 1193 leg.; INPA 284829 • ibid; −02.1782, −059.0180; 13 Feb. 2019; V. Klein 274 leg.; INPA 286225.

Identification. Holoepiphyte. Herb erect. Pseudobulb oblong, laterally flattened 1.5–3.3 × 0.6–0.8 cm. Leaves 1 per pseudobulb, oblong, 14.3–27.2 × 0.8–1.6 cm, emarginate apex. Inflorescence 3.1–4.7 cm long, lateral, single-flower. Flowers 1, attractive, yellow; dorsal sepal 1.2–1.7 × 0.3–0.5 cm, elliptical, obtuse apex; lateral sepals 1.0–1.6 × 0.3–0.5 cm, elliptical, obtuse apex; petals 1.0–1.6 × 0.2–0.4 cm, lanceolate, acute apex; lip 1.3–1.6 × 0.6–0.7 cm, minutely trilobed, dark purple. Fruits fusiform 1.8–3.2 × 0.6–0.9 cm.

Geographic distribution. Neotropical. Occurs in South America (Bolivia, Brazil Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela). In Brazil this species occurs in the North and Central-West regions (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. This species is common in OAC and OFC. Occurs mainly in the ZII and ZIII regions of the phorophytes. Observed with flowers and fruits throughout the year.

***Maxillaria tenuis* C.Schweinf.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1841, −059.0204; alt. 40 m; 2 Jan. 20176; V. Klein 91 leg.; INPA 280923.

***Maxillaria violaceopunctata* Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1831, −059.0334; alt. 40 m; 16 Feb. 2017; V. Klein 99 leg.; INPA 280936.

***Notylia aromatica* Barker ex Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1912, −059.01334; alt. 40 m; 11 Oct. 2017; V. Klein 246 leg.; INPA 281052 • ibid; −059.1711, −059.0305; 16 Oct. 2017; V. Klein 248 leg.; INPA 281053.

***Octomeria erosilabia* C.Schweinf.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1809, −059.0355; alt. 40 m; 26 Mar. 2017; V. Klein 113 leg.; INPA 280948 • ibid; −02.1813, −059.0345; 18 Jun. 2017; V. Klein 180 leg.; INPA 281003.

Octomeria grandiflora Lindl.

Figure 7C

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1789, −059.0354; alt. 40 m; 16 Feb. 20197 V. Klein 81 leg.; INPA 280919 • ibid; −02.1810, −059.0211; 15 Jun. 2017; V. Klein 147 leg.; INPA 280978.

Identification. Holoepiphyte. Herb erect. Stem cylindrical at base and flattened at apex, 5.1–6.6 × 0.2–0.3 cm. Leaves 1 per pseudobulb, lanceolate, 6.1–7.6 × 0.7–0.9 cm, emarginate apex. Inflorescence 0.3–0.4 cm long, terminal, in a fascicle. Flowers 1–3, discreet, yellowish; dorsal sepal 0.6–0.8 × 0.2–0.3 cm, elliptical to oblong, cuneate apex; lateral sepals 0.6–0.9 × 0.2–0.3 cm, elliptical, cuneate apex; petals 0.6–0.9 × 0.15– 0.2, elliptical, acute apex; lip 0.4–0.6 × 0.25–0.4 cm, trilobed, yellow with red macules on disc. Fruits not observed.

Geographic distribution. Neotropical. Occurs in South America (Brazil, Colombia, Ecuador, Peru, and Venezuela). In Brazil this species is widely distributed, occurs in all regions (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. This species is common in OFC and DFC, mainly in small sub-canopy trees. Occurs mainly in the ZII region of the phorophytes. Observed with flowers and fruits between February and November.

Octomeria sagittata (Rchb.f.) Garay

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1847, −059.1732; alt. 40 m; 21 Apr. 2017; V. Klein 120 leg.; INPA 280955.

Octomeria scirpoidea (Poepp. & Endl.) Rchb.f.

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1825, −059.0345; alt. 40 m; 14 Jun. 2017; V. Klein 144 leg.; INPA 280975 • ibid; −02.1821, −059.0433; 18 Jun. 2017; V. Klein 182 leg.; INPA 281004.

Octomeria taracuana **Schltr.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1923, −059.0212; alt. 40 m; 2 Jan. 2017; V. Klein 97 leg.; INPA 2808935.

Octomeria yauaperyensis **Barb.Rodr.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1874, −059.0247; alt. 40 m; 21 Jun. 2017; V. Klein 182 leg.; INPA 281006 • ibid; −02.1800, −059.0212; 12 Aug. 2017; V. Klein 214 leg.; INPA 281028.

Orleanesia amazonica **Barb.Rodr.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1935, −059.1882; alt. 40 m; 5 Nov. 2016; V. Klein 55 leg.; INPA 280898 • ibid; −02.1774, −059.0213; 17 Jun. 2017; L.O. Demarchi 947 leg.; INPA 284769.

Pabstiella yauaperyensis **(Barb.Rodr.) F.Barros**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1737, −059.0356; alt. 40 m; 16 Nov. 2017; V. Klein 249 leg.; INPA 281054 • ibid; −02.1833, −059.0423; 15 May 2018; V. Klein 261 leg.; INPA 281064.

Polystachya concreta **(Jacq.) Garay & Sweet**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1827, −059.1882; alt. 40 m; 15 Jun. 2017; V. Klein 152 leg.; INPA 280983 • ibid; −02.19217, −059.0225; 5 Jun. 2018; V. Klein 239 leg.; INPA 281049.

Polystachya stenophylla **Schltr.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1935, −059.0882; alt. 40 m; 9 Nov. 2016; V. Klein 78 leg.; INPA 280915 • ibid; −02.1847, −059.1756; 5 May 2018; V. Klein 265 leg.; INPA 281068.

Prosthechea aemula **W.E.Higgins**

Figure 7D, E

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1856, −059.02357; alt. 40 m; 9 Nov. 2016; V. Klein 80 leg.; INPA 280918 • ibid; −02.1812, −059.0202; 2 Feb. 2017; V. Klein 104 leg.; INPA 280941 • ibid; −02.1831, −059.0240; 3 May 2017; V. Klein 136 leg.; INPA 280967.

Identification. Holoepiphyte. Herb erect. Pseudobulb elliptical, 3.2–6.4 × 0.6–1.2. Leaves 1 per pseudobulb, elliptical to lanceolate, 13.6–17.3 × 1.1–1.5 cm, attenuate apex. Inflorescence 3.4–6.2 cm long, terminal, in a raceme. Flowers 2–4, attractive, greenish-white; dorsal sepal 2.2–2.4 × 0.4–0.6 cm, lanceolate, attenuate apex; lateral sepals 2.2–2.4 × 0.4–0.6 cm, lanceolate-falcate, attenuate apex; petals 2.2–2.4 × 0.2–0.35 cm, lanceolate, attenuate apex; lip 1.4–1.6 × 1.0–1.3 cm, sub-orbiculate, concave, white with purple vein. Fruits wide-elliptical, 3.2–3.5 × 1.5–1.7.

Geographic distribution. Neotropical. This species is widely distributed in Central and South America. In Brazil this species occurs in all the regions (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. This species is abundant and common in all local campinarana phytophysiognomies, forming large clusters on the phorophytes. Occurs mainly in the ZIII and ZIV regions. Observed with flowers and fruits between January and June.

***Prosthechea crassilabia* (Poepp. & Endl.) Carnevali & I.Ramírez**

Figure 7F, G

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1866, −059.0232; alt. 40 m; 8 Aug. 2016; V. Klein 48 leg.; INPA 280892 • ibid; −02.1812, −059.0202; 17 Jun. 2017; V. Klein 148 leg.; INPA 280979 • ibid; −02.1906, −059.0190; 28 Apr. 2018; L.O. Demarchi 1153 leg.; INPA 284812.

Identification. Holoepiphyte. Herb erect. Pseudobulb ovoid, 5.5–9.7 × 1.0–1.2. Leaves 2 per pseudobulb, elliptical to lanceolate, 16.2–24.9 × 1.5–2.7 cm, retuse apex. Inflorescence 5.5–21.4 cm long, terminal, in a raceme. Flowers 6–22, attractive, greenish with purplish macules; dorsal sepal 0.9–1.1 × 0.3–0.5 cm, oblong, attenuate apex; lateral sepals 0.9–1.1 × 0.3–0.5 cm, elliptical, cuneate apex; petals 0.9–1.1 × 0.1–0.15 cm, oblanceolate, rounded apex; lip 0.8–0.9 × 0.6–0.7 cm, obtrullate, white with purple veins. Fruits not observed.

Geographic distribution. Endemic to Brazil, distributed in all regions of the country (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. This species occurs in OAC and OFC. Usually growing in ZII and ZIII regions of the phorophytes. Observed with flowers between June and November.

***Quekettia microscopica* Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1812, −059.0426; alt. 40 m; 11 Jan. 2018, V. Klein 250 leg.; INPA 281055.

***Rudolfiella aurantiaca* (Lindl.) Hoehne**

Figure 7H

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1803, −059.0432; alt. 40 m; 13 Oct. 2015; L.O. Demarchi 697 leg.; INPA 274324 • ibid; −02.1852, −059.0274; 2 Oct. 2018; V. Klein 269 leg.; INPA 286920.

Identification. Holoepiphyte. Herb erect. Pseudobulb ovoid tetragonal, 3.5–5.2 × 2.2–3.1. Leaves 1 per pseudobulb, elliptical to lanceolate, 16.2–24.9 × 1.5–2.7 cm, acute apex. Inflorescence 5.5–21.4 cm long, terminal, in a raceme. Flowers 12–23, attractive, yellow with brown macules; dorsal sepal 1.0–1.2 × 0.4–0.5 cm, oblong, rounded apex; lateral sepals 1.0–1.2 × 0.4–0.6 cm, oblong-falcate, attenuate apex; petals 1.0–1.2 × 0.15–0.2 cm, linear-falcate, attenuate apex; lip 0.9–1.1 × 0.7–0.9 cm, trilobed, yellow with brown macules. Fruits not observed.

Geographic distribution. Restricted to the Amazon basin. Occurs in South America (Brazil, Bolivia; Colombia, Peru, Suriname, and Venezuela). In Brazil this species occurs in the North Region (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. The species occur in OAC and OFC. Usually growing in ZII region of the phorophytes. Observed with flowers in October.

***Scaphyglottis reflexa* Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1713, −059.0433; alt. 40 m; 8 Nov. 2016; V. Klein 75 leg.; INPA 280813 • ibid; −02.1812, −059.0202; 17 Jun. 2017; V. Klein 164 leg.; INPA 280991.

***Scaphyglottis sickii* Pabst**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1821, −059.0322; alt. 40 m; 14 Jun. 2017; V. Klein 142 leg.; INPA 280873 • ibid; −02.1862, −059.0212; 8 May 2018; V. Klein 237 leg.; INPA 281047.

***Scaphyglottis stellata* Lodd. ex Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1831, −059.0240; alt. 40 m; 10 Jun. 2017; V. Klein 200 leg.; INPA 281018.

***Scuticaria steelei* (Hook.) Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1823, −059.0322 alt. 40 m; 28 Apr. 2017; V. Klein 133 leg.; INPA 280964.

***Sobralia bletiae* Rchb.f.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1872, −059.0316 alt. 40 m; 28 Jun. 2017; V. Klein 183 leg.; INPA 281005.

***Sobralia granitica* G.A.Romero & Carnevali**

Figure 7I

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1902, −059.0156 alt. 40 m; 8 Aug. 2016; V. Klein 48 leg.; INPA 280891 • ibid; −02.1805, −059.0221; 5 Aug. 2016; V. Klein 51 leg.; INPA 280894 • ibid; −02.1709, −059.0091; 15 Jun. 2017; V. Klein 145 leg.; INPA 281002.

Identification. Accidental epiphyte. Herb erect. Stem cylindrical, 64.8–150.5 × 0.3–0.5 cm. Leaves 9–16, distichous along the stem, lanceolate, plicate, 17.7–24.33 × 3.0–3.6 cm, acute apex. Inflorescence 5.5–21.4 cm long, terminal, in a raceme. Flowers 2–4, attractive, white; dorsal sepal 5.5–5.8 × 1.3–1.5 cm, oblong, attenuate apex; lateral sepals 5.3–5.5 × 1.1–1.3 cm, elliptical-falcate, obtuse apex; petals 5.3–5.5 × 1.0–1.2, elliptical, obtuse apex; lip 5.2–5.4 × 3.8–4.0 cm, discreetly trilobed to obovate, white with yellow veins, lateral lobes hugging the column. Fruits oblong, 4.8–5.3 × 1.7–2.2 cm.

Geographic distribution. Restricted to the Amazon basin. Occurs in South America (Brazil, Colombia, and Venezuela). In Brazil this species occurs in the North Region. (Flora do Brasil 2020; Govaerts et al. 2021).

Ecological and phenological information. This species is common in OSC. It is generally observed with terrestrial habit, but occasionally occurs as epiphyte in the lower parts (ZI and ZII) of the phorophytes. Observed with flowers and fruits between June and November.

***Specklinia picta* (Lindl.) Pridgeon & M.W.Chase**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1802, −059.0423 alt. 40 m; 11 Jan. 2018; V. Klein 254 leg.; INPA 281058.

***Trichosalpinx orbicularis* (Lindl.) Luer**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1752, −059.0333 alt. 40 m; 5 Nov. 2016; V. Klein 56 leg.; INPA 280895 • ibid; −02.1812, −059.0121; 17 Jun. 2017; V. Klein 163 leg.; INPA 280990.

***Vanilla bicolor* Lindl.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1822, −059.0356 alt. 40 m; 23 Apr. 2017; V. Klein 124 leg.; INPA 280959 • ibid; −02.1805, −059.0221; 25 Apr. 2017; V. Klein 129 leg.; INPA 280960.

Polypodiaceae J.Presl

***Cochlidium serrulatum* (Sw.) L.E.Bishop**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1862, −059.0100; alt. 40 m; 11 May 2019; V. Klein 303 leg.; INPA 286948 • ibid; −02.1906, −059.0190;25 Fev. 2020; V. Klein 398 leg.; INPA 289216.

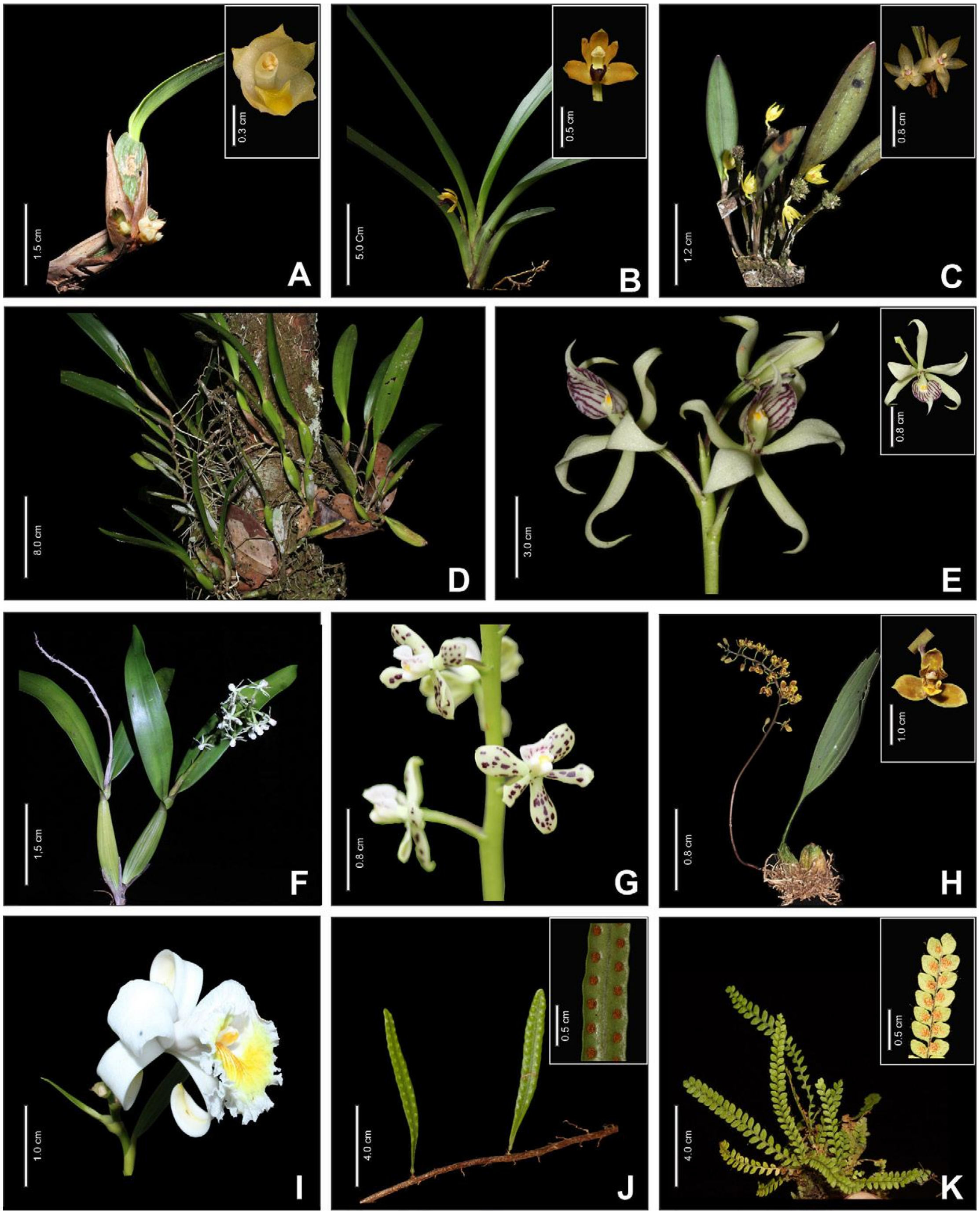

Figure 7. Species of vascular epiphytes with greater value of epiphytic importance (VEI) for the white-sand ecosystems of the Uatumã Sustainable Development Reserve. **A.** *Maxillaria parviflora*. **B.** *Maxillaria superflua*. **C.** *Octomeria surinamensis*. **D, E**. *Prosthechea aemula*. **F, G.** *Prosthechea crassilabia*. **H.** *Rudolfiella aurantiaca*. **I.** *Sobralia granitica*. **J.** *Microgramma baldwinii*. **K.** *Moranopteris nana*.

***Microgramma baldwinii* Brade**

Figure 7J

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1782, −059.0180; alt. 40 m; 5 May 2019; V. Klein 297 leg.; INPA 286943 • ibid; −02.1906, −059.0190; 7 Sep. 2019; V. Klein 332 leg.; INPA 286968.

Identification. Holoepiphyte. Herb pendant. Stem cylindrical, 80–250.0 × 0.15–0.25 cm, long-creeping stem, covered by light brown scale. Leaves 5–22, distichous along the stem; sterile leaves, elliptical, 3.3–5.2 × 0.5–1.1 cm, acute apex; fertile leaves lanceolate to linear, 4.0–6.2 × 0.3–0.8 cm, acute apex. Sori round, distributed in two linear rows, without indusium, printed on the leaf blade, leaving marks (scar) on the upper side of the leaf.

Geographic distribution. Amazon basin. Occurs in South America (Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, and Venezuela). In Brazil the species occurs in the North Region (Flora do Brasil 2020; Tropicos 2020).

Ecological and phenological information. The species is common in all local campinarana phytophysiognomies. Usually, the species is spread over the entire length of phorophytes, is common in ZII and ZIV regions. Observed in fertile stage between February and May.

***Moranopteris nana* (Fée) R.Y. Hirai & J. Prado**

Figure 7K

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1852, −059.0240; alt. 40 m;11 May 2019; V. Klein 304 leg.; INPA 286949.

Identification. Holoepiphyte. Herb erect. Stem cylindrical, 0.5–1.1 × 0.05–0.10 cm, covered by yellow-brown to orange-brown scales. Leaves 4–6, laminae linear, pinnatisect; 4.3–9.8 × 1.0–2.0. cm, acute apex; fertile leaves lanceolate to linear, 4.0–6.2 × 0.3–0.8 cm, acute apex. Sori one per segment, round, (0.5–)1.2–1.5 mm in diameter.

Geographic distribution. Neotropical. Widely distributed in the Central and South America. In Brazil the species occurs in the North, Northeast, and Central-West regions (Flora do Brasil 2020; Tropicos 2020).

Ecological and phenological information. This species occurs in moist areas of OFC and DFC. Usually grows in ZI region of the phorophytes. Observed in fertile stage between May and August.

Pleopeltis bombycina **(Maxon) A.R.Sm.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1852, −059.0240; alt. 40 m; 26 Nov. 2006; C.E. Zartman 6248 leg.; INPA 226324 • ibid; −02.1906, −059.0190; 20 May 2021; V. Klein 426 leg.; INPA289242.

Serpocaulon triseriale **(Sw.) A.R.Sm.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1845, −059.0234; alt. 40 m; 25 Feb 2020; V. Klein 393 leg.; INPA 289211.

Pteridaceae E.D.M.Kirchn.

Vittaria lineata **(L.) Sm.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1852, −059.0240; alt. 40 m; 20 Mar. 2007; C.E. Zartman 7064 leg.; INPA 226368 • ibid; −02.1906, −059.0190; 25 Feb. 2020; V. Klein 392 leg.; INPA289210.

Schizaeaceae Kaulf.

Actinostachys pennula **(Sw.) Hook.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1856, −059.0203; alt. 40 m; 16 Jul. 2017; V. Klein 169 leg.; INPA 286914.

Rubiaceae Juss.

Hillia illustris **(Vell.) K.Schum.**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Uatumã SDR; −02.1866, −059.0232; alt. 40 m; 12 Dec. 2016; L.O. Demarchi 1619 leg.; INPA 288699.

Urticaceae Juss.

***Coussapoa asperifolia* Trécul**

Material examined. BRAZIL • Amazonas, São Sebastião do Uatumã, Ramal da Morena; −01.9155, −059.4734; alt. 40 m; 3 Sep. 1987; F.D. Mattos 177 leg.; INPA 148153.

Discussion

Knowledge of the composition and distribution of species in Amazonian campinaranas has mainly focused on tree communities (e.g., Vicentini 2004; Fine and Kembel 2011; Stropp et al. 2011; García-Villacorta et al. 2016; Demarchi et al. 2018; Costa et al. 2020), while for vascular epiphytes, the numbers of studies are still relatively modest (Braga 1982; ter Steege and Cornelissen 1989; Gottsberger and Morawetz 1993; Coomes and Grubb 1996; Marí et al. 2016; Klein and Piedade 2019).

The campinaranas of the Uatumã SDR present remarkable variation in the structure of their vegetation, even within small distances, and form a set of physiognomies with differences in the richness and density of vascular epiphytes. The forested (OFC) and arboreal (OAC) campinarana areas present the most species and individuals of vascular epiphytes (Appendix Table A1). In these typologies, the tree communities are more diverse, and the trees have larger sizes (diameter and height) (Targhetta et al. 2015; Demarchi et al. in press). Structural variables of the trees, mainly related to the size and canopy area, are positively correlated with the increase in richness and abundance of epiphytes (Zotz and Vollrath 2003; Laube and Zotz 2007; Wang et al. 2016; Quaresma et al. 2017). The sum of the structural characteristics, together with a greater diversity of phorophytes, provides greater environmental heterogeneity and availability of new microhabitats, enabling the establishment of different epiphytic groups (Zotz and Vollrath 2003; Woods et al. 2015).

Another important factor to be considered is species adaptations. Differences in the occurrence of taxa among phytophysiognomies may reflect morphological, anatomical, and physiological adaptations that enable different groups to establish and occupy different micro-habitats without overlap (Agudelo et al. 2019). Some epiphytes (e.g., *Brassavola martiana*, *Epidendrum strobiliferum,* and *Tillandsia adpressiflora*) present carbon-fixation pathways of the crassulacean acid metabolism (CAM) type, which allows epiphytes to settle in environments with higher luminous incidence, such as the phytophysiognomies of OAC and OSC (Braga 1977a; Bonates and Braga 1992; Bonates 1993). On the other hand, species more sensitive to light and which undergo rapid desiccation (e.g., *Hymenophyllum polyanthos* and *Trichomanes humboldtii*) occurred more frequently in areas with higher humidity such as the DAC and DFC phytophysiognomies. Zuquim et al. (2012) observed that the composition of ferns in campinaranas show a strong correlation with the opening of the canopy. A similar pattern was reported by Daly et al. (2016), who highlighted that *Elaphoglossum discolor* and *Trichomanes bicorne* Hook were characteristic of campinaranas that undergo seasonal flooding, while other species (e.g., *Codonanthe carnosa* (Gardner) Hanst) are common in open campinaranas.

In addition to the vegetation structure (size, density, and composition of tree species) and species adaptations (morphological, anatomical, physiological, and ecological), other environmental and microclimatic characteristics may be associated with the distribution of species in these phytophysiognomies. Studies in different regions, report differences in species distribution as a function of light and moisture gradients hat vary at the forest–atmosphere interface (Johansson 1974; Krömer et al. 2007; Sporn et al. 2010; Marcusso et al. 2019). Similarly, Larrea and Wener (2010), when evaluating the distribution of the vascular epiphytes assemblage in environments with different canopy structure, attributed changes in species composition primarily to microclimate alterations towards higher levels of light and desiccation stress. Future studies relating environmental variables to the floristic and functional composition of vascular epiphytes are fundamental to elucidate the questions about the distribution patterns and occurrences of the species and the different phytososionamies of Amazonian campinaranas.

Our results revealed a high number of species (112 spp.) when compared to the quantitative studies carried out by ter Steege and Cornelissen (1989) in campinarana forests of Guyana (67 spp.), by Gottsberger and Morawetz (1993) in the southwest of the Brazilian Amazon (7 spp.), by Coomes and Grubb (1996) in campinaranas of Venezuela (12 spp.), and by Mari et al. (2016) in 36 focal *A. heterophylla* phorophytes in areas of campinarana of the central Amazon (68 spp.). Contrary to the studies mentioned above, in which the species were recorded only within the sample units (plots), we also carried out rambles throughout the area, which may explain the greater richness found. Kersten and Waechter (2011) reported that floristic sampling, even in a few sample units, is sufficient to evaluate the structural parameters of the communities, but they highlighted that the sampling of trees around the plots favors more accurate floristic lists and increases the chance of inclusion of rare species, besides bringing important biogeographic information. The quantitative results that we obtained corroborate the postulation of Kersten and Waechter (2011), since if we considered only the species in the plots (62 spp.), the richness of the vascular epiphytes of the campinaranas of the Uatumã SDR would be underestimated by approximately 45%.

Also of importance when comparing the species richness observed in the current study with other studies published for the Amazonian campinaranas is the structure of the analyzed vegetation. In the campinaranas studied by ter Steege and Cornelissen (1989), the trees reached heights of up to 30 m and there is a high density of individuals (500-600 ind/ha), but those authors emphasized that the vegetation is formed by a large proportion of small trees. Similarly, for the campinaranas analyzed in Venezuela, Coomes and Grubb (1996) also reported the absence of trees with diameter ≥30 cm and Gottsberger and Morawetz (1993) characterized their study area as being formed by isolated trees and grass savanna. Thus, substrate availability and phorophyte size can be a limiting factor for the occurrence of epiphyte species, since the colonization by epiphytes is positively correlated with phorophyte size and composition in local tree communities (Burns et al. 2010; Marcusso et al. 2019). Our results are closer to those observed by Mari et al. (2016), with 36 species shared between the studies. In addition to the geographical proximity of the areas, the campinaranas of Central Amazonia have different phytophysiognomies, ranging from open areas to forest formations, dominated by large trees, such as *Aldina heterophyla* that can reach diameters greater than 80 cm and is recognized as one of the main phorophytes for epiphytes in these environments (Mari et al. 2016; Klein and Piedade 2019).

The representativeness at family level follow the pattern described for the Neotropical regions (Gentry and Dodson 1987), with Orchidaceae, Bromeliaceae, and Araceae representing 80% of the species. This pattern is also widely reported for different Amazonian environments (Nieder et al. 2000; Benavides et al. 2011; Obummuler et al. 2011, 2014; Irume et al. 2013; Quaresma and Jardim 2013; Boelter et al. 2014; Quaresma et al. 2017, 2018) and includes campinarana environments (ter Steege and Cornelissen 1989; Mari et al. 2016). The selection of some characteristics, such as velamen-coated roots, water storage structures, a thick cuticle, an aquifer hypodermis, specialized stomata, and CAM metabolism, reflect adaptations that have enabled these families great success in colonizing the forest canopy (Dubuisson et al. 2009; Zotz 2016; Agudelo et al. 2019). This feat is so evident that the tropical regions of South America are considered the main center of diversification for several epiphyte lineages, especially for Bromeliaceae and Orchidaceae (e.g., Kreier et al. 2008; Mendoza et al. 2017; Pérez-Escobar et al. 2017).

Most of the vascular epiphytes recorded in this study (87%) have wide geographical distributions and occur in virtually all Neotropical humid lowlands around the Amazon basin. This broad pattern of distribution can be attributed to two main factors: the high ecophysiological plasticity (Ibisch et al. 1996; Kessler 2001; Fontoura and Santos 2010) and the high dispersal ability of the main groups (Tremblay 1997; Kessler 2001, 2002; Kreft et al. 2004; Küper et al. 2004; Acevedo et al. 2020). Nieder et al. (1999) highlighted that the extensive lowland plains of the Amazon (altitude <400 m) favor the long dispersion of propagules, which for most epiphytes is anemochoric, and which results in a flora with a low degree of heterogeneity. Although most epiphytes have wide distributions, campinaranas are recognized as being a habitat of an endemic and specialized flora (Fine et al. 2010; Fine and Kembel 2011; Fine and Baraloto 2016; Guevara et al. 2016). Among the species of epiphytes restricted to the campinaranas, we can highlight *Cattleya wallisii*, *Elaphoglossum discolor*, *Hylaeorchis petiolaris*, and *Sobralia granitica* (Flora do Brasil 2020).

A small number of species (6 spp.) was responsible for more than 70% of the recorded epiphyte abundance, while the majority of the species (47 spp.) can be considered "rare" locally, since they have an abundance of less than five individuals. The presence of few abundant species and many species with a low abundance of individuals is a recurrent pattern for epiphytic communities (Nieder et al. 2000; Kersten and Silva 2002; Quaresma et al. 2017). However, several species considered rare were recorded in the qualitative survey (outside the plots), which leads to the belief that the "rarity" for many species is only an artifact of sampling.

Prosthechea aemula stood out as the most abundant species (336 individuals), while *Brassavola martiana* colonized more phorophytes (28), which is a pattern similar to that shown for other Amazonian campinaranas (Braga 1977b; Mari et al. 2016). The high representativeness of these species may indicate that both have adaptations or functional traits that cause them to have greater success in the colonization of campinaranas. *P. aemula* allocates energy to rapid vegetative growth, constantly adding new pseudobulbs, which leads to the formation of large clusters of individuals on the phorophytes (Braga 1977b, 1981). The species also presents a set of phenological and floral characteristics, such as a resupinate lip and longitudinal striae, which act as nectar guides, and osmophores that release a strong aroma, which direct the floral visitor, thus resulting in greater reproductive success (Braga 1977b; Krahl 2020). For *B. martiana*, physiological adaptations that allow to alternate the pathway of atmospheric carbon fixation from C_3 to CAM during dry and hot periods are reported (Bonates and Braga 1992; Bonates 1993, 2007). The CAM metabolic pathway is associated with strategies for water conservation and confers advantages in environments that have periods of water stress (Lambers and Oliveira 2019). Crassa leaves, a thick cuticle and stomatal predominance in the abaxial epidenderm also enable *B. martiana* to withstand the water stress that is characteristic of the epiphytic habit and potentiated in campinarana environments, and may justify the wide local distribution of the species (Bonates 2007).

In recent years, the environments of campinarana have been undergoing increasing processes of fragmentation and suppression of vegetation (Ferreira et al. 2013; Adeney et al. 2016; Demarchi et al. 2019), which is extremely worrying considering the low resilience of these environments and the fact that they are poorly represented in conservation units (Capurucho et al. 2020). A continuous effort by researchers to catalog the diversity of the plants in these ecosystems is necessary, especially for the epiphytic flora, which is sensitive to minor environmental changes. Information on the local distribution patterns of taxa and issues involving the interaction of epiphytes with their respective phorophytes are key points to be considered in subsequent studies. A better understanding of the processes that structure the dynamics of plant communities in campinarana environments, including the epiphytic component, is essential in order to guide discussions and planning that have the aim of the conservation and preservation of the biodiversity of these fragile Amazonian environments.

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Authors' Contributions

Conceptualization: VPK, LOD, ACQ, MTFP. Data curation: VPK, LOD, ACQ. Formal analysis: VPK. Funding acquisition: ACQ, MTFP. Investigation: VPK, LOD, ACQ. Methodology: VPK, LOD. ACQ, JC. Project administration: VPK, ACQ, MTFP. Resources: ACQ, MTFP. Software: VPK, JC. Supervision; ACQ, MTFP. Validation; VPK, LOD, ACQ, JC, MTFP. Visualization: VPK, LOD, ACQ, JC, MTFP. Writing – original draft: VPK, LOD, ACQ, JC, MTFP. Writing – review & editing: VPK, LOD, ACQ, JC, MTFP.

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Appendix

Table A1. Vascular epiphytes flora in a white-sand ecosystem in Uatumã Sustainable Development Reserve. Ecological categories: Hol (characteristic epiphytes); Fac (Facultative epiphytes); Acc (accidental epiphyte) and Hem (hemiepiphytes). Types of campinaranas: **OSC** (Open Shrubby Campinarana); **DSC** (Dense Shrubby Campinarana); **OAC** (Open Arboreal Campinarana); **DAC** (Dense Arboreal Campinarana); **OFC** (Open Forested Campinarana) and **DFC** (Dense Forested Campinarana). Geographic distribution: (PAN) pantropical; (NEO) Neotropical; (BA) restricted to the Amazon basin; (EN) restricted to Brazil; (SA) Amazon basin + other Brazilian vegetations

Group/family/species	Life form	Types of campinarana	Geographic distribution	Voucher
FERNS				
Aspleniaceae				
Asplenium serratum L.	Hol	OFC	NEO	INPA 277951 286951
Dryopteridaceae				
Elaphoglossum discolor (Kuhn) C.Chr.	Hol	OFC DFC DAC	SA	INPA 286913
Elaphoglossum glabellum J.Sm.	Hol	OFC	NEO	INPA 286956 286957
Elaphoglossum obovatum Mickel	Hol	OFC DFC DAC	NEO	INPA 286945 286913
Elaphoglossum plumosum (Fée) T.Moore	Hol	OFC DFC DAC OAC	SA	INPA 286915 286944
Hymenophyllaceae				

Hymenophyllum polyanthos (Sw.) Sw.	Hol	OFC DFC DAC DSC	PAN	INPA 286950 286970
Trichomanes crispum L.	Hol	OFC DFC DAC	NEO	INPA 286946
Trichomanes humboldtii (Bosch) Lellinger	Fac	OFC DFC DAC DSC	BA	INPA 286947
Polypodiaceae				
Cochlidium serrulatum (Sw.) L.E.Bishop	Hol	OFC DFC	PAN	INPA 286948
Micrgramma baldwinii Brade	Hol	OFC DFC DAC OAC DSC OSC	BA	INPA 277937 286943
Moranopteris nana (Fée) R.Y. Hirai & J. Prado	Hol	OFC DFC	NEO	INPA 286949 87746
Pleopeltis bombycina (Maxon) A.R.Sm.	Hol	OFC DFC	NEO	INPA 87423 226324
Serpocaulon attenuatum (C. Presl) A.R. Sm.	Hol	OFC	NEO	INPA 10553
Pteridaceae				
Vittaria lineata (L.) Sm.	Hol	OFC	PAN	INPA 226368
Schizaeaceae				
Actinostachys pennula (Sw.) Hook.	Hol	OFC OAC	NEO	INPA 286914
ANGIOSPERMS				
Araceae				
Anthurium bonplandii Bunting	Hol	OFC OAC	BA	INPA

				286939 286940
Anthurium eminens Schott	Hem	OFC	NEO	INPA 277951
Anthurium gracile (Rudge) Lindl.	Hol	OFC DFC OAC OSC	NEO	INPA 286963 286983
Anthurium obtusum (Engl.) Grayum	Hol	OFC DFC	NEO	INPA 286912
Philodendron billietiae Croat	Hem	OFC	BA	INPA 241196
Philodendron distantilobum K.Krause	Hem	OFC OAC	BA	INPA 225245
Philodendron megalophyllum Schott	Hem	OFC	NEO	INPA 274318
Philodendron pulchrum G.M.Barroso	Hem	OFC DFC	NEO	INPA 192925
Thaumatophyllum spruceanum Schott	Hem	OFC	BA	MNHN 1750689
Bromeliaceae				
Aechmea beeriana L.B.Sm. & M.A.Spencer	Fac	OFC OAC	BA	INPA 288546
Aechmea bromeliifolia (Rudge) Baker	Fac	OFC OAC	NEO	INPA 87295 225305
Aechmea huebneri Harms	Fac	OFC OAC OSC DSC	NEO	INPA 288387
Aechmea longifolia (Rudge) L.B.Sm. & M.A.Spencer	Hol	OFC OAC	NEO	INPA 225296
Aechmea mertensii (G.Mey.) Schult. & Schult.f.	Hol	OFC OAC OSC	NEO	INPA

				288500 225303
Aechmea rodriguesiana (L.B.Sm.) L.B.Sm.	Hol	OFC	EN	INPA 178866
Aechmea setigera Mart. ex Schult. & Schult.f.	Fac	OFC OAC	NEO	INPA 87712
Araeococcus micranthus Brongn.	Hol	OFC OAC	NEO	INPA 288516
Billbergia violacea Bee	Hol	OFC	BA	INPA 127339
Bromelia grandiflora Mez	Acc	OFC OAC	EN	IAN 83619
Neoregelia eleutheropetala (Ule) L.B.Sm.	Hol	OFC	NEO	INPA 207064
Tillandsia adpressiflora Mez	Hol	OFC DFC DAC OAC DSC OSC	BA	INPA 287405
Tillandsia bulbosa Hook.f.	Hol	OFC	NEO	INPA 278025 288695
Cactaceae				
Epiphyllum phyllanthus (L.) Haw.	Hol	OFC	NEO	INPA 87667
Clusiaceae				
Clusia insignis Mart.	Hem	OFC DFC OAC DAC	NEO	INPA 274278
Clusia nemorosa G.Mey.	Hem	OFC DFC OAC	NEO	INPA 151875 274269
Cyclanthaceae				
Ludovia lancifolia Brongn.	Hol	OFC	NEO	INPA

				288684
Gesneriaceae				
Codonanthopsis crassifolia (H. Focke) Chautems & Mat. Perret	Hol	OFC DFC OAC OSC	NEO	INPA 286982
Codonanthopsis ulei Mansf.	Hol	OFC	BA	INPA 277928
Moraceae				
Ficus mathewsii (Miq.) Miq.	Hem	OFC	NEO	INPA 272956
Orchidaceae				
Acianthera discophylla Luer & Carneval	Hol	DAC	BA	INPA 280994
Acianthera fockei (Lindl.) Pridgeon & M.W.Chase	Hol	OFC OAC	BA	INPA 280908 280927
Acianthera miqueliana (H.Focke) Pridgeon & M.W.Chase	Hol	OFC	BA	INPA 280909
Aganisia fimbriata Rchb.f.	Hol	OFC	BA	INPA 286917
Batemannia colleyi Lindl.	Hol	OFC	BA	INPA 280962
Bifrenaria longicornis Lindl.	Hol	OFC OAC	BA	INPA 280944 280981
Brassavola martiana Lindl.	Hol	OFC DFC DAC OAC DSC OSC	BA	INPA 280932 281023
Bulbophyllum setigerum Lindl.	Hol	DAC	BA	INPA 280985
Campylocentrum fasciola (Lindl.) Cogn.	Hol	OAC	NEO	INPA 286980

Catasetum discolor (Lindl.) Lindl	Hol	OFC DFC OAC	BA	INPA 280947 280965
Catasetum rivularium Barb.Rodr.	Hol	OFC	BA	INPA 284797 284801
Catasetum tigrinum Rchb.f.	Hol	DFC	EN	INPA 195192
Cattleya wallisii (Linden) Linden ex Rchb.f	Hol	OFC OAC	EN	INPA 280907
Caularthron bicornutum (Hook.) Raf.	Hol	OFC OAC	NEO	INPA 280896
Dichaea anchoraelabia C.Schweinf.	Hol	OFC	BA	INPA 280951
Dichaea picta Rchb.f.	Hol	OFC OAC	BA	INPA 280946 281063
Encyclia chloroleuca (Hook.) Neumann	Hol	OFC	NEO	INPA 281046
Encyclia conchaechila Barb.Rodr.) Porto & Brade	Hol	DSC	BA	INPA 280910 281021
Encyclia mapuerae (Huber) Brade & Pabst	Fac	OSC OAC	BA	INPA 280903 281022
Epidendrum apuahuense Mansf.	Hol	OFC DAC	BA	INPA 278517 278519
Epidendrum bahiense Rchb.f.	Hol	OFC OAC DSC OSC	NEO	INPA 280889

				280952
Epidendrum carpophorum Barb.Rodr.	Hol	OFC OAC	NEO	INPA 280952 280969
Epidendrum compressum Griseb.	Hol	OFC	NEO	INPA 281051 281059
Epidendrum micronocturnum Carnevali & G.A.Romero	Hol	OFC OAC DAC DSC	BA	INPA 280957 280968
Epidendrum microphyllum Lindl.	Hol	OFC OAC	NEO	INPA 280942
Epidendrum orchidiflorum (Salzm.) Lindl.	Acc	OAC OSC	SA	INPA 280912
Epidendrum rigidum Jacq.	Hol	OAC	NEO	INPA 280950 280953
Epidendrum sculptum Rchb.f.	Hol	OFC OAC	NEO	INPA 280966 281048
Epidendrum strobiliferum Rchb.f.	Hol	OFC DFC OAC OSC	NEO	INPA 280954 281067
Eriopsis sceptrum Rchb.f. & Warsz.	Hol	OFC	BA	INPA 45915
Jacquiniella globosa Schltr.	Hol	OAC OSC	NEO	INPA 280958
*Hylaeorchis petiolaris (*Schltr.) Carnevali & G.A.Romero	Hol	OFC CAD	BA	INPA 280943 280992

Madisonia kerrii Luer	Hol	OFC	BA	INPA 280977
Maxillaria brasiliensis Brieger & Illg	Hol	OFC	EN	INPA 280961
Maxillaria camaridii Rchb.f.	Hol	OFC DFC OAC	NEO	INPA 280939
Maxillaria crassifolia (Lindl.) Rchb.f.	Hol	OFC OAC	NEO	INPA 280940
Maxillaria desvauxiana Rchb.f.	Hol	OFC	NEO	INPA 280917 280974
Maxillaria kegelii Rchb.f.	Hol	OFC	BA	INPA 280949 281057
Maxillaria parviflora (Poepp. & Endl.) Garay	Hol	OFC DFC OAC	NEO	INPA 280893 281020
Maxillaria superflua Rchb.f.	Hol	OFC DFC OAC DAC	NEO	INPA 280963 280938
Maxillaria tenuis C.Schweinf.	Hol	OFC	BA	INPA 280929
Maxillaria violaceopunctata Rchb.f.	Hol	OFC	NEO	INPA 280936
Notylia aromatica Barker ex Lindl.	Hol	OFC	BA	INPA 281052 281053
Octomeria erosilabia C.Schweinf.	Hol	OFC DFC OAC	BA	INPA 280948 281003

Octomeria grandiflora Lindl.	Hol	OFC DFC OAC	NEO	INPA 280919 280978
Octomeria sagittata (Rchb.f.) Garay	Hol	OFC	EN	INPA 280955
Octomeria scirpoidea (Poepp. & Endl.) Rchb.f.	Hol	OAC DAC	NEO	INPA 281004 280975
Octomeria taracuana Schltr.	Hol	DAC	BA	INPA 280935
Octomeria yauaperyensis Barb.Rodr.	Hol	DAC	BA	INPA 281006 281028
Orleanesia amazonica Barb.Rodr.	Hol	OAC	BA	INPA 280898
Pabstiella yauaperyensis (Barb.Rodr.) F.Barros	Hol	OFC	BA	INPA 281064 281054
Polystachya concreta (Jacq.) Garay & Sweet	Hol	OFC OAC	NEO	INPA 281049 280983
Polystachya stenophylla Schltr.	Hol	OFC OAC	BA	INPA 280915 281068
Prosthechea aemula W.E.Higgins	Hol	OFC DFC OAC DAC OSC DSC	NEO	INPA 280918 280967
Prosthechea crassilabia (Poepp. & Endl.) Carnevali & I.Ramírez	Hol	OFC OAC	SA	INPA 280892 280890

Quekettia microscopica Lindl.	Hol	OFC	BA	INPA 281055
Rudolfiella aurantiaca (Lindl.) Hoehne	Hol	OFC OAC	BA	INPA 274324 286920
Scaphyglottis reflexa Lindl.	Hol	OFC	NEO	INPA 280913 280991
Scaphyglottis sickii Pabst	Hol	OAC OSC	NEO	INPA 280973 281047
Scaphyglottis stellata Lodd. ex Lindl.	Hol	OFC OAC	NEO	INPA 281018
Scuticaria steelei (Hook.) Lindl.	Hol	OFC	BA	INPA 280964
Sobralia bletiae Rchb.f.	Hol	OFC	NEO	INPA 281005
Sobralia granitica G.A.Romero & Carnevali	Acc	OAC OSC	BA	INPA 280891 280894
Specklinia picta (Lindl.) Pridgeon & M.W.Chase	Hol	OFC OAC	NEO	INPA 280951 281058
Trichosalpinx orbicularis (Lindl.) Luer	Hol	OFC OAC	NEO	INPA 280899 280990
Vanilla bicolor Lindl.	Hemi	DFC	NEO	INPA 280959 280960
Rubiaceae				

Hillia illustris (Vell.) K.Schum.	Acc	OFC	NEO	INPA 288699
Urticaceae				
Coussapoa asperifolia Trécul	Hemi	OFC	NEO	INPA 148153

CAPÍTULO 5

Viviane Pagnussat Klein, Layon Oreste Demarchi, Adriano Costa Quaresma, Talitha Mayumi Francisco e Maria Teresa Fernandez Piedade. **Vascular epiphytes of white sand ecosystem "campinarana".** Guia Submetido e em revisão na plataforma eletrônica Field Guides.

Apresentação

Guias fotográficos são ferramentas de inestimável valor, tanto para taxonomistas e pesquisadores, quanto para aqueles que necessitam de auxílio na identificação das espécies. Os guias agregram importantes informações taxonômicas e registros fotográficos que permitem ao leitor uma identificação mais rápida e precisa a respeito das espécies presentes em determinado ambiente. Nesse sentido, a plataforma de guias “Field Guides” (https://fieldguides.fieldmuseum.org/) tem contribuído muito para divulgação e disponibilização de guias de inúmeros grupos biológicos de várias localidades de todo o mundo.

Este guia fotográfico tem como objetivo auxiliar a identificação de epífitas vasculares ocorrentes nos ecossistemas de areia branca (campinaranas) da Amazônia central. As espécies foram coletadas, identificadas e encontram-se depositadas no herbário do Instituto Nacional de Pesquisas da Amazônia. As espécies aqui representadas foram amostradas durante as expedições de campo realizadas pelos autores deste trabalho em cinco áreas de campinaranas. O guia conta com registros de 134 espécies de epífitas vasculares e encontra-se em revisão pela equipe técnica da plataforma Field Guides.

Registros de espécies como, *Bulbophyllum setigerum* Lindl. (Orchidaceae), *Codonanthopsis dissimulata* (H.E. Moore) Wiehler (Gesneriaceae), *Macroclinium mirabile* (C. Schweinf.) Dodson (Orchidaceae), *Madisonia kerrii* (Braga) Luer (Orchidaceae), *Mezobromelia pleiosticha* (Griseb.) Utley & H.Luther (Bromeliaceae) e *Hecistopteris pumila* (Spreng.) J.Sm. (Pteridaceae) são muito importantes uma vez que essas plantas são de difícil coleta e contam atualmente com pouquíssimos registros fotográficos e registros em herbário. Registro de plantas comuns, como *Codonanthopsis crassifolia* (H. Focke) Chautems & Mat. Perret (Gesneriaceae), permitem observar a grande variabilidade fenotípica dentro do grupo. Além disto, registros de espécies, como *Epidendrum apuahuense* Mansf. (Orchidaceae), o qual foi recentemente redescoberto e neotipificado, permitem uma maior divulgação e conhecimento dos padrões de distribuição de espécies pouco conhecidas (Klein et al. 2019).

Vascular epiphytes of white-sand ecosystems “*campinaranas*” of the Central Amazonia

2

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16
Aechmea longifolia
BROMELIACEAE

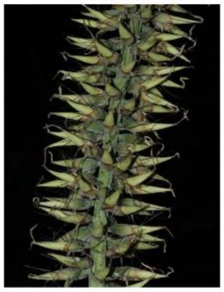

17
Aechmea longifolia
BROMELIACEAE


18
Aechmea mertensii
BROMELIACEAE


19
Aechmea mertensii
BROMELIACEAE


20
Aechmea rodriguesiana
BROMELIACEAE


21
Aechmea setigera
BROMELIACEAE


22
Aechmea setigera
BROMELIACEAE


23
Aechmea vallerandii
BROMELIACEAE


24
Aechmea vallerandii
BROMELIACEAE


25
Araeococcus micranthus
BROMELIACEAE


26
Araeococcus micranthus
BROMELIACEAE


27
Billbergia violacea
BROMELIACEAE


28
Billbergia violacea
BROMELIACEAE


29
Guzmania brasiliensis
BROMELIACEAE


30
Guzmania brasiliensis
BROMELIACEAE

Vascular epiphytes of white-sand ecosystems “*campinaranas*” of the Central Amazonia

3

Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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31
Mezobromelia pleiosticha
BROMELIACEAE

32
Mezobromelia pleiosticha
BROMELIACEAE

33
Neoregelia eleutheropetala
BROMELIACEAE

34
Neoregelia eleutheropetala
BROMELIACEAE

35
Tillandsia adpressiflora
BROMELIACEAE

36
Tillandsia adpressiflora
BROMELIACEAE

37
Tillandsia adpressiflora
BROMELIACEAE

38
Tillandsia bulbosa
BROMELIACEAE

39
Tillandsia bulbosa
BROMELIACEAE

40
Apteria aphylla
BURMANNIACEAE

41
Epiphyllum phyllanthus
CACTACEAE

42
Epiphyllum phyllanthus
CACTACEAE

43
Clusia insignis
CLUSIACEAE

44
Clusia insignis
CLUSIACEAE

45
Clusia nemorosa
CLUSIACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

4

Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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46
Clusia nemorosa
CLUSIACEAE


47
Ludovia lancifolia
CYCLANTHACEAE


48
Ludovia lancifolia
CYCLANTHACEAE


49
Ludovia lancifolia
CYCLANTHACEAE


50
Elaphoglossum discolor
DRYOPTERIDACEAE


51
Elaphoglossum discolor
DRYOPTERIDACEAE


52
Elaphoglossum glabellum
DRYOPTERIDACEAE


53
Elaphoglossum glabellum
DRYOPTERIDACEAE


54
Elaphoglossum obovatum
DRYOPTERIDACEAE


55
Elaphoglossum obovatum
DRYOPTERIDACEAE


56
Elaphoglossum plumosum
DRYOPTERIDACEAE


57
Elaphoglossum plumosum
DRYOPTERIDACEAE


58
Elaphoglossum raywaense
DRYOPTERIDACEAE


59
Codonanthopsis crassifolia
GESNERIACEAE


60
Codonanthopsis crassifolia
GESNERIACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

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Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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61
Codonanthopsis crassifolia
GESNERIACEAE

62
Codonanthopsis dissimulata
GESNERIACEAE

63
Codonanthopsis dissimulata
GESNERIACEAE

64
Codonanthopsis ulei
GESNERIACEAE

65
Codonanthopsis ulei
GESNERIACEAE

66
Hymenophyllum polyanthos
HYMENOPHYLLACEAE

67
Trichomanes crispum
HYMENOPHYLLACEAE

68
Trichomanes martiusii
HYMENOPHYLLACEAE

69
Trichomanes spruceanum
HYMENOPHYLLACEAE

70
Trichomanes spruceanum
HYMENOPHYLLACEAE

71
Lindsaea lancea
LINDSAEACEAE

72
Ficus mathewsii
MORACEAE

73
Nephrolepis rivularis
NEPHROLEPIDACEAE

74
Acianthera discophylla
ORCHIDACEAE

75
Acianthera fockei
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems “*campinaranas*” of the Central Amazonia

6

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76
Acianthera miqueliana
ORCHIDACEAE


77
Acianthera miqueliana
ORCHIDACEAE


78
Aganisia fimbriata
ORCHIDACEAE


79
Aganisia fimbriata
ORCHIDACEAE


80
Batemannia colleyi
ORCHIDACEAE


81
Bifrenaria longicornis
ORCHIDACEAE


82
Bifrenaria longicornis
ORCHIDACEAE


83
Bifrenaria venezuelana
ORCHIDACEAE


84
Brassavola martiana
ORCHIDACEAE


85
Brassavola martiana
ORCHIDACEAE


86
Brassavola martiana
ORCHIDACEAE


87
Bulbophyllum setigerum
ORCHIDACEAE


88
Bulbophyllum setigerum
ORCHIDACEAE


89
Campylocentrum fasciola
ORCHIDACEAE


90
Catasetum ciliatum
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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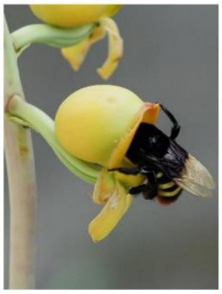
91
Catasetum ciliatum
ORCHIDACEAE


92
Catasetum ciliatum
ORCHIDACEAE


93
Catasetum rivularium
ORCHIDACEAE


94
Catasetum rivularium
ORCHIDACEAE


95
Catasetum tigrinum
ORCHIDACEAE


96
Catasetum tigrinum
ORCHIDACEAE


97
Cattleya wallisii
ORCHIDACEAE


98
Caularthron bicornutum
ORCHIDACEAE


99
Caularthron bicornutum
ORCHIDACEAE


100
Dichaea anchoraelabia
ORCHIDACEAE


101
Dichaea picta
ORCHIDACEAE


102
Encyclia chloroleuca
ORCHIDACEAE


103
Encyclia conchaechila
ORCHIDACEAE


104
Encyclia conchaechila
ORCHIDACEAE


105
Encyclia mapuerae
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

8

Viviane Pagnussat Klein[1,2], **Layon Oreste Demarchi**[1,2], **Adriano Costa Quaresma**[3], **Maria Teresa Fernandez Piedade**[1]
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106
Encyclia mapuerae
ORCHIDACEAE

107
Epidendrum apuahuense
ORCHIDACEAE

108
Epidendrum apuahuense
ORCHIDACEAE

109
Epidendrum bahiense
ORCHIDACEAE

110
Epidendrum carpophorum
ORCHIDACEAE

111
Epidendrum carpophorum
ORCHIDACEAE

112
Epidendrum compressum
ORCHIDACEAE

113
Epidendrum compressum
ORCHIDACEAE

114
Epidendrum micronocturnum
ORCHIDACEAE

115
Epidendrum micronocturnum
ORCHIDACEAE

116
Epidendrum microphyllum
ORCHIDACEAE

117
Epidendrum orchidiflorum
ORCHIDACEAE

118
Epidendrum orchidiflorum
ORCHIDACEAE

119
Epidendrum rigidum
ORCHIDACEAE

120
Epidendrum schlechterianum
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

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Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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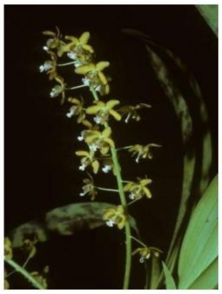
121
Epidendrum schlechterianum
ORCHIDACEAE


122
Epidendrum sculptum
ORCHIDACEAE


123
Epidendrum sculptum
ORCHIDACEAE


124
Epidendrum strobiliferum
ORCHIDACEAE


125
Epidendrum strobiliferum
ORCHIDACEAE


126
Eriopsis sceptrum
ORCHIDACEAE


127
Jacquiniella globosa
ORCHIDACEAE


128
Hylaeorchis petiolaris
ORCHIDACEAE

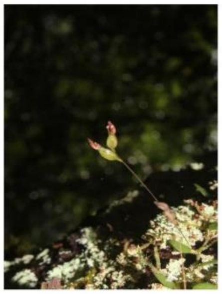

129
Hylaeorchis petiolaris
ORCHIDACEAE


130
Macroclinium mirabile
ORCHIDACEAE


131
Macroclinium mirabile
ORCHIDACEAE


132
Macroclinium mirabile
ORCHIDACEAE


133
Madisonia kerrii
ORCHIDACEAE


134
Madisonia kerrii
ORCHIDACEAE


135
Maxillaria brasiliensis
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

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Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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136
Maxillaria brasiliensis
ORCHIDACEAE


137
Maxillaria brasiliensis
ORCHIDACEAE


138
Maxillaria crassifolia
ORCHIDACEAE


139
Maxillaria crassifolia
ORCHIDACEAE


140
Maxillaria desvauxiana
ORCHIDACEAE


141
Maxillaria desvauxiana
ORCHIDACEAE


142
Maxillaria kegelii
ORCHIDACEAE


143
Maxillaria kegelii
ORCHIDACEAE


144
Maxillaria lutescens
ORCHIDACEAE


145
Maxillaria lutescens
ORCHIDACEAE


146
Maxillaria parviflora
ORCHIDACEAE


147
Maxillaria pendens
ORCHIDACEAE


148
Maxillaria pendens
ORCHIDACEAE


149
Maxillaria obtusa
ORCHIDACEAE


150
Maxillaria obtusa
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems “*campinaranas*” of the Central Amazonia 11

Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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151
Maxillaria obtusa
ORCHIDACEAE


152
Maxillaria subrepens
ORCHIDACEAE


153
Maxillaria subrepens
ORCHIDACEAE


154
Maxillaria superflua
ORCHIDACEAE


155
Maxillaria superflua
ORCHIDACEAE


156
Maxillaria tenui
ORCHIDACEAE


157
Maxillaria violaceopunctata
ORCHIDACEAE


158
Maxillaria violaceopunctata
ORCHIDACEAE


159
Maxillaria uncata
ORCHIDACEAE


160
Maxillaria uncata
ORCHIDACEAE


161
Notylia aromática
ORCHIDACEAE


162
Notylia aromatica
ORCHIDACEAE


163
Octomeria erosilabia
ORCHIDACEAE


164
Octomeria erosilabia
ORCHIDACEAE


165
Octomeria grandiflora
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems “*campinaranas*” of the Central Amazonia

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Viviane Pagnussat Klein[1,2], **Layon Oreste Demarchi**[1,2], **Adriano Costa Quaresma**[3], **Maria Teresa Fernandez Piedade**[1]
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166
Octomeria grandiflora
ORCHIDACEAE


167
Octomeria grandiflora
ORCHIDACEAE


168
Octomeria sagittata
ORCHIDACEAE


169
Octomeria sagittata
ORCHIDACEAE


170
Octomeria scirpoidea
ORCHIDACEAE


171
Octomeria scirpoidea
ORCHIDACEAE


172
Octomeria taracuana
ORCHIDACEAE


173
Octomeria yauaperyensis
ORCHIDACEAE


174
Orleanesia amazonica
ORCHIDACEAE


175
Orleanesia amazonica
ORCHIDACEAE


176
Pabstiella yauaperyensis
ORCHIDACEAE


177
Pabstiella yauaperyensis
ORCHIDACEAE


178
Polystachya concreta
ORCHIDACEAE


179
Polystachya concreta
ORCHIDACEAE


180
Polystachya foliosa
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia 13

Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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181
Polystachya foliosa
ORCHIDACEAE


182
Prosthechea aemula
ORCHIDACEAE


183
Prosthechea aemula
ORCHIDACEAE


184
Prosthechea aemula
ORCHIDACEAE


185
Prosthechea crassilabia
ORCHIDACEAE


186
Prosthechea crassilabia
ORCHIDACEAE


187
Quekettia microscopica
ORCHIDACEAE


188
Rodriguezia lanceolata
ORCHIDACEAE

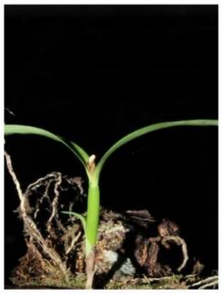

189
Rudolfiella aurantiaca
ORCHIDACEAE


190
Rudolfiella aurantiaca
ORCHIDACEAE


191
Scaphyglottis reflexa
ORCHIDACEAE


192
Scaphyglottis reflexa
ORCHIDACEAE


193
Scaphyglottis reflexa
ORCHIDACEAE


194
Scaphyglottis sickii
ORCHIDACEAE


195
Scaphyglottis sickii
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia 14

Viviane Pagnussat Klein[1,2], Layon Oreste Demarchi[1,2], Adriano Costa Quaresma[3], Maria Teresa Fernandez Piedade[1]
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196
Scaphyglottis stellata
ORCHIDACEAE


197
Scaphyglottis stellata
ORCHIDACEAE


198
Scuticaria steelei
ORCHIDACEAE


199
Scuticaria steelei
ORCHIDACEAE


200
Sobralia bletiae
ORCHIDACEAE


201
Sobralia bletiae
ORCHIDACEAE


202
Sobralia granitica
ORCHIDACEAE


203
Sobralia granitica
ORCHIDACEAE


204
Sobralia sessilis
ORCHIDACEAE


205
Sobralia sessilis
ORCHIDACEAE


206
Sobralia sessilis
ORCHIDACEAE


207
Specklinia picta
ORCHIDACEAE


208
Specklinia picta
ORCHIDACEAE


209
Trichocentrum recurvum
ORCHIDACEAE


210
Trichocentrum recurvum
ORCHIDACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

15

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Photos: Viviane Klein and Layon O. Demarchi. Produced by the authors. Support: CNPq and FAPEAM fellowship; Program PELD – MAUA (MCTIC/CNPq/FAPs-GN: 441590/2016-0). Acknowledgments: Amazonas Environmental State Secretary (SEMA) and the bilateral project Amazon Tall Tower Observatory (ATTO).
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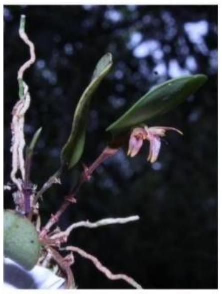
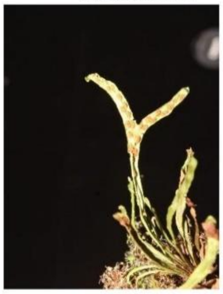
211
Trichosalpinx orbicularis
ORCHIDACEAE


212
Trichosalpinx orbicularis
ORCHIDACEAE


213
Trichosalpinx orbicularis
ORCHIDACEAE


214
Vanilla bicolor
ORCHIDACEAE


215
Vanilla bicolor
ORCHIDACEAE


216
Cochlidium furcatum
POLYPODIACEAE


217
Cochlidium pumilum
POLYPODIACEA

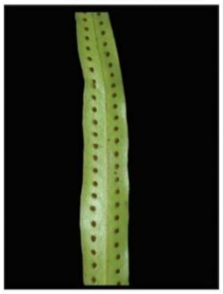

218
Cochlidium serrulatum
POLYPODIACEAE


219
Cochlidium serrulatum
POLYPODIACEAE


220
Microgramma baldwinii
POLYPODIACEAE


221
Microgramma baldwinii
POLYPODIACEAE


222
Microgramma percussa
POLYPODIACEAE


223
Microgramma percussa
POLYPODIACEAE


224
Moranopteris nana
POLYPODIACEAE


225
Moranopteris nana
POLYPODIACEAE

Vascular epiphytes of white-sand ecosystems “*campinaranas*” of the Central Amazonia

16

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226
Pleopeltis bombycina
POLYPODIACEAE


227
Pleopeltis bombycina
POLYPODIACEAE


228
Pleopeltis hirsutissima
POLYPODIACEAE


229
Pleopeltis hirsutissima
POLYPODIACEAE


230
Serpocaulon sessilifolium
POLYPODIACEAE


231
Serpocaulon sessilifolium
POLYPODIACEAE


232
Hecistopteris pumila
PTERIDACEAE


233
Vittaria lineata
PTERIDACEAE


234
Vittaria lineata
PTERIDACEAE


235
Hillia illustris
RUBIACEAE


236
Hillia illustris
RUBIACEAE


237
Hillia illustris
RUBIACEAE


238
Actinostachys pennula
SCHIZAEACEAE


239
Actinostachys pennula
SCHIZAEACEAE


240
Coussapoa asperifolia
URTICACEAE

Vascular epiphytes of white-sand ecosystems "*campinaranas*" of the Central Amazonia

17

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241 General characteristics of the Amazon *campinaranas*

242 Phorophyte *Aldina heterophylla* with large amount of vascular epiphytes

243 Clusters of vascular epiphytes on phorophytes in *campinaranas*

244 Diversity of vascular epiphytes on phorophytes

White sand ecosystems, "*campinaranas*", are distributed over approximately 5% of the Amazon region. In regions of the Upper Rio Negro these formations occupy large and continuous areas of land, while in the rest of the basin they occur as small islands surrounded by other forest types, mainly by *terra firme* forests. These environments are characterized by having sandy, oligotrophic soils that are extremely poor in nutrients, which results in highly adapted vegetation, with many endemic taxa (photo 241). Vascular epiphytes are one of the most representative and abundant plant components of these ecosystems. A large number of tree species are phorophytes for epiphytes in these environments, however, the species *Aldina heterophylla* (Fabaceae, photo 242) stands out for hosting greater abundance and species richness of epiphytes than any other species. Large clusters of species can be observed on this phorophyte (photos 243 and 244).

Special thanks to the taxonomists who helped with identification in specific families and groups: Edlley Pessoa, Mario Blanco and Amauri Krahl (Orchidaceae), Lourdes Soares and Mariana Irume (Araceae), Alain Chautems (Gesneriaceae), Gabriela Zuquim and Thaís Elias (Ferns), Matheus Nogueira (Bromeliaceae). And also to parataxonom José Ferreira Ramos for helping with identification and to Kleuto Moraes for helping with collections. We also thank the technicians Valdeney Araújo, Elizabeth Rebouças, Celso Rabelo and the ATTO project team for their help with logistics and field support.

SÍNTESE GERAL

O presente estudo foi realizado com um intenso esforço de campo, e traz importantes informações sobre a riqueza, abundância, diversidade e composição das comunidades de epífitas vasculares presentes nos ecossistemas de areia branca (campinaranas) da Amazônia central. O uso de diferentes abordagens estatísticas nos permitiu testar hipóteses sobre a distribuição das comunidades de epífitas vasculares, e relacionar os padrões observados com variáveis ambientais e estruturais da vegetação. Este estudo é também pioneiro em utilizar as abordagens de redes ecológicas complexas para avaliar a estrutura e organização das interações entre epífitas e forófitos na Amazônia, e testar a estabilidade das interações a perturbações ambientais.

Nossos resultados revelaram que os ecossistemas de areia branca da Amazônia central reúnem uma considerável riqueza e abundância epifítica, além de espécies endêmicas e raras. Observamos no capítulo 1 que a composição das espécies de epífitas difere entre as áreas estudadas, mesmo que próximas geograficamente, e que características intrínsecas das áreas como tamanho, distância dos ambientes florestais adjacentes e a estrutura da vegetação (área basal e altura média do dossel) influenciam a composição das espécies presentes em cada área estudada. Os resultados do capítulo 2, nos indicam que as características dos forófitos, como a altura, o diâmetro e a identidade taxonômica são os melhores preditores para prever a distribuição horizontal e vertical das epífitas nestes ambientes. Ao testarmos como as epífitas se distribuem no gradiente vertical, utilizando as zonas ecológicas propostas Johansson (1974), pudemos detectar diferenças significativas na riqueza, abundância de indivíduos e composição de espécies entre as regiões da copa e do fuste dos forófitos, indicando um padrão de estratificação e de modularidade. No capítulo 3, nossos resultados mostram que as interações epífitas-forófitos possuem uma estrutura aninhada, com baixa especialização e baixa modularidade, o que significa que a maioria das espécies de epífitas é generalista interagindo com a maioria das espécies de forófitos. Neste capítulo também simulamos a perda de forófitos altamente conectados às epífitas para testar a estabilidade do sistema às perturbações ambientais. Assim, pudemos constatar que os ecossistemas de areia branca da Amazônia central são frágeis e apresentam baixa robustez às alterações ambientais, e que a retirada de apenas uma espécie de forófito generalista, *Aldina heterophylla,* pode ocasionar a extinção secundária de aproximadamente 25% das espécies de epífitas vasculares. No capítulo 4, apresentamos um checklist e descrevemos detalhadamente como se distribuem as comunidades de epífitas vasculares em uma das áreas de estudo, a Reserva do Desenvolvimento Sustentável do Uatumã. Também, analisamos parâmetros estruturais e identificamos e discutimos as espécies com maior valor de importância epifítica para essa área. Outro importante resultado deste capítulo, foi verificar que a distribuição das epífitas vasculares difere entre as distintas fitofisionomias de areia branca presentes nessa mesma campinarana; provavelmente estas diferenças estão relacionadas ao fato que a estrutura e composição das espécies arbóreas variam em relação à profundidade do lençol freático. Por fim, no capítulo 5, utilizamos 225 registros fotográficos de 134 espécies de epífitas vasculares para construir um guia de campo para auxilar na identificação desse grupo de espécies nos ecossistemas de areia branca (campinaranas) da Amazônia central. Este guia é uma importante contribuição para aumentar o conhecimento botânico das espécies presentes nestes ecossistemas.

Com este acúmulo de informações sobre a diversidade, estrutura, composição e distribuição de epífitas vasculares em ambientes de areia branca da Amazônia Central, acreditamos ter contribuído para aumentar o conhecimento a respeito da flora epifítica e dos padrões que estruturam a composição de espécies e as interações epífitas-forófitos nestes ambientes. Considerando que em anos recentes as ações antrópicas exploratórias têm se intensificado sobre estes frágeis ecossistermas, esperamos que os resultados contidos neste trabalho possam também contribuir para a tomada de decisões sobre conservação da biodiversidade dessas áreas e seus múltiplos componentes vegetais.

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