

**INTERAÇÕES PLANTA-POLINIZADOR EM ECOSISTEMAS DE
VEREDAS: DE OFERTA DE RECURSOS FLORAIS PARA A
COMUNIDADE À REDE DE INTERAÇÕES DE PALMEIRAS-CHAVE**

Andressa Laís Lacerda Luna

Montes Claros - MG
Fevereiro - 2024

Mestranda: Andressa Laís Lacerda Luna

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Dissertação apresentada à Universidade Estadual de Montes Claros como parte das exigências do Curso de Mestrado Acadêmico em Botânica Aplicada, área de concentração em Botânica Aplicada para a obtenção do título de Mestre.

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APROVADA em 28 de fevereiro de 2024.

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Orientadora

Montes Claros - MG
Fevereiro - 2024

AGRADECIMENTOS

Em primeiro lugar a Deus por ter concedido que eu pudesse alcançar os objetivos nessa jornada e ter me oferecido muito mais do que eu desejei. Sem Ele e a interseção da virgem Maria nenhuma graça teria sido alcançada e eu não teria forças diante das dificuldades, sem a Tua infinita bondade não sou capaz de superar todas as adversidades.

A minha família, os meus pais Eulisete Luna e Izildinha Luna, meu irmão João Eduardo Luna e minha avó Iracema Brito, por tanto amor, dedicação, esforço e incentivo para que eu pudesse ir em busca dos meus objetivos e chegar até aqui. Agradeço por serem meu suporte, meu direcionamento e o meu maior exemplo em todos os momentos, por me encorajarem quando eu desanimei diante das dificuldades. Em todos os pequenos detalhes eu vejo o cuidado de vocês!

Ao meu noivo e companheiro de vida, Pedro Melo, por me ajudar diversas vezes nesse processo e em tantos outros, sendo tão prestativo, paciente e companheiro, sempre me incentivando a seguir em busca dos meus objetivos e sonhos. A minha amiga de tantos anos, Julyene Alkmim, por toda a compreensão em todos os momentos, sempre me incentivando a alcançar meus sonhos.

A minha orientadora Isla Azevedo, por ser exemplo de dedicação e companheirismo, nunca deixando o desânimo tomar conta quando está presente. Sempre me lembrando do meu potencial e mostrando que sou capaz. Você sempre será referência profissional para o meu crescimento, desde quando entrei para a Universidade e te conheci, ainda no primeiro período da graduação. Sou imensamente grata por toda compreensão, incentivo e generosidade comigo e com meu trabalho. A minha coorientadora Camila Souza, sempre tão empática e prestativa. Agradeço imensamente por me apresentar o universo que é o estudo de redes ecológicas e pela oportunidade de trabalhar com esse estudo encantador! Todos os seus ensinamentos foram fundamentais para o desenvolvimento desse trabalho. Também a minha coorientadora Yule Nunes, pelo apoio e generosidade, por ser exemplo profissional e de humildade, por todos os incentivos para que eu pudesse permanecer estudando e buscando os meus objetivos. Tenham a certeza de que o mundo seria melhor se existissem mais pessoas como vocês. Aprendi não só sobre o que é fazer pesquisa e sobre interações ecológicas, mas também sobre valores e virtudes.

A minha equipe de campo, mas também amigos tão queridos, sempre presentes em todos os momentos bons e ruins Lucas Souza, José Gustavo Neves, Raíssa Santos e Sara Benavides. Agradeço imensamente por toda a ajuda, seja nas coletas de campo, nas análises estatísticas, nas escritas e correções dos trabalhos. Saiba que sempre poderão contar comigo, serei eternamente grata. A Anna Priska, Esther Lorrany, Naylla Letícia e Lara, por serem tão prestativas e eficientes me ajudando na observação das centenas de lâminas de pólen. Aos meus amigos Cristina Veloso e João Carlos Figueiredo, sempre me dando suporte e apoiando os meus objetivos. Ao Daniel Alcântara por ter nos ajudado a planejar como seriam as coletas em espécies tão altas quanto as palmeiras estrelas desse trabalho, sem a sua ajuda teríamos enfrentado muito mais dificuldade em nosso estudo. Receba toda a minha gratidão. E a tantos outros. Conheci pessoas prestativas, bondosas e dispostas a enfrentar as dificuldades que são encontradas em campos, com muito companheirismo.

A banca examinadora (Dr. Pedro Bergamo, Dra. Vanessa Marcelo, Dra. Marly Antonielle de Ávila e Dra. Rúbia Fonseca) por aceitarem o convite e pelas contribuições que com certeza irão enriquecer esse trabalho.

Ao Laboratório de Ecologia Vegetal da Universidade Estadual de Montes Claros.

A FAPEMIG, CNPq, CAPES, PELD-VEREDAS e RESA pelo suporte financeiro nas diversas etapas do trabalho.

A Universidade Estadual de Montes Claros e Instituto Estadual de Florestas pelo apoio logístico e suporte durante a realização das coletas do trabalho.

E, enfim, a todos que contribuíram de forma direta e indireta na minha formação acadêmica e realização desse trabalho, meus sinceros agradecimentos.

Sou imensamente grata a todos!

RESUMO

A polinização é um dos serviços ecossistêmicos essenciais para a humanidade, permitindo a sobrevivência da grande maioria das angiospermas. A distribuição dos recursos florais e a época de floração são essenciais para manter e preservar os serviços de polinização nos ecossistemas. A variação intraespecífica nos atributos dos indivíduos e a sua localização na paisagem podem ter influência nas interações com seus polinizadores e o papel de cada um desses indivíduos em uma rede de interações. Identificamos as síndromes de polinização de espécies lenhosas em um ecossistema de vereda e caracterizamos a disponibilidade de recursos de polinização entre habitats. Além disso, buscamos descrever a estrutura da rede de indivíduos de *M. armata* e seus polinizadores, avaliando como a variação dos atributos e a localização dos indivíduos podem atuar na determinação do papel na rede. Para *M. flexuosa*, também procuramos identificar os seus potenciais polinizadores, levando em consideração a plasticidade fenotípica da espécie, capaz de influenciar na diversidade dos polinizadores, apresentando os polinizadores que compartilham flores masculinas e femininas. Para caracterização da disponibilidade de recursos, realizamos monitoramento fenológico durante 24 meses e examinamos a ocorrência de floração por meio de estatística circular. As diferenças na ocorrência da síndrome de polinização entre meses e habitats foram determinadas por meio de análise de modularidade. Em relação a rede de interações das palmeiras-chave, selecionamos indivíduos femininos e masculinos e realizamos a medição de diferentes atributos como altura, circunferência a altura do peito, número de inflorescências, registro de espécies próximas florescendo e grupo de polinizadores. Foi montada uma rede de interações de indivíduos para *M. armata* e *M. flexuosa* e calculada a especialização e modularidade para toda a rede, com dois índices, em nível de indivíduos para *M. armata* e *M. flexuosa*, e de espécies para seus polinizadores: grau e força da espécie. Encontramos oito síndromes de polinização, sendo a melitofilia o tipo de polinização mais frequente entre as espécies lenhosas da vereda. A floração ocorre durante todo o ano na comunidade e atinge seu pico durante a transição da estação seca para a chuvosa. A distribuição das síndromes e a disponibilidade de recursos diferiu entre os habitats. A modularidade mostrou complementaridade entre os habitats, com disponibilidade contínua de recursos em todo o ecossistema. A rede de interações para *M. armata* apresentou estrutura especializada e modular. Os grupos de polinizadores mais frequentes foram as abelhas, seguido das vespas e besouros. Houve diferença na frequência de visitas entre os indivíduos femininos e masculinos, sugerindo uma estratégia utilizada pela espécie. As abelhas tiveram maior grau e força de espécie, enquanto indivíduos com maior número de inflorescências e menos espécies florescendo em sua vizinhança, tiveram maior grau e força de interação. Para a palmeira *M. flexuosa*, insetos como abelhas, vespas, besouros, moscas e hemípteras foram observados nas inflorescências, com 16 espécies de polinizadores coletadas em ambos os sexos florais. A rede de interações não foi significativamente especializada e modular. As inflorescências nos indivíduos masculinos atraíram maior número de polinizadores, sendo as abelhas com maior força de espécie e abelhas, besouros e vespas apresentaram maior grau na rede. Informações sobre essas interações são necessárias para compreender a funcionalidade do ecossistema de vereda.

Palavras-chave: síndromes florais; polinização em palmeiras; competição, efeito de vizinhança, polinização por engano, dioécia

ABSTRACT

Pollination is one of the essential ecosystem services for humanity, enabling the vast majority of angiosperms to survive. The distribution of floral resources and the flowering season are essential for maintaining and preserving pollination services in ecosystems. Intraspecific variation in the attributes of individuals and their location in the landscape can influence interactions with their pollinators and the role of each of these individuals in a network of interactions. We identified the pollination syndromes of woody species in a *vereda* ecosystem and characterized the availability of pollination resources between habitats. In addition, we sought to describe the structure of the network of *M. armata* individuals and their pollinators, evaluating how variation in attributes and the location of individuals can act in determining their role in the network. For *M. flexuosa*, we also tried to identify its potential pollinators, taking into account the phenotypic plasticity of the species, which can influence the diversity of pollinators, featuring pollinators that share male and female flowers. To characterize the availability of resources, we carried out phenological monitoring over 24 months and examined the occurrence of flowering using circular statistics. The differences in the occurrence of the pollination syndrome between months and habitats were determined using modularity analysis. With regard to the network of interactions between the key palms, we selected female and male individuals and measured different attributes such as height, circumference at breast height, number of inflorescences, records of nearby species flowering and the group of pollinators. A network of interactions between individuals was set up for *M. armata* and *M. flexuosa* and specialization and modularity were calculated for the entire network, using two indices, at the level of individuals for *M. armata* and *M. flexuosa*, and species for their pollinators: degree and strength species. We found eight pollination syndromes, with melittophily being the most frequent type of pollination among the woody species in the *vereda*. Flowering occurs throughout the year in the community and reaches its peak during the transition from the dry to the rainy season. The distribution of syndromes and the availability of resources differed between habitats. Modularity showed complementarity between habitats, with continuous availability of resources throughout the ecosystem. The network of interactions for *M. armata* showed a specialized and modular structure. The most frequent groups of pollinators were bees, followed by wasps and beetles. There was a difference in the frequency of visits between female and male individuals, suggesting a strategy used by the species. Bees had a higher degree and strength of species, while individuals with a greater number of inflorescences and fewer species flowering in their vicinity had a higher degree and strength of interaction. For the *M. flexuosa* palm, insects such as bees, wasps, beetles, flies and hemiptera were observed on the inflorescences, with 16 species of pollinators collected from both floral sexes. The network of interactions was not significantly specialized or modular. The inflorescences on male individuals attracted the greatest number of pollinators, with bees having the greatest species strength and bees, beetles and wasps showing the greatest degree in the network. Information on these interactions is necessary to understand the functionality of the *vereda* ecosystem.

Keywords: floral syndromes; pollination in palm trees; competition; neighborhood effect; pollination by deceit; dioecy

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1 INTRODUÇÃO GERAL

2

3 As interações entre as espécies são importantes para manter a biodiversidade e processos

4 ecológicos de um ecossistema. A polinização é considerada uma interação mutualística, que

5 proporciona benefícios para as plantas e seus polinizadores aumentando sua adaptação,

6 ampliando a sobrevivência e sucesso reprodutivo entre os participantes dessa interação (Rech,

7 2014). Os padrões espaciais e temporais de floração influenciam as interações entre plantas e

8 polinizadores (Dupont *et al.* 2014; Soares *et al.* 2021). Dessa forma, a diversidade e frequência

9 das interações podem apresentar variações sazonais (Cortés-Flores *et al.* 2017; Genini *et al.*

10 2021), sendo esperado em comunidades vegetais, constância das interações ao longo do ano,

11 devido as florações de diferentes espécies (Cortés-Flores *et al.* 2017; Genini *et al.* 2021).

12 O aparecimento e diversidade dessas interações são influenciadas pela fenologia das

13 espécies, visto que os polinizadores necessitam de recursos alimentares contínuos e podem

14 mudar seu comportamento de forrageamento em resposta a disponibilidade de espécies com

15 flores (Maruyama *et al.* 2013; Rosas-Guerrero *et al.* 2014; Genini *et al.* 2021). Portanto, a

16 distribuição temporal da floração tem influência importante no sucesso reprodutivo das plantas

17 e ocorre em resposta a diferentes fatores como disponibilidade de água, temperatura e

18 comprimento do dia, mas também pelas interações entre plantas e polinizadores (Springate;

19 Kover, 2014; Cortés-Flores *et al.* 2017; Soares *et al.* 2021).

20 As síndromes de polinização envolvem a especialização das plantas em grupos

21 específicos de polinizadores, exercendo pressões seletivas semelhantes sobre características

22 florais (Faegri; van der Pijl 1979; Fenster *et al.* 2004). Nesse contexto, essa associação pode ser

23 mais forte nas espécies que utilizam da polinização cruzada, sendo altamente dependentes dos

24 agentes polinizadores (Rosas-Guerrero *et al.* 2014). Assim, os diferentes períodos de floração

25 em espécies lenhosas associada as distintas síndromes de polinização podem favorecer a

26 manutenção de uma comunidade de polinizadores ao longo do ano, sendo interpretada como
27 uma estratégia para atrair polinizadores (Cortés-Flores *et al.* 2017).

28 De forma semelhante ao que ocorre no nível de comunidade, é esperado que aconteça
29 mudanças nas interações a nível individual, quando as plantas florescem em momentos
30 diferentes e interagem com diferentes polinizadores (Valverde *et al.* 2016). A relação individual
31 entre plantas e seus polinizadores pode ser caracterizada como uma rede ecológica (Fortuna *et*
32 *al.* 2008; Soares *et al.* 2021). As redes possuem organização hierárquica, em que cada espécie
33 é ao mesmo tempo parte de um todo ou um todo de partes (Dupont *et al.* 2011). Diferente da
34 abordagem ao nível de comunidade, as redes baseadas em indivíduos podem ser utilizadas para
35 analisar variações significativas entre as populações de espécies de plantas e polinizadores para
36 os efeitos de aptidão, demografia, fluxo gênico e padrões que seriam dificilmente detectados
37 em redes ao nível de espécie (Gómez *et al.* 2011; Guimarães, 2020; Tonos *et al.* 2021).
38 Atualmente, o interesse nas redes de polinização ao nível individual tem crescido (Valverde *et*
39 *al.* 2016), porém, ainda pouco estudadas, principalmente em relação a plantas com sexos
40 separados, espacial ou temporalmente (Vizentin-Bugoni *et al.* 2018; Arroyo-Correa *et al.*
41 2021).

42 Os fatores internos e externos de cada planta dentro das populações polinizadas por
43 animais são importantes para avaliar o comportamento de forrageamento dos polinizadores
44 (Arroyo-Correa *et al.* 2021). Os indivíduos vegetais diferem no seu fenótipo levando a
45 variações no seu nicho de polinização devido a preferências distintas de diferentes guildas de
46 polinizadores (Gómez *et al.* 2014; Arroyo-Correa *et al.* 2021). Estas diferenças nas
47 características individuais contribuem para gerar padrões nas interações (Valverde, 2016),
48 afetando a dinâmica populacional e a estruturação local das interações bióticas (Arroyo-Correa
49 *et al.* 2021). Além disso, as variações nas características dos indivíduos vegetais podem

50 influenciar o estabelecimento de interações, afetando a estrutura da rede de polinização baseada
51 no indivíduo (Dupont *et al.* 2014; Arroyo-Correa *et al.* 2021).

52 As interações entre as palmeiras e seus polinizadores são complexos e variam no tempo
53 e espaço (Barfod *et al.* 2011), apresentando diversas estratégias de polinização (Henderson,
54 1986; Listabarth, 2001; Barfod *et al.* 2011). Atualmente é descrito que as palmeiras podem ser
55 polinizadas pelo vento (anemofilia), pelos animais e por ambos (ambofilia) (Rios *et al.* 2014;
56 Barbosa *et al.* 2021). A polinização animal em palmeiras é predominantemente relatada por
57 besouros, abelhas e moscas (Barfod *et al.* 2011; Barbosa *et al.* 2021; Auffray *et al.* 2023). A
58 dioícia - sistema reprodutivo onde os indivíduos apresentam sexos separados (indivíduos
59 masculinos e femininos) é relativamente incomum entre as angiospermas, porém é recorrente
60 em palmeiras neotropicais (Renner; Ricklefs, 1995; Auffray *et al.* 2023). Essas espécies
61 dependem do polinizador para o transporte de pólen, pois são incapazes de se autopolinizar
62 (Bawa, 1985; Renner; Ricklefs, 1995). Por isso, diversas espécies de palmeiras desenvolveram
63 estratégias reprodutivas para a atração de polinizadores, como exibição floral, perfume e
64 acessibilidade (Ashman, 2009; Barrett; Hough, 2013; Pincebourde *et al.* 2016; Barbosa *et al.*
65 2021; Auffray *et al.* 2023). Por outro lado, as características das inflorescências são importantes
66 influenciadoras na composição dos polinizadores, que podem variar em riqueza e abundância
67 de espécies (Barfod *et al.* 2011).

68 Muitas espécies de palmeiras são consideradas espécies-chave em vários ecossistemas
69 tropicais (Barfod *et al.* 2011; Eiserhardt *et al.* 2011; Ávila *et al.* 2022,2023). A palmeira
70 *Mauritiella armata* (Mart.) Burret, conhecida como Xiriri, possui significativa importância
71 ecológica e social (Martins *et al.* 2014; Ávila *et al.* 2022). É amplamente distribuída na América
72 do Sul associada a solos úmidos, formando povoamentos aglomerados (Lorenzi *et al.* 2010;
73 Ávila *et al.* 2022). *M. armata* é uma espécie dióica, necessita de polinização biótica e como

estratégia reprodutiva para a polinização cruzada e consequentemente sucesso reprodutivo, apresenta sincronia na floração das inflorescências masculinas e femininas (Ávila *et al.* 2022).

A palmeira *Mauritia flexuosa* L.f., popularmente conhecida como Buriti, é filogeneticamente próxima de *M. armata* (Virapongse *et al.* 2017; Ávila *et al.* 2022, 2023). Também apresenta grande importância ecológica e econômica, principalmente pela alta produção de frutos para a fauna local e povos tradicionais (Virapongse *et al.* 2017; Ávila *et al.* 2023). Também é uma espécie dióica, apresenta sincronia da floração entre indivíduos femininos e masculinos para que ocorra a polinização cruzada (Ávila *et al.* 2023). Os padrões de floração e frutificação dessa palmeira diferem em ambientes com diferentes condições (Mendes *et al.* 2017). Portanto, a espécie responde às variações ambientais que ocorrem em cada região de forma complexa e variável (Ávila *et al.* 2023), influenciando diretamente nas interações com seus polinizadores. Além disso, também apresenta divergência nos polinizadores relatados na literatura (Barfod *et al.* 2011; Mendes *et al.* 2017). Possui ampla distribuição no Brasil, sendo encontrado em diferentes ecossistemas e no Cerrado brasileiro é encontrada em ecossistemas úmidos, como solos alagados devido ao afloramento do lençol freático, conhecido por veredas (Melo *et al.* 2020; Nunes *et al.* 2022; Ávila *et al.* 2023).

Encontrado em áreas úmidas do Cerrado brasileiro, os ecossistemas de veredas são comunidades higrófilas, relacionadas a lençóis freáticos rasos (Araújo *et al.* 2002; Nunes *et al.* 2022). Nesses ecossistemas, a vegetação é formada por uma camada herbáceo-arbustiva que predomina e áreas abertas e solos úmidos, e o estrato arbóreo ocorre próximo a região do afloramento do lençol freático, como solos permanentemente saturados de água (Araújo *et al.* 2002; Nunes *et al.* 2015, 2022). As veredas da região sudeste do Brasil, são relativamente ricas em espécies arbóreas quando comparadas a outras veredas (Resende *et al.* 2013; Nunes *et al.* 2022). Os estudos referentes as espécies vegetais desses ecossistemas, incluindo suas espécies-

chave, são necessários para o preenchimento de lacunas e compreensão dos serviços ecossistêmicos prestados.

Os serviços de polinização necessitam de documentação e entendimento dos seus mecanismos, identificando os principais estímulos que atuam para sua manutenção (Auffray *et al.* 2023). Portanto, procuramos entender a distribuição dos recursos florais para os polinizadores na comunidade de vereda e identificamos as síndromes de polinização presentes nesse ecossistema, buscando compreender a dinâmica reprodutiva do ambiente em relação as espécies vegetais. Além disso, caracterizamos a rede de interações dos indivíduos das espécies-chave presentes nesse ecossistema, as palmeiras *M. armata* e *M. flexuosa*, buscando entender o papel dos indivíduos e dos grupos de polinizadores na rede de interações, quais atributos responsáveis por atrair o maior número de parceiros e os potenciais polinizadores dessas espécies.

Os resultados alcançados com esta dissertação estão organizados em três capítulos: (1) artigo publicado na *Flora*, relacionando a variação temporal e espacial dos recursos florais de espécies lenhosas em um ecossistema de vereda e a distribuição das síndromes, mostrando a complementariedade entre os habitats, com disponibilidade contínua de recursos em todo o ecossistema; (2) artigo formatado para a revista *Annals of Botany* caracterizando a rede de interações entre a palmeira-chave *M. armata* e seus polinizadores no ecossistema de veredas, através de métricas como especialização e modularidade, identificando os processos responsáveis pelo papel desses indivíduos na rede; (3) artigo formatado nas normas da *Plant Biology*, identificando e caracterizando as interações entre *M. flexuosa* e seus polinizadores, através da descrição da estrutura da rede, e analisando os atributos responsáveis por atrair o maior número de parceiros.

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CAPÍTULO 1

Artigo publicado na Revista *Flora*

<https://doi.org/10.1016/j.flora.2023.152425>

Temporal and spatial variation of floral resources of woody species in a *vereda* ecosystem: uniformity and habitat complementarity

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Abstract

Floral resource distribution, pollinator community structure, and flowering season are essential for maintaining and preserving pollination services in ecosystems. In humid Cerrado areas, *veredas* are considered hygrophilous communities, marked by the presence of the *Mauritia flexuosa* palm tree emerging in the wetter zones. Waterlogged portions present dense hygrophilous forests, whereas open areas predominant present herbaceous and shrubby components. We identified the pollination syndromes of woody species in a *vereda* ecosystem and characterized the pollination resource availability between habitats (hygrophilous forest and open area). The study was conducted on a *vereda* located in the north of Minas Gerais, Brazil. We characterized pollination syndromes using information on floral attributes, pollinator observations, and a literature survey. We performed phenological monitoring for 24 months and examined the occurrence of flowering using circular statistics. The differences in pollination syndrome occurrence among months and habitats were determined using modularity analysis. We found eight pollination syndromes, with melittophily being the most frequent pollination type among the woody species in the studied *vereda*. Flowering occurs throughout the year in the community and peaks from September to November during the transition from the dry to the wet season. In hygrophilous forest the species flowered preferentially in November, whereas in open area, preferentially between September and October. The syndromes distribution differed between the habitats, as well as resource availability. This difference between habitats can influence pollinator diversity. Modularity showed complementarity among the habitats, with continuous resource availability throughout the entire ecosystem. Species present in the hygrophilous forest provide their resources mainly during the rainy season, whereas species from the open area, during the dry season. Information on these interactions is necessary to understand the functionality of a *vereda* ecosystem, through the characterization of the resource's availability, and maintenance of pollination services in the ecosystem. In addition, our results demonstrate the importance of the *vereda* ecosystem as an important area in the availability of resources for the Cerrado formation. This information can strengthen protection laws and contribute to sustainable practices that boost the conservation of pollinators in the biome.

Keywords: Cerrado, floral syndromes, hygrophilous communities, melittophily, modularity, phenology

1. Introduction

Biodiversity includes species richness in a habitat and their interactions (Sabatino et al., 2010; Ballantyne et al., 2017). Pollination is a mutualistic interaction where flowers provide food and pollinators provide pollination service (Maruyama et al., 2013; Rech et al., 2014; Wardhaugh, 2015). Within pollination interactions, we can define pollination syndromes that consist of a set of floral characteristics (floral resources, colors, fragrances, and morphology) that are associated with the attraction and utilization of a possible specific group of animals as pollinators, with the floral characteristics correlated through independent evolutionary events (Fenster et al., 2004). In relation the different types of pollination syndromes and potential interactions between plants and possible pollinators, spatial and temporal variations combined with the abundance and distribution of floral resources are structuring factors for pollinator communities (Olesen et al., 2008; Burkle and Alarcon, 2011; Carstensen et al., 2014). Therefore, resource availability, conditioned by the flowering season, is essential for interactions and the maintenance of pollination (CaraDonna et al., 2014, 2017; Kantsa et al., 2018).

Several plant communities have different flowering seasons among their species, making resources available over a prolonged period (Dorado and Vazquez, 2014). Distinct species with sequential flowering seasons provide continuous resources for pollinators (Rosas-Guerrero et al., 2014). However, some regions might present restricted pollination seasons, resulting in seasonal variations in the diversity and frequency of pollination systems (Cortés-Flores et al., 2017; Genini et al., 2021). These environments present more diverse pollination systems, especially during flowering peaks. The diversity of consumers increases with the variety of resources (Cortés-Flores et al., 2017). The synchronicity between flowering and pollinators' activity is still poorly understood in ecosystem services. However, these

interactions are valuable for maintaining biodiversity, and information about them aids understanding of the functionality and maintenance of pollination services and ecological processes (Morellato et al., 2016).

The Cerrado is a Neotropical savanna with a high floristic diversity (Mendonça et al., 2008; Silva et al., 2012; Maruyama et al., 2013). Field studies in this biome revealed a diversity of pollination syndromes, with bees as the leading pollinators (Oliveira and Gibbs, 2000; Barbosa and Sazima, 2008; Ishara and Maimoni-Rodella, 2011; Baronio et al., 2021). Although the Cerrado presents well-drained soils throughout most its plant formations, it also has seasonally waterlogged areas, e.g., *veredas* (Araújo et al., 2002; Nunes et al., 2015, 2022). *Veredas* are an important source of water and food for wildlife (Bahia et al., 2009; Alencar-Silva and Maillard, 2011) owing to the seasonal climate characteristics of the Cerrado (Malheiros 2016). These ecosystems are considered hygrophilous communities presenting variations in floristic composition and zoned structure according to humidity and depth of the water table, which characterize distinct microhabitats (Araújo et al., 2002; Nunes et al., 2015, 2022). Commonly, there is a dense hygrophilous forest in the center of the *vereda*, where water logging is continuous around streams, and tree species predominate. In the open areas, the soil is wet, and the vegetation is composed of shrubs, undershrubs, herbs, and grasses (Nunes et al., 2015, 2022).

Anthropic disturbances and climate changes have damaged many *vereda* areas before we understand their composition, structure, ecosystem services, and functional diversity (Fagundes and Ferreira, 2016; Nunes et al., 2022; Silva et al., 2022). Identifying pollination syndromes and characterizing resource availability along the year in a *vereda* ecosystem will enable a better understanding of the reproductive dynamics in these environments in relation the plant species. It is important to highlight that this type of study is the first in the studied

ecosystem. Here, we focus on woody species selected based on a previous phytosociological study (Nunes et al., 2022) carried out in a *vereda* ecosystem. We did not include the herbaceous layer which is dominated by plants from the Poaceae and Cyperaceae which are pollinated by the wind (Friedman and Barrett, 2009; Rech et al., 2014; Linder et al., 2018), even though some establish interactions with potential pollinators (Schulze-Albuquerque et al., 2020). Therefore, we sought to answer the following questions: (i) which woody species pollination syndromes are present in *veredas*? (ii) are resources continuously available in this ecosystem? and (iii) do the distribution of pollination syndromes and seasonal resource availability differ among the *vereda* microhabitats (hygrophilous forest and open area)?

2. Materials and methods

2.1 Study site

We studied the Almescla *vereda* in the environmental protection area of the Pandeiros River (APA Rio Pandeiros) (15°20'54.9" S, 44°53'84.5" W), Bonito de Minas, Minas Gerais, Brazil (Fig. 1a). The *veredas* in the northern region of the state of Minas Gerais present an Organosol and Melanic Gleysol, which are soils formed by the accumulation of plant residues in varying degrees of decomposition and in environments with prolonged water saturation. The Almescla *vereda* presents a Mesic Organosol (soil consisting of organic matter, saturated with water; Nunes et al. 2015; Veloso et al. 2018). The present study considered two different habitats: hygrophilous forest (HF) on wet soil with predominant tree species and open area (OF) on wet to dry soil with the predominance of shrubs (Nunes et al., 2022; Fig. 1).

The Köppen classification defines the regional climate as Aw: tropical, with a dry winter and a rainy summer (Alvares et al., 2013). The dry season lasts for 5 months (May to

September). The rainy season occurs from November to January (Azevedo et al., 2014). The annual rainfall is 920 mm, and the average temperature is 26.8 °C (Azevedo et al., 2014). In the region, rainfall starts in October and is higher between November and April. In May, the weather transitions from rainy to dry, lasting until September. Between March 2018 and February 2020, the average temperature increased from 18 °C (July) to 37 °C (November). The rainiest month was November 2018, with 294.8 mm (Fig. 2).

2.2 Species, floral attributes, and pollination syndromes

We selected the woody species of angiosperms, including trees, shrubs, subshrubs and also palm species, according to a previous phytosociological study carried out in the Almescla vereda in 2017 (Nunes et al., 2022). For the phytosociological study, plots distributed in the vereda in transects parallel to the watercourse were used. In the habitat characterized as a hygrophilous forest, 30 plots of 10 m × 20 m were distributed along a transect, with a distance of 150 m between them. All tree and shrub individuals within these plots with DBH $\geq$ 5 cm (diameter at breast height – measuring 1.30 m above ground level) were identified and marked with numbered aluminum plates. Within each plot, smaller plots of 5 × 5 m were also delimited for sampling tree-shrub individuals from the lower and/or regenerating strata. In these subplots, all tree-shrub individuals with a DBH $\geq$ 3 cm were also registered and numbered with aluminum plates. In the habitat defined as an open area, two transects were allocated separated by 20 m. In these transects, 38 plots of 10 m × 20 m were distributed, with a distance of 150 m between them, arranged parallel to demarcated plots in the hygrophilous forest. All shrub individuals with DBS (diameter at the base of the soil) $\geq$ 5 cm were marked and registered with aluminum plates. Likewise, subplots of 5 m × 5 m were allocated within these plots to sample shrub-

subshrub individuals. Thus, all individuals with DBS ≥ 3 cm were marked and registered using aluminum plates. Individual identification was carried out in the field and through collected material (vegetative or reproductive) for identification through specialized literature (Nunes et al., 2022). The present study analyzed 86.9 % of the species found in the phytosociological survey; 29 species in the hygrophilous forest and 31 in the open areas. For the other species, due to the absence of reproductive material, data collection in loco, and information in the literature, it was not possible to identify the pollination syndrome.

We analyzed the species in loco during flowering and recorded the shape/type (dish, campanulate, flag, gullet, tube, brush and inconspicuous), color (white, red, greenish, yellow, orange, lilac/violet, pink), and scent (characterized as pleasant, unpleasant, or imperceptible). Flower anthesis for each species was determined using information available in the literature or observations during diurnal sampling (Tables S1 and S2). The observations were conducted between 7 AM and 6 PM, and for the nocturnal species, information about anthesis and main pollinator was determined through information collected in the literature and the characteristics that the flowers presented as typical of nocturnal pollination syndromes. We gathered literature information whenever reproductive material was absent. We conducted our search to gather information in the literature using Web of Science (<https://login.webofknowledge.com/>), Scopus (<https://www.scopus.com/>), Google Scholar (<https://scholar.google.com.br/>), and Scielo (<https://www.scielo.br/>). We used a combination of the following keywords in English (and their equivalents in Portuguese/Spanish): “pollinators”, “pollination syndromes” and “pollination”, always together with the name of the plant species. In addition to observing the floral attributes of the evaluated plant species, we also made phytocentric observations of floral visitors and potential pollinators. During the monthly observations for flowering characterization, we performed ten minutes of focal observations of each flowering plant within

the plots. The observation time was variable for each species, depending on occurrence, phenology, and abundance. To include variations in the timing of plantpollinator interactions, we recorded all plots at different times throughout the day during the sampling period (Souza et al., 2017, 2018, 2021). Thus, the pollination syndrome characterization considered floral attributes and pollinator sightings through field observations and literature: cantharophily (pollination by beetles), phalaenophily (moths), sphingophily (hawkmoths), psychophily (butterflies), melittophily (hymenoptera), myophily (flies), ornithophily (birds), chiropterophily (bats) (Faegri and van der Pijl, 1979), anemophily (wind pollination), and ambophily (anemophily + melittophily) (Bullock, 1994) (Table S2). Some plant species showed more than one pollination syndrome; that is, the species was pollinated by several groups of pollinators, which is why they were classified as multiple pollination syndromes.

2.3 Resource availability

Phenological data were collected every month over 24 months (March 2018 to February 2020). We recorded, during observations, the presence of flowers in each individual (Bencke and Morellato, 2002). The estimated occurrence and intensity of flowering distribution allowed us to evaluate the season and duration of resource availability and determine the seasonality over the study period. To estimate the intensity of flowering and supply of resources in the different evaluated habitats of *vereda*, all flowering individuals were quantified, and the sum of these individuals was calculated to identify the intensity of the flowering peak and assess the seasonality in each habitat. We calculated the circular standard deviation, circular mean, and vector length (r) to represent data grouping around the mean for flowering period (as proposed by Morellato et al. 2010). The Rayleigh test (z) indicated a unimodal distribution at $p < 0.05$,

i.e., seasonality in the flowering pattern (Zar, 2013). Angles represented the months: e.g. January = 0°, February = 30°, December = 330°, in 30° increments. The circular analysis was conducted in the Oriana 4.0 software (Kovach, 1994).

We used the modularity index to evaluate how pollination syndrome occurrences differ among the sample months by quantifying the abundance of species with a particular syndrome in a particular month (modified from Genini et al. 2021). In this way, modularity quantified the prevalence of species with certain syndromes in specific months, and whether the syndromes would occur more in specific months than in others, forming modules. The modularity was calculated using the DIRTLPawb+ algorithm (Beckett, 2016) and the computeModules function in Bipartite package (Dormann et al., 2008). In addition to the raw modularity, we used the Patefield null model, which fixes the matrix size and the marginal totals, which is species richness/syndromes and observed months, while shuffling occurrence randomly (Patefield, 1981). We consider the modularity and consequent separation of the syndromes in the different modules to be significant if the observed value was greater than those generated by the null model. For each *vereda* area, we conducted a separate modularity analysis (hygrophilous forest and open area).

3. Results

Animals pollinated a large proportion of woody plants in the Almescla *vereda*, which were included in eight pollination syndromes. Bee pollinated species (mellitophily) were the most frequent, representing 83 % of all species. Beetles (cantharophily) and Butterflies (psychophily) accounted for 4 % of species each, and the other syndromes for only a single plant species each (Table S1). Melittophily was the most frequent syndrome in both habitats, in 87 % of the open area species and 79 % of the hygrophilous forest species.

Cantharophily and psychophily were present in both *vereda* habitats. Cantharophily occurred among species of the same genus: *Xylopia aromatica* (Lam.) Mart. in the open areas and *Xylopia emarginata* Mart. in the hygrophilous forest. Pollination by birds and moths, ambophily, and anemophily remained restricted to the hygrophilous forest. Sphingophily occurred only in the open areas.

Different species with flowers were present throughout the year, with flowering concentrated between September and November, a period of transition from the dry season to the rainy season. Flowering peaks occurred in October in both years (Fig. 3), when the temperature also increased (Fig. 2). Flowering in the hygrophilous forest was seasonal in the first year ($r = 0.557$), with a peak in October, and irregular during the second year ($r = 0.389$). Although the second year did not show significant seasonality, species preferably flowered in November (Fig. 4). Open areas presented irregular flowering in both years ($r = 0.339$ and $r = 0.276$, respectively). Again, even though the vector (r) did not indicate seasonality, species preferably flowered between September and October (Fig. 4), a transition between the dry and rainy seasons (Figs. 2 and 3).

Although flowering occurred throughout the year, resource availability was continuous only for melittophily and cantharophily. Resources were available for cantharophily throughout the year only occurred due to *X. aromatica* extended flowering, which is present in both environments. Species with floral attributes related to psychophily, sphingophily, chiropterophily, phalaenophily, and ornithophily did not have continuous resource offer. Flowering occurred only for a few months, especially between July and October (Table S1; Fig. 3).

The distribution of pollination syndromes among different sample months followed a modular pattern, considering species richness and abundance. Modularity was significant in

both environments (hygrophilous forest: species richness $Q = 0.21$, $p < 0.03$; abundance $Q = 0.32$, $p < 0.01$. Open area: species richness $Q = 0.39$, $p < 0.01$; abundance $Q = 0.13$, $p < 0.01$. Fig. 5a and b), generating three to four modules. Some modules included more than three months, corresponding to the longer flowering period of a given syndrome.

These results showed that the variety of pollination syndromes in the hygrophilous forest generated three modules. The first module (rainy season) was dominated by melittophily and also included anemophily, ambophily, and cantharophily. The second module (dry season) was also dominated by melittophily, but all other pollination syndromes were present, and was the only module containing ornithophily, phalaenophily, chiropterophily, and psychophily. The last module (transition between the rainy and dry seasons) revealed less dominance by mellitophily, and greater representation by ambophily and cantharophily. Syndrome abundance modularity in the hygrophilous forest showed a similar pattern. A module in the rainy season was associated with melittophily. The second one occurred mainly during the dry season and associated abundance with ambophily, ornithophily, phalaenophily, chiropterophily, and psychophily. The third module (transition between seasons) was associated with cantharophily and anemophily (Fig. 5a).

Open areas presented contrasting resource availability compared with the hygrophilous forest. There were four modules for the diversity of pollination syndromes. The first, during the dry season, was associated with melittophily, whereas the second, in September, with ambophily, chiropterophily, and psychophily. The third and fourth modules occurred mainly during the rainy season and were associated with cantharophily and sphingophily, respectively. Abundance of syndromes had only two modules. The first, also during the dry season, was associated with melittophily and psychophily. The second, mainly during the rainy season, was associated with ambophily, chiropterophily, cantharophily, and sphingophily (Fig. 5b).

499

500 **4. Discussion**

501 This study revealed that the *Almescla vereda* woody plant community had a high
502 richness of pollination syndromes, with melittophily as the most frequent type, followed by
503 cantharophily and psychophily. Melittophily was more representative in this system than
504 reported in other tropical seasonal environments, both wet and dry. It is important to highlight
505 that in our study we only analyzed the woody species present in the environment. Additionally,
506 we limited the study only to pollinator groups and pollination syndromes, since we did not
507 perform the identification of pollinator species. We therefore emphasize the importance of
508 studies that also include herbaceous species of the *vereda*. Bees are the main pollinators of
509 arboreous-shrubby species in the Cerrado (Oliveira and Gibbs, 2000; Ishara and Maimoni-
510 Rodella, 2011). Melittophily includes most of the plant species in the cerrado *sensu stricto* (Reis
511 et al., 2012; Silva et al., 2012; Gottsberger and Silberbauer-Gottsberger, 2018), and also with
512 bees dominating pollination in rupestrian grasslands (Santos et al., 2020; Martins et al., 2021;
513 Monteiro et al., 2021). In dry tropical forests, species with floral attributes related to bee
514 pollination accounted for 57 % of the total number of species (Cortes-Flores et al., 2017). In
515 wet environments, e.g., riparian forests, the most frequent pollination syndromes are
516 melittophily and cantharophily (Martins and Antonini, 2016). The high species richness of
517 tropical communities encourages pollination by animals, favoring interactions and a diversity
518 of pollination syndromes (Ollerton et al., 2011), and thus a higher dependency on biotic
519 pollination (Ollerton et al., 2006; Dorado and Vazquez, 2014). Among them, entomophilous
520 interactions caused the radiation and specialization of plants with modern flowers (Wardhaugh,
521 2015), with bees and beetles as the most frequent pollinators (Bawa et al., 1985; Wardhaugh,
522 2015; Souza et al., 2016, 2017; Moreira and Freitas, 2020).

Melittophily and cantharophily, the overall most frequent syndromes, were also common in both habitats on the studied *vereda*. Studies indicate that species pollinated by bumblebees and beetles comprise trees, shrubs, and herbs, whereas smaller insects such as small bees prefer the lower portions of vegetations (Gottsberger and Silberbauer-Gottsberger, 2018). The distribution of other pollination syndromes differed among environments, with the majority being recorded in the hygrophilous forest during the dry season. This environment presented a higher diversity of species with flowers, sustaining more diverse pollination syndromes. Furthermore, this environment showed high availability of resources for several types of pollinators during a time when floral resources are generally scarce in the environment and the surrounding landscape. Thus, the hygrophilous forest potentially acted as a refuge for pollinators. However, it is worth noting that, despite the richness of pollination syndromes found in this environment, a single species, *Inga vera* Willd. (Fabaceae), supplied resources for birds, moths, and bats, and was classified under all three syndromes. In the open area, we observed the opposite of what was registered for the syndromes in the hygrophilous forest, with melittophily occurring mainly during the dry season and the remaining syndromes modulated in the rainy season. Therefore, resource availability seasons and habitats differed among themselves. This arrangement in different environments in a *vereda* ecosystem can influence pollinator diversity. Higher plant species richness and pollinator interaction result in a broader ecosystem function (Cardinale et al., 2012; Bartomeus et al., 2013). Butterflies, sphingids, moths, and bats can also act as potential pollinators mainly because they can be the main pollinators for trees and shrubs in Cerrado physiognomies (Gottsberger and Silberbauer-Gottsberger, 2018). Phalaenophily and sphingophily are common in lower and open vegetations that can benefit from resource extraction by these animals (Reis et al., 2012). Furthermore, because the Cerrado is a mosaic of different formations, where we observe the complementarity

of habitats (Maruyama et al., 2014), the migration of these species to other areas when the *vereda* is in periods with scarce diversity of species with different syndromes is possible.

Although flowering occurred throughout the year, a continuous resource availability of woody species occurred only for melittophily and cantharophily, indicating that each season provided favorable and unfavorable conditions for each pollinator group of woody species. Plants of the *Byrsonima* (Malpighiaceae) and *Miconia* (Melastomataceae), present in both habitats, stood out in melittophily by presenting flowering mainly during the dry season, whereas *X. aromatica* (Annonaceae) supplied cantharophily resources throughout the year. Flowers pollinated by bees throughout the year may be associated with the variety of strategies in the flowering period presented by different species in that system (Genini et al., 2021). Other pollinators of woody species had resources available for only a few months, with some species flowering only during a specific season. Restricted flowering tends to adjust the diversity of pollination syndromes in seasonal environments (Genini et al., 2021). However, periods with insufficient food supply can lead to network disruption and decreases in the diversity and abundance of pollinators (Abrahamczyk et al., 2011). Incompatibility between resource availability and pollinator foraging activity can cause reductions in pollination services (Petanidou et al., 2014), affecting seed production (Satake et al., 2013).

Resource availability seasons also differed among the environments. Although we used the activity index, which evaluates only the presence or absence of flowers in the individuals, the sum of individuals manifesting flowering allows us to assess the intensity and resource availability at a given time and in each environment. In the hygrophilous forest, flowering occurred mainly in October and November, when the rainy season begins. In the open area, flowering was more intense earlier, in September and October, with temperature increases and the transition from the dry to the rainy season. Therefore, we observed that species from the

hygrophilous forest behaved similar to those from riparian forests, whereas species from the open area behaved similar to those from the Cerrado, with solid seasonality and flowering of frequent species occurring during the dry season (Oliveira 2008; Pirani et al., 2009). Many species from riparian forests present flowering peaks during the rainy season and under higher temperatures that can stimulate flowering in tropical species (Talora and Morellato, 2000; Reys et al., 2005). The predominance of animal pollination is related to higher temperatures and rainfall because these conditions increase nectar production as a resource for pollinators (Rech et al., 2016).

Our results for the woody species of the studied *vereda* indicate that the two types of habitats (hygrophilous forest and open area) complement their resource availability for pollinators. Species from hygrophilous forest supply their leading pollinators (Hymenoptera) during the rainy season, whereas species from open area supply their pollinators during the dry season. Therefore, resources are continuously available throughout the entire ecosystem. The same occurs for the other syndromes. However, each syndromes occur specifically in each environment. Studies have highlighted the importance of maintaining populations of pollinators and plant species, preserving these interactions, and ensuring the function and stability of ecological communities (Säterberg et al., 2013). Changes in the flowering start, peak, and duration, along with the activity and life cycle of consumers, can influence the scarcity of resources and collapse the consumer population (Berg et al., 2010; Donnelly et al., 2011). The richness of pollinator functional groups increases the reproductive success of plants, thereby increasing the production of fruits and seeds (Albrecht et al., 2012). Therefore, the number of pollinators increases plant diversity, and the diversity of pollinators increases the capacity and persistence of plants in the community over time (Albrecht et al., 2012). However, it is worth noting that some studies have reported that an increase in the number of floral visitors can lead

to a reduction in the number of interaction links, modifying the structure of interactions between plants and pollinators, and affecting the reproductive success of plant species (Valido et al., 2019; Page and Williams, 2023).

5. Conclusion

The analyzed *vereda* woody plant community presented a richness of pollination syndromes related to floral complexity, with melittophily as the most frequent. The distribution of pollination syndromes differed among the habitats of this ecosystem, and only a few occurred in both environments. The same was observed for resource availability. In the community, flowering occurred throughout the year, with peaks during the transition from the dry season to the rainy season. However, resources were continuously available only for melittophily and cantharophily. The modularity in both environments showed complementarity among them. In the hygrophilous forest, the leading pollinators were present in the rainy season, whereas in the open areas, they were present during the dry season. It is important to highlight that the results of this study are related only to the *vereda* in question, and that these results may differ in other similar environments. The *vereda* presented conditions to sustain pollinators in a diversified manner, being fundamental for the reproductive and functional dynamics of the ecosystem and for preserving biodiversity. In addition, these results demonstrate how essential the ecosystem is as areas for the availability of resources in the Cerrado. In addition, these results demonstrate how essential this ecosystem is as areas for the availability of resources in the Cerrado. It is important to reinforce that this study is the first in a *vereda* ecosystem. The information from this study can strengthen and assist in sustainable management practices that promote the conservation of pollinators in the Cerrado areas.

618 **Authorship contribution statement**

619 ALLL, YRFN, IFPA and CSS conducted the conception and design of the work. YRFN, IFPA,
620 ALLL and JGSN conducted data collection. ALLL, CSS, IFPA and PEO conducted statistical
621 analysis, draft of the work and previous manuscript reviews.

622

623 **Declaration of Competing Interest**

624 The authors have no competing interests to declare that are relevant to the content of this article.

625

626 **Funding**

627 This research was supported by the Long-term Ecological Research Network (PELD-VERE)
628 of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 441440/2016-
629 9; 441583/2020-2; 308877/2019-5), Coordenação de Aperfeiçoamento de Pessoal de Nível
630 Superior (CAPES 88887.136273/2017–00), and Fundação de Amparo à Pesquisa do Estado de
631 Minas Gerais (FAPEMIG APQ-04816-17; CRAPPM- 00539-18; APQ-04816-17; FAPEMIG/
632 RED-00253-16).

633

634 **Acknowledgments**

635 Postgraduate Program in Applied Botany, to the grassland assistance of the Plant Ecology
636 Laboratory (Universidade Estadual de Montes Claros) and logistical support from the Instituto
637 Estadual de Florestas, in the Minas Gerais State.

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641 **Supplementary materials**

642 Supplementary material associated with this article can be found, in the online version, at
643 [doi:10.1016/j.flora.2023.152425](https://doi.org/10.1016/j.flora.2023.152425).

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893 **Figure 1.** Location of the Almescla *vereda*, APA Pandeiros, Bonito de Minas, MG, Brazil. Almescla *vereda*:
894 hygrophilous forest and open area. The hygrophilous forest is composed of a dense forest community, and the
895 open area is composed of shrubs, herbs, and grass.

896 **Figure 2.** The total monthly rainfall (bars) and the average minimum, mean, and maximum temperatures (lines)
897 from March 2018 to March 2020, collected by the meteorological station installed in the Almescla *vereda*, Bonito
898 de Minas, MG, Brazil.

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900 **Figure 3.** The number of flowering individuals between March 2018 and February 2020 in the Almescla *vereda*
901 community, Bonito de Minas, MG, Brazil.

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903 **Figure 4.** Circular histograms: flowering peak frequency (number of flowering individuals) in the hygrophilous
904 forest and open area habitats in the Almescla *vereda* community over 2 years (March 2018 to February 2020:
905 Period 1 = March/2018 – February/2019; Period 2 = March/2019 – February/2020). Arrows indicate the mean
906 angle, and their lengths correspond to the mean vector (r) value or the degree of seasonality.

907

908 **Figure 5.** Modularity results quantifying the prevalence of species richness with a determinate syndrome during
909 both years in the hygrophilous forest and open areas (March 2018 to February 2020). On the left is the distribution
910 matrix of the different syndromes between the twelve months of the year, and each square and color correspond
911 to a different module. On the right side we have the percentage of occurrence of syndromes (species richness)
912 between the different months sampled. The stronger the shade of blue, the high the frequency of occurrence of that
913 syndrome in the indicated month (richness or abundance) Pollinators images were obtained from
914 www.divulgare.net.

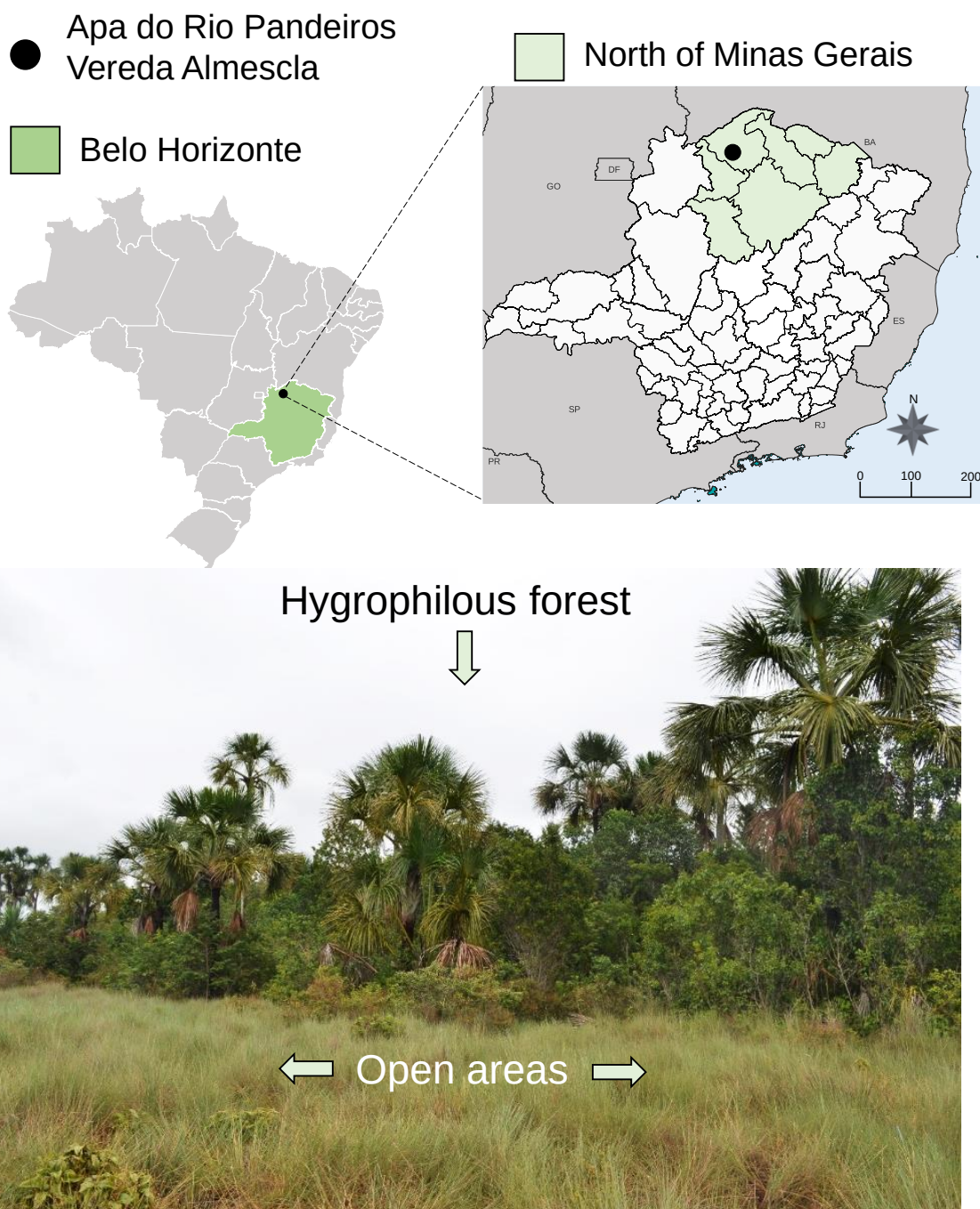
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Table 1. Spearman correlation (with $p < 0.05$) between the flowering phenophase and the climatic variables of the habitats in the plant community of the *vereda* Almescla, MG, Brazil.

Abiotic variables	Hygrophilous forest		Open area	
	Correlation	p-value	Correlation	p-value
Maximum temperature (°C)	0.49	0.01	0.48	0.01
Minimum temperature (°C)	0.05	0.8	-0.05	0.81
Medium temperature (°C)	0.33	0.1	0.19	0.35
Precipitation	-0.04	0,8349	-0.19	0.34
Photoperiod	0.32	0.12	-0.15	0.45



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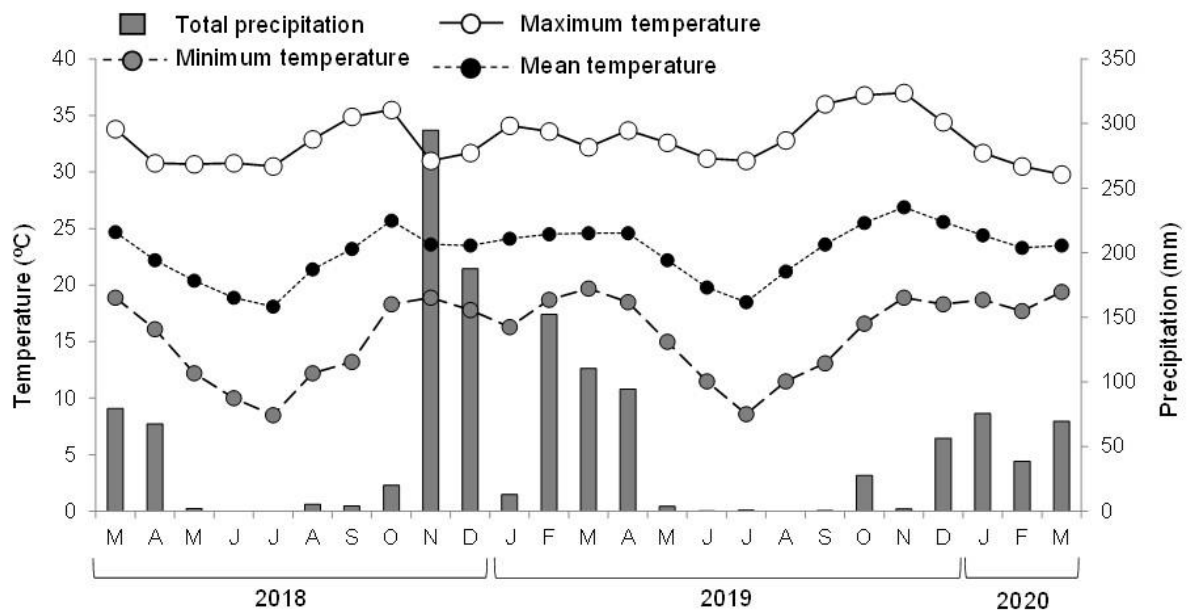
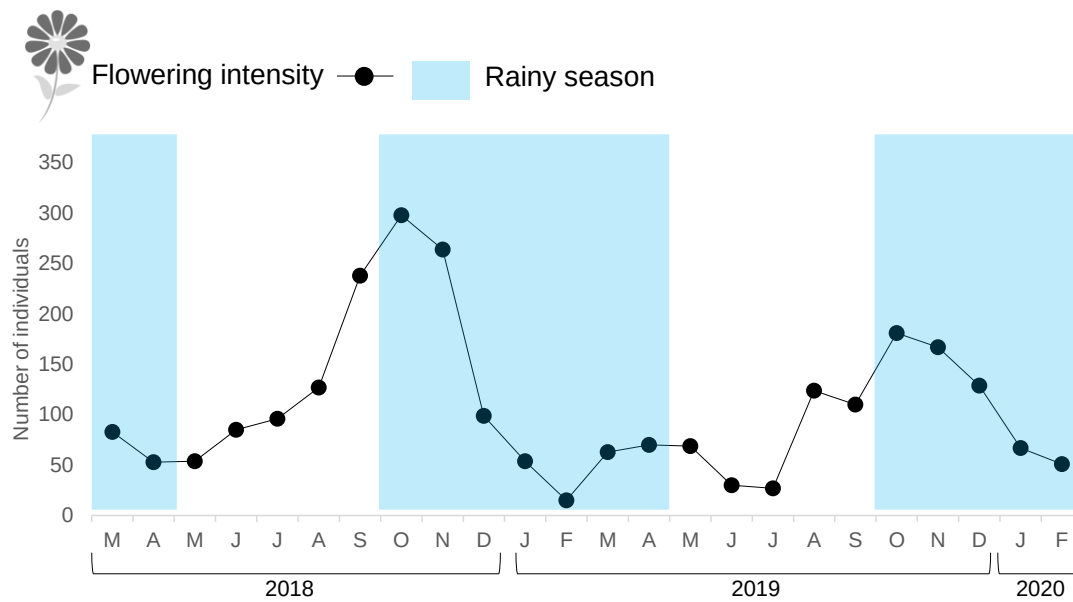


Figure 02.

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961 Figure 03.

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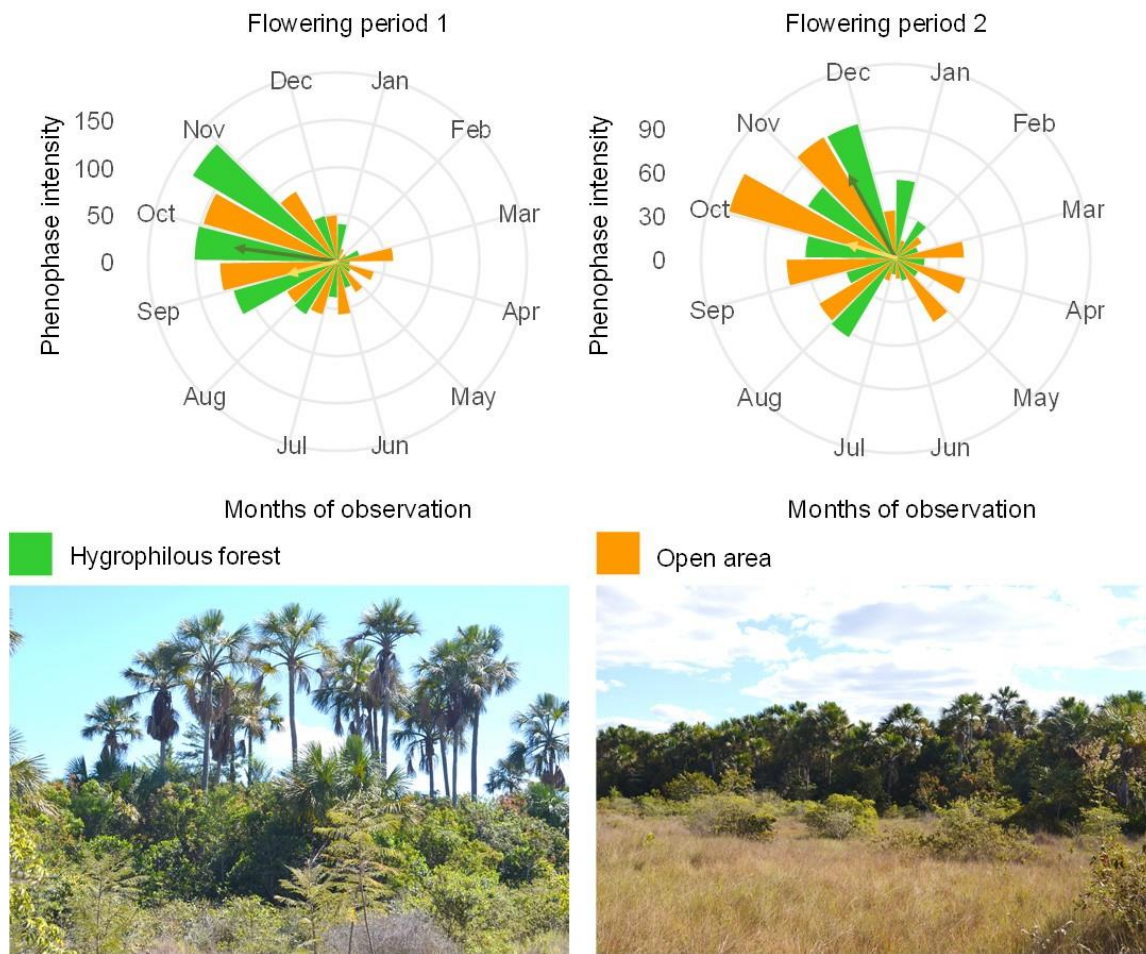
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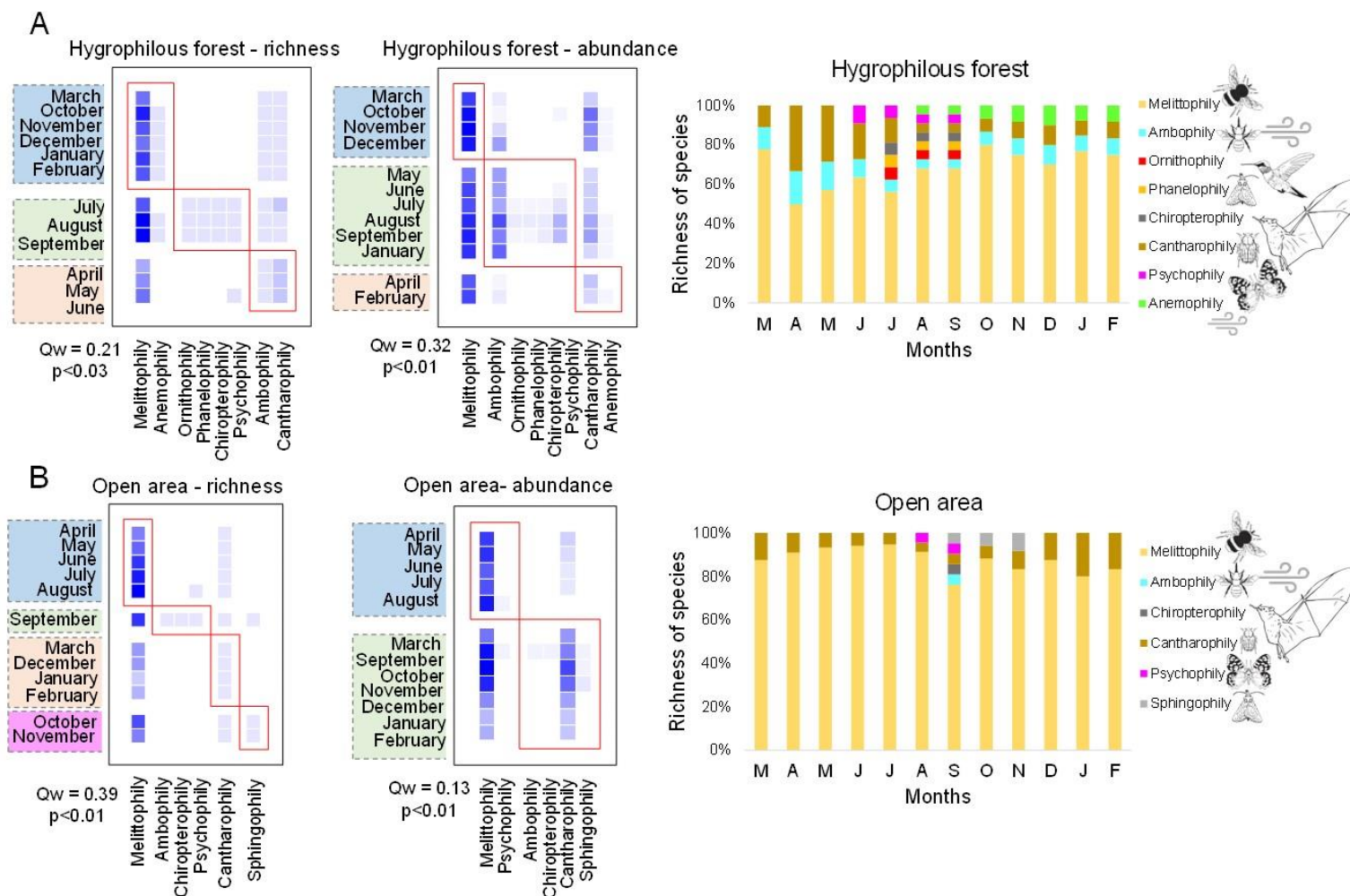


Figure 05.

Table S1. Pollination syndromes, habitat (HF=Hygrophilous Forest, OA=Open Area) and floral resources distribution (phenology) of plant species from Almescla vereda, Minas Gerais, Brazil. Data for the present study were sampled between March 2018 to February 2020.

Family	Species	Habitat	Pollination syndromes	Flowering period	Reference
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.*	HF	Melittophily	July – February	Present study
Annonaceae	<i>Annona</i> sp.	HF	Cantharophily	-	Silva <i>et al.</i> 2012; Farchado <i>et al.</i> 2015
	<i>Xylopia aromatica</i> (Lam.) Mart.	OA	Cantharophily	All year	Present study
	<i>Xylopia emarginata</i> Mart.	HF	Cantharophily	April - July	Present study
Apocynaceae	<i>Himatanthus obovatus</i> (Müll. Arg.) Woodson	OA	Phanelophily	September - November	Present study
Aquifoliaceae	<i>Ilex affinis</i> Gardner*	OA	Melittophily	January – August	Present study
	<i>Ilex</i> sp.*	HF	Melittophily	-	Almeida <i>et al.</i> 2010
Arecaceae	<i>Mauritia flexuosa</i> L.f.	HF/OA	Melittophily /wind	November – March	Present study
	<i>Mauritiella armata</i> (Mart.) Burret*	HF/ OA	Melittophily	October – January	Present study
Burseraceae	<i>Protium spruceanum</i> (Benth.) Engl.*	HF	Melittophily	August - October	Present study
	<i>Protium</i> sp.*	HF	Melittophily	-	Silva Lóz <i>et al.</i> 2019
Calophyllaceae	<i>Calophyllum brasiliense</i> Cambess.	HF	Melittophily	-	Present study
	<i>Kielmeyera speciosa</i> A.St.-Hil.	OA	Melittophily	-	Present study
Caryocaraceae	<i>Caryocar brasiliense</i> Cambess.	OA	Chiropterophily	September	Present study
Connaraceae	<i>Connarus</i> sp.	OA	Melittophily	-	Rodrigues <i>et al.</i> 2014
Chloranthaceae	<i>Hedyosmum Brasiliense</i> Mart. ex Miq.	HF	Anemophily	August – February	Moffatt 2012; Doria <i>et al.</i> 2012
Chrysobalanaceae	<i>Hirtella glandulosa</i> Spreng.	OA	Psychophily	August - September	Silva <i>et al.</i> 2012
Clusiaceae	<i>Symphonia globulifera</i> L.f.	HF	Melittophily	-	Silva <i>et al.</i> 2018

Dilleniaceae	<i>Curatella americana</i> L.	OA	Melittophily	July - October	Present study
Elaeocarpaceae	<i>Sloanea retusa</i> Uittien*	HF	Melittophily	-	Coode 2004
Euphorbiaceae	<i>Croton urucurana</i> Baill.*	HF	Melittophily	January – March	Kinoshita 2006
Fabaceae	<i>Dimorphandra mollis</i> Benth.	OA	Melittophily	December - January	Present study
	<i>Enterolobium gummiferum</i> (Mart.) J. F. Macbr.	OA	Melittophily	-	Present study
			Phanelophily, Ornithophily,		Yamamoto <i>et al.</i> 2007;
	<i>Inga vera</i> Willd.	HF	Chiropterophily (multiple pollination syndrome)	July - September	Almeida <i>et al.</i> 2010
	<i>Tachigali aurea</i> Tul.	OA	Melittophily	-	Present study
	<i>Zygia latifolia</i> (L.) Fawc. & Rendle	HF	Psychophily	July - October	Present study
Lauraceae	<i>Nectandra cissiflora</i> Nees.*	HF	Melittophily	-	Present study
	<i>Nectandra megapotamica</i> (Spreng.) Mez*	HF	Melittophily	-	Present study
Malpighiaceae	<i>Byrsonima intermedia</i> A. Juss.	OA	Melittophily	March - May	Present study
	<i>Byrsonima pachyphylla</i> A.Juss.	OA	Melittophily	All year	Present study
	<i>Byrsonima umbellata</i> Mart ex. A. Juss.	HF	Melittophily	June – October	Present study
	<i>Byrsonima sericea</i> DC.	OA	Melittophily	April – October	Present study
Melastomataceae	<i>Clidemia sericea</i> D. Don	OA	Melittophily	April – October	Melo <i>et al.</i> 1999
	<i>Macairea radula</i> (Bonpl.) DC.	OA	Melittophily	March – December	Present study
	<i>Miconia albicans</i> (Sw.) Triana	OA	-	April - November	Present study
	<i>Miconia burchellii</i> Triana	OA	Melittophily	March - September	Present study
	<i>Miconia corallina</i> Spring	OA	Melittophily	May - November	Present study
	<i>Miconia chamissois</i> Naudin	OA	Melittophily	June – October	Present study
	<i>Miconia elegans</i> Cogn	OA	Melittophily	March – November	Present study
	<i>Miconia ibaguensis</i> (Bonpl.) DC.	OA	Melittophily	June – October	Present study

	<i>Miconia prasina</i> (Sw.) DC.	OA	Melittophily	June - December	Present study
	<i>Miconia</i> sp.	OA	Melittophily	-	Silva <i>et al.</i> 2012
Meliaceae	<i>Guarea kunthiana</i> A.Juss.	HF	Melittophily	-	Present study
Moraceae	<i>Ficus</i> sp.	HF		-	Almeida <i>et al.</i> 2010; Silveira <i>et al.</i> 2020
			Micro-Hymenoptera (wasps)		
Myrtaceae	<i>Eugenia</i> sp.	HF		September	Silva <i>et al.</i> 2012; Silveira <i>et al.</i> 2020
			Melittophily		
	<i>Myrcia</i> sp.	HF	Melittophily	July – September	Silva <i>et al.</i> 2012
Phyllanthaceae	<i>Hyeronima alchorneoides</i> Allemão	HF	Melittophily	January – October	Present study
	<i>Richeria grandis</i> Vahl	HF	Melittophily	August – November	Present study
Primulaceae	<i>Myrsine umbellata</i> Mart.	HF	Melittophily	August - September	Present study
	<i>Ladenbergia cujabensis</i> Klotzsch	HF	Phanelophily, Psychophily,		Wolff 2006
Rubiaceae			Sphingophily (multiple pollination syndrome)	-	
	<i>Ladenbergia</i> sp.	HF	Phanelophily, Psychophily,		Wolff 2006
			Sphingophily (multiple pollination syndrome)	-	
Styracaceae	<i>Styrax oblongus</i> (Ruiz & Pav.) A. DC.	HF	Melittophily	August - November	Present study
Urticaceae	<i>Cecropia pachystachya</i> Trecul.	HF	Ambophily	All year	Monjoin & Wandji 2018
Vochysiaceae	<i>Vochysia guianensis</i> Aubl.	OA	Melittophily	February - August	Present study
	<i>Vochysia rufa</i> Mart.	OA	Melittophily	-	Present study
	<i>Vochysia</i> sp.1	OA	Melittophily	August	Silva <i>et al.</i> 2012
	<i>Vochysia</i> sp.2	OA	Melittophily	May - August	Silva <i>et al.</i> 2012
	<i>Vochysia</i> sp.3	OA	Melittophily	-	Silva <i>et al.</i> 2012

*Species mostly visited by bees but receive visits from other groups such as wasps and flies.

Table S2. Period of pollinator activity, anthesis, corolla shape, color, scent, floral resource and group of pollinators for each pollination syndrome in *vereda* Almescla, Minas Gerais, Brazil.

Pollination Syndromes	Floral traits						Pollinators
	Activity time	Anthesis	Corolla shape	Color	Scent	Resource	Group
Melittophily (Hymenoptera)	Diurnal	Diurnal	Open, dish, tubular, infundibuliform and with landing platform	Ranging from yellow, blue and lilac, with visual néctar and pollen guides	Mild or strong, with a pleasant odor	Nectar, pollen, oil, resins and floral volatiles	Mainly bees
Cantharophily (pollination by beetles)	Diurnal, nocturnal, crepuscular	Diurnal, nocturnal, crepuscular	Dish type, with the sexual organs exposed forming a pollination chamber	Greenish, cream and whitish	Mild or strong, with a pleasant odor	Floral tissues	Beetles
Myophily, Sapromyophily (flies)	Diurnal	Diurnal	Dish type, with exposed sexual organs or flowers with traps that keep flies temporarily trapped	Red, brown, yellow, greenish usually with colored spots, strong shine	Mild or strong (putrid), unpleasant	Nectar, pollen	Flies
Psychophily (butterflies)	Diurnal	Diurnal	Long-tubular corolla, delicate and erect, generally hypocrateriform, brush-shaped or with floral calcars	Red, yellow, orange, blue, white, purple and pink, usually with nectar guides	Mild with a pleasant odor	Nectar	Butterflies
Phalaenophily (moths), Sphingophily (hawkmoths)	Nocturnal	Nocturnal	Tubular (very long and narrow tube) and in a horizontal or pendent position, hypocrateriform, and brush-shaped	White and greenish-white, cream, without nectar guides	Strong (sweet) even narcotic	Nectar	Moths and Sphingids
Ornithophily (birds)	Diurnal	Diurnal	Tubular, in a horizontal or pendant position, also in the shape of a brush, gullet, labiate and mechanically strengthened	Red associated with yellow, also orange, blue, lilac, white, usually without nectar guides	Absent	Nectar	Birds
Chiropterophily (bats)	Nocturnal	Nocturnal	Large, resistant flower, positioned outside the foliage, or campanulate, labiated, brush-shaped, with a large number of stamens	White, greenish, brown and without nectar guides	Strong	Nectar, pollen	Bats

Anemophily (wind pollination)	Diurnal, Nocturnal	Diurnal, Nocturnal	Inconspicuous, large stigmas and exposed stamens	Greenish, whitish	Absent	Pollen	Wind
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CAPÍTULO 2

Artigo formatado de acordo com a Revista *Plant Biology*

Plant pollinator individual-based network: neighborhood effect and pollination in the dioecious tropical palm *Mauritiella armata*

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Short title for use as running head: Plant pollinator individual-based network

Keywords: *Mauritiella armata*, palm pollinator, dioecy, plant height; competition, neighborhood effect.

ABSTRACT

- *Mauritiella armata* (Arecaceae), has great ecological and social importance and is considered a keystone species in their habitat of occurrence. Intraspecific variation in the attributes of individuals (sex, size, resource) and their location in the landscape (neighborhood effect) can influence interactions with pollinators and the role of these individuals in a network of interactions. Here, we describe the network structure of the *M. armata* individuals and their pollinators and evaluate how the variation in attributes and location of individuals can determine their role in the network.
- Individuals were selected from three areas of *veredas* (humid environment) from Cerrado formation, in the semiarid region of southeastern Brazil. Female and male individuals were sampled, and different attributes were measured, such as height, circumference at breast height - CAP, number of inflorescences, registration of nearby species blooming, and group of pollinators. Histochemical evaluations were carried out to verify the difference in attractiveness and type of resource offered by the flowers. An interaction network of *M. armata* individuals was constructed, and the specialization and modularity for the entire network were calculated. We also used two species-level indices (degree and species strength) to understand the variation in the role of individuals and the correlation with attributes.
- The network had a specialized and modular structure. The most frequent group of pollinators was bees, followed by wasps and beetles. There was no difference in the frequency of visits between individuals from different areas, but between female and male individuals, suggesting a strategy used by the species. Bees had a greater degree and species strength, while individuals with a greater number of inflorescences and fewer species blooming in their neighborhood had a high degree and species strength.
- We highlight the importance of considering intraspecific variations of individuals for the network formation, contributing to the understanding of the network structure of individuals of dioecious plants and their pollinators in tropical areas.

57

58 **INTRODUCTION**

59 In a plant population, individuals tend to differ in the use of available resources, and this
60 intraspecific variation is responsible for shaping different ecological processes (Araújo *et al.*,
61 2011; Dall *et al.*, 2012). These processes encompass the interactions between plants and their
62 pollinators (Zywiec *et al.*, 2012; Tur *et al.*, 2014; Arroyo-Correa *et al.*, 2021). This variation
63 among individuals in a population tends to define their role in the community, shaping possible
64 influences on inter- and intraspecific interactions (Bergamo *et al.* 2020).

65 The spatial location of individuals within their populations and the community in which
66 they are inserted can affect their interactions with pollinators, and consequently, the patterns of
67 pollinator sharing among individuals and their role in a network of interactions (Tur *et al.* 2014;
68 Arroyo-Correa *et al.* 2021; Friedemann *et al.* 2022). Therefore, these ecological interactions
69 can influence individual fitness and demography, causing adaptations in the population traits
70 (Arroyo-Correa *et al.* 2021). However, in addition to spatial location, if individuals of the same
71 species present variations in their interactions and in their importance for the maintenance of
72 pollinators that form the network, there tends to be an important role in variability in space,
73 time, and mainly in traits of these individuals (such as height and attractions offered). These
74 individual trait variations can shape the occurrence of interactions and the individual-based
75 network structure (*sensu* Araújo *et al.* 2008; Guimarães Jr. 2020; Arroyo-Correa *et al.* 2021;
76 Friedemann *et al.* 2022).

77 Palm trees have been recognized as keystone species in many tropical ecosystems and
78 are crucial for maintaining the organization and diversity of the ecological communities in
79 which they are part (Cámara-Leret *et al.*, 2017; Muscarella *et al.*, 2020; Cerqueira *et al.*, 2023;
80 Ávila *et al.* 2023). Palms are abundant in tropical areas (Wing *et al.* 1993; Morley 2000;

Eiserhardt *et al.* 2011), and a fundamental resource for pollinator and frugivore communities (Terborgh 1986; Zona & Anderson, 1989; Barford *et al.*, 2011; Muñoz *et al.* 2019; Friedemann *et al.* 2022). Furthermore, this group of plants has practically all parts usable, both by local populations (food, crafts, construction, traditional medicine) and industry (in the production of cosmetics, fabrics, fuel, and medicines) (Balick 1988; Zambrana *et al.* 2007; Sosnowska & Balslev, 2009; Van der Hoek *et al.* 2019).

Mauritiella armata (Arecaceae) is a dioecious palm that has great ecological and social importance, presenting high density where it is present (Resende *et al.* 2012; Ávila *et al.* 2022). Due to their high nutritional value and phytochemical composition, species such as *M. armata* have attracted the attention of researchers and the industrial sector, due to their potential to integrate the food, pharmaceutical and cosmetic sectors (Souza *et al.* 2020). *Mauritiella armata* occurs in flooded environments, in humid areas of the Cerrado, known as *veredas*, and its presence, together with the palm tree *Mauritia flexuosa*, is considered to define these environments (Ávila *et al.* 2022; Nunes *et al.* 2022). Furthermore, human disturbances damaged many vereda areas before we understood their composition, structure, ecosystem services and functional diversity, making this environment highly threatened (Nunes *et al.* 2022; Ávila *et al.* 2022; Luna *et al.* 2024). As a consequence of its dioecious sexual system, *M. armata* needs a biotic agent to perform the pollination. The synchrony in flowering between male and female individuals of *M. armata*, floral traits, and the absence of pollen dispersion through the wind, indicate a type of strategy presented by the species for pollination to occur, possibly through entomophily (Ávila *et al.*, 2022).

Interactions between *M. armata* and pollinators, as well as other diverse species, can occur at different levels of organization, including the individual level (Levin 1992; Margalef 1963; Guimarães Jr. 2020). Thus, as proposed for the ecology of interactions as drivers of

species diversity and occurrence (MacArthur & Levins 1967; Benkman 1999), individuals of *M. armata* represent basic interaction units of the ecological systems in which they are found, and by representing a keystone species that is dioecious and dependent on pollinators, their interactions tend to affect the demography and evolution of their populations in *veredas* communities. These ecological interactions between *M. armata* individuals, in turn, can connect populations of different species that occur in this formation through the supply of resources that can increase the attractiveness of floral visitors (May 1972; Cohen 1977; Pascual & Dunne, 2006; Guimarães Jr. 2020).

Here, we describe the interaction network structure of the palm *Mauritiella armata* and its pollinators and evaluate how variation in traits and resource availability can determine the role of these individuals in the network. We aimed to: (1) identify the pollinators of *M. armata* and describe the structure of the network of individuals and their pollinators (specialization and modularity), characterizing the individuals and groups of pollinators with the most important roles in the network of interactions; and (2) identify the processes responsible for variation in the role of *M. armata* individuals in the network, such as quantity of flowers produced, height of individuals, attractiveness and floral resources of female and male individuals, and spatial location of these individuals in the community. Therefore, we expect that *M. armata* individuals with greater resource availability and smaller size can occupy more central positions in the network (greater degree and strength of the individual). Finally, the spatial context, such as the number of nearby species in flowering (neighborhood effect), can also influence the individual role in the network, where individuals with greater neighborhoods (greater grouped resource diversity) have a more central role in the network.

MATERIAL AND METHODS

129 *Study area*

130 The study was conducted in three *veredas* in the northern region of the State of Minas
131 Gerais, southeastern Brazil. The *veredas* Panelas (15°15'56.03" S; 44°57'20.65" W) and
132 Almescla (15°20'54.9" S; 44°53'84.5" W) are located in the Área de Proteção Ambiental (APA)
133 do Rio Pandeiros, municipality of Bonito de Minas, and the Peruaçu *vereda* (15°01'10.5" S;
134 44°42'15.3" W) in the Parque Estadual Veredas do Peruaçu, municipality of Cônego Marinho
135 (Fig. 1).

136 *Veredas* in the region have two distinct habitats that differ in structure and floristic
137 composition. In open areas, herbaceous and shrub species predominate, characterizing a
138 savanna formation, with moist to dry soil. The interior of the *veredas* had a typical structure of
139 hygrophilous forests, with a prominent water table composed mainly of tree species.
140 *Mauritiella armata* occurs frequently in these two described habitats (Nunes *et al.* 2015; Ávila
141 *et al.* 2016, 2022; Nunes *et al.* 2022; Silva *et al.* 2022). The soil in the region is dystrophic and
142 sandy (Nunes *et al.* 2015) and is classified as Histosol (IUSS Working Group 2015; Nunes *et*
143 *al.* 2022). According to the Köppen classification, the climate of the region is Aw, tropical, with
144 dry winters and rainy summers (Alvares *et al.* 2013). The dry period lasts for five months (May
145 to September), mainly during winter, and the rainy period is defined as between November and
146 January (Azevedo *et al.* 2014). The average annual precipitation in the study area is 920 mm,
147 and the average temperature is 26.8°C (Ávila *et al.* 2022).

148

149 *Mauritiella armata* – species description and evaluated traits

150

151 *Mauritiella armata* is a canopy and sub-canopy palm with thin stems that can be solitary
152 or multiple, forming clumps measuring up to 20 m in height (Souza *et al.* 2020) (Fig. 2). The
153 stems and leaves are covered with thorns (Borchsenius *et al.* 1998; Hiura & Rocha, 2018; Souza

et al. 2020). The species is found in the Guianas, in low-altitude areas in the Amazon Basin, in the Northeast and Center of Brazil, and in humid environments (Souza *et al.* 2020). The fruits are globular, small, fleshy, approximately 3 cm in size, and covered with reddish-brown scales (Borchsenius *et al.* 1998; Souza *et al.* 2020). Its male inflorescences can reach up to 215 cm, with a large production of small flowers, whereas its female inflorescences are smaller, up to 160 cm, with the production of larger flowers (Ávila *et al.* 2022). It exhibits peak flowering at the end of the dry season and beginning of the rainy season (September to October), with synchrony between females and males, mainly in response to temperature. Fruiting occurs during the rainy season and peaks in December and January (Ávila *et al.* 2022).

The traits of *M. armata* individuals and their interaction data were sampled in September 2022, during the peak flowering period of the species. For this, in the three sampled *veredas*, 12 individuals were selected (six females and six males), maintaining the proportion (Fig. 1). The selection of individuals from different populations was conducted with the aim of representing greater variability between individuals and their pollinators. The individuals were chosen based on flower production and accessibility for observing inflorescences, given the extreme difficulty of sampling interactions in palm species. This reflects the knowledge gap and the limited number of studies on the floral biology of palm species and their pollinators. The selected individuals were marked with metal identification plates and georeferenced. Other plant species in the neighborhood within a 10 m radius were counted and recorded in relation to the presence and quantity of flowers. In addition, the height (meters) and circumference at breast height (CAP) of all sampled *M. armata* individuals were measured, as well as the number of inflorescences produced during field observation.

To verify whether there is a difference in the attractiveness and type of resource offered between male and female individuals of *M. armata*, flowers were collected during pre-anthesis

and anthesis, and immersed in a neutral red solution (Kirk 1970) for 5 min to detect lipophilic substances. Morphological traits were recorded using a digital camera attached to a stereomicroscope (Zeiss Stemi 305, Axion Cam ICC 3, Jena, Germany). For histochemical evaluations, samples of petals, stamens, and staminodes were fixed in Karnovsky solution (Karnovsky 1965) for 24 h, dehydrated in an ethanol series, and embedded in 2-hydroxyethylmethacrylate resin (Leica Microsystems, Heidelberg, Germany) (Paiva *et al.* 2011). Transverse and longitudinal sections of 5 μ m density were obtained using a rotating microtome (Histocore Autocut, Leica Biosystems, Heidelberg, Germany). Tests were conducted with Lugol reagent for starch (Johansen 1940), xyloidine-ponceau for proteins (Vidal 1970), reagent Nadi for terpenoids (David & Carde, 1964), and toluidine blue (0.05%, pH 4.7 (O'Brien *et al.* 1964, modified), whose metachromasia allows the identification of mucilages and phenolic compounds. All sections were analyzed and images were obtained using a photomicroscope (Zeiss Lab A1, Axion Cam ICC 3, Jena, Germany).

Interactions sampling between pollinators and individuals of Mauritiella armata

The pollinators of each *M. armata* individual sampled were observed for approximately three hours at each stage (six hours in total), between 7:00 am and 5:00 pm, alternating between the morning and afternoon periods, totaling approximately 72 h of sampling (10 days of observation in total). We only included legitimate interactions when the floral visitor came into contact with the reproductive structures of the flowers, indicating the potential for pollination. Furthermore, the presence of pollen on the body of the pollinator was used as a proxy for *M. armata* pollination. These legitimate visitors will be called “pollinators” here, although we did not further evaluate their role in fruit production for *M. armata* individuals (see Souza *et al.*

2018, 2021). After the visit was recorded, the pollinators were captured with the aid of an entomological net with an extender and a ladder, and stored in individual bottles with ethyl acetate and absorbent paper. The pollinators were examined under a stereomicroscope to observe the presence of pollen. To sample pollen in the pollinator body, small cubes of gelatin stained with fuchsin were used on the bodies of insects, and the gelatin was then placed on microscopic slides (Dafni 1992; Bosch *et al.* 2009; Souza *et al.* 2021). The pollen grains sampled from each pollinator were recorded for the presence and absence of pollen and were differentiated into hetero- and conspecific pollen. After pollen removal, the pollinators were organized in entomological boxes or in bottles with 70% alcohol, morphotyped, and identified at the lowest possible taxonomic level. They were later incorporated into the collection at the Unimontes Plant Ecology Laboratory.

Network metrics and statistical analysis

We constructed an individual-based network of *M. armata* interactions (Alcantara *et al.* 2022; Vissoto *et al.* 2022). This network was built using a matrix in which palm individuals were included in rows and pollinator species in columns. The matrix was completed based on the frequency of interactions between each individual palm and pollinator species. First, sampling effort was evaluated for the *M. armata* network (Chacoff *et al.* 2012; Vizentin-Bugoni *et al.* 2016) to analyze the detection of all possible interactions between palm individuals and their pollinators, during sampling. For this purpose, each combination of an individual and a pollinator species was considered as a “species” and the frequency of each interaction between network pairs represented their “abundance” (Vizentin-Bugoni *et al.* 2016; Alcantara *et al.* 2022). The diversity of interactions was estimated using the Chao1 estimator of species richness

(Chao 1984; Colwell & Coddington, 1994), and the sampling effort was calculated as the ratio between the observed and estimated in relation to the richness of interactions (Chacoff *et al.* 2012). The Chao 1 estimator was calculated using the INEXT package (Hsieh *et al.* 2014) in R (R Development Core Team 2022).

To analyze the interaction network of palm individuals, two network-level metrics were calculated to understand how individuals partition their interactions within the community. Specialization for the entire network was calculated using the H_2' index, which describes how palm individuals distribute their interactions based on the availability of partners throughout the community (Blüthgen *et al.* 2006), and the modularity index, which quantifies the prevalence of interactions within subsets of individuals in the network. Modularity analyses also returned the module occupied by each pollinator species and palm individual in the network because of their affinity and frequency of interaction. The modularity index was calculated using the DIRTLPawb+ algorithm (Beckett 2016) using the *computeModules* function in the Bipartite package in the R program (Dormann *et al.* 2008). As networks indices can be affected by the number of species or individuals interacting in the community and sampling effort (Fründ *et al.* 2016), in addition to the observed values obtained, metrics were also compared using a null model. Here, the Vaznull null model (Vázquez *et al.* 2005) was used, which restricts the connectance, network size, and total number of interactions in each randomization. The estimated confidence interval was 95% for each metric of the 10,000 simulated values, and a significant value of the metric was considered when greater than the confidence interval generated by the randomization of the null model used.

In addition to these two network-level indices, two individual/species-level indices were also calculated for *M. armata* and pollinators that capture distinct properties of an individual or species in the network: 1) degree, expressing the number of interaction partners (pollinators)

that each palm individual interacts with in the network; 2) species or individual strength, which measures the extent to which the set of individuals/species depends on a specific pollinator species or individual (Bascompte *et al.* 2006). All species level indices were quantified using the `specieslevel()` function in the Bipartite package in R (Dormann *et al.* 2008).

We assessed whether the modules formed in the interaction network corresponded to the distribution of the different groups of pollinators sampled from *M. armata* individuals, using the chi-square test. The same test was conducted to verify whether the modules corresponded to the distribution of individuals in the different populations studied (Veredas Peruaçu, Pannels and Almescla). The two calculated individual/species-level indices (degree and strength) were compared to the attributes of palm individuals and pollinator groups using linear models. Furthermore, we assessed whether the frequency of visits varied between male and female individuals (due to the difference in the type of attraction and resources available) and whether there was also variation in the frequency of visits according to the *vereda* where the individual was located. We performed a correlation analysis between the evaluated attributes, and because of the high correlation of some attributes (>0.50 ; Fig. S1), we used only habitat, individual sex, CAP, neighborhood, and number of inflorescences produced in the models.

Thus, the indices of palm individuals and pollinators were used as the response variable, and for *M. armata* individuals, the CAP, habitat, sex of the individual, neighborhood, and number of inflorescences produced were used as predictor variables in the models. For pollinators, the functional group was used as a predictor variable. The following categories were used: bees, beetles, wasps, and others (including groups with less than three species, such as butterflies, ants, flies, and Hemiptera). In addition, the frequency of visits was used as a response variable, and the location of the individual sampled and gender were used as predictor

variables. All statistical analyzes were conducted in the R program (R Development Core Team 2022).

Results

Mauritiella armata – floral and resource description: What traits and resources male and female flowers use to attract visitors?

In *M. armata*, the male flowers are sessile, consisting of three sepals and greenish-yellow petals, with two verticils of yellowish stamens, free fillets, and dorsifixed anthers (Fig. 3A). The petals and stamens tested positive for lipophilic compounds, which were more intensely detected in anthers (Fig. 3B). The epidermis of petals is uniseriate and papillose in some regions; it has a thin cuticle impregnated with terpenoids. The mesophyll is narrow and consists of phenolic-containing idioblasts, fiber bundles, and two or three layers of parenchyma cells with terpenoid droplets (Fig. 3C). Pollen grains are rich in reserves, such as mucilage (Fig. 3D), starch (Fig. 3E), and essential oils mainly in vegetative cells (Fig. 3F). Essential oils are also more representative of exines and form a pollenkit.

The female flowers are sessile and trimeric, with connate sepals and petals of green color. The petals are adnate at the base of the staminoidal ring, which is composed of six infertile, yellowish stamens (Fig. 3G). The petals and anthers of the staminodes tested positive for lipophilic compounds (Fig. 3H). The petals had a uniseriate epidermis with a thin cuticle and multicellular trichomes with thickened and lignified walls, and terpenoids were detected in all of these structures, including the mesophyll (Fig. 3I). The anthers of the staminodes are well-developed, presenting four pollen sacs with a uniseriate epidermis, endothecium, middle layer, and two to three layers of secretory tapetum. No pollen grains were formed, with only tetrads of microspores observed, which indicates that the process was interrupted at the end of

microsporogenesis. The microspores were united by callose and were rich in mucilage (Fig. 3J), proteins (Fig. 3K) and terpenoids (Fig. 3L); they also occur in the epidermis and tapetum.

Mauritiella armata – interactions patterns in the individual based-network

In total, 588 visits were recorded in the female and male flowers of *M. armata*, involving 34 species of pollinators in the 12 individuals (Table S1). The most frequent pollinators were the bees *Apis mellifera* (with 261 visits), followed by *Trigona* sp. (n = 81), *Tetragonisca angustula* (n = 71), *Trigona spinipes* (n = 43) and *Paratrigona lineata* (n = 16). Bees were the richest group (11 species), followed by wasps (10 species), and beetles (four species). The interaction network had a sampling effort of 79% (Fig. S2), was significantly specialized ($H_2' = 0.56$, confidence interval = 0.005 - 0.087) and modular ($Q = 0.51$, confidence interval = 0.094 - 0.1277; Fig. 4). Five modules were detected that were not related to the different groups of pollinators sampled ($X^2 = 18,017$; $df = 24$; $p = 0.80$), sex ($X^2 = 2.53$; $df = 4$; $p = 0.64$), or location of *M. armata* individuals sampled from different populations ($X^2 = 8.6$; $df = 8$; $p = 0.37$; Fig. 4). The frequency of visits did not differ between individuals from the different sampled populations ($F = 2.13$; $p = 0.12$; Fig. 5A). However, the frequency of visits was higher in females (mean $\pm$ standard deviation: $\bar{x} = 6.88 \pm 5.11$) than males ($\bar{x} = 3.58 \pm 5.02$; $F = 4.77$; $p = 0.03$; Fig. 5B).

For *M. armata* pollinators, bees and beetles had similar degrees and species strengths in the network, with bees having the highest degree ($F = 3.46$; $p = 0.03$; Fig. 5C) and species strength ($F = 3.34$; $p = 0.03$; Fig. 5D) than in the other groups (ants, flies, butterflies, and wasps). As for the role of *M. armata* individuals and the variation in their attributes, the degree or number of partners in the network was negatively related to the height and CAP of the individual ($F = 6.58$; $p = 0.02$; $R^2 = 0.34$; Fig. 6A), and the richness of species that formed its

neighborhood ($F = 5.57$; $p = 0.03$; $R^2 = 0.30$; Fig. 6B). However, the number of partners in the network (degree) was positively related to the number of inflorescences produced by individuals ($F = 3.83$; $p = 0.04$; $R^2 = 0.21$; Fig. 6C). In relation to the strength of the network, individuals with greater species richness in their neighborhoods had lower strength in the interaction network ($F = 4.23$; $p = 0.05$; $R^2 = 0.23$; Fig. 6D). No significant effects were found between the habitat and sex of individuals on their role in the network of interactions (degree and strength of the individual; Table 1).

The presence of *M. armata* pollen was verified in 28 (29.1%) of the 96 pollinators. The 28 pollinators belonged to 11 insect species: *Apis mellifera*, *Trigona spinipes*, *Tetragonisca angustula*, *Trigona* sp., *Augochlora* sp., and Apidae sp., a species of ant, the wasp *Brachygastra* sp., and two unidentified species. Bees were the group in which we found the highest records of *M. armata* pollen, mainly in individuals of the species *Apis mellifera*, *Trigona spinipes*, and *Tetragonisca angustula*. It is important to highlight that these species of bees were recorded visiting male and female individuals, and were considered in this study as potential pollinators for *M. armata*. Furthermore, it was possible to verify the presence of several pollen morphotypes (heterospecific pollen) representing different plant species in the neighborhood.

DISCUSSION

Here, we found that generalist insects belonging to different groups, such as bees, wasps, and beetles, are potential pollinators of *M. armata*. Bees were the most important group, with the highest degree and species strength. *Mauritiella armata* individuals with the greatest number of inflorescences and lowest CAP were the most important, with the greatest degree and strength. No correlation was observed between the proximity or sex of *M. armata* individuals with established interactions and the modules conformation in the network.

However, contrary to initial expectations, more neighboring species in flowering, more lower the degree and strength of the individuals in the network. The availability of resources and the height of flowering individuals have already been considered influential traits in mutualistic interactions between plants and pollinators (Dupont *et al.* 2014). Local variation in individuals within a population can also influence these mutualistic interactions (Gómez *et al.* 2011; Guimarães Jr. 2020; Arroyo-Correa *et al.* 2021; Friedemann *et al.* 2022). This study provides results that reinforce these relationships, contributing to the comprehension of the individual-based network structure in semiarid areas and exploring the relationship between intrinsic and extrinsic characteristics as structuring mechanisms that shape the patterns of these interactions.

The dependence of dioecious plants on pollinators is a critical factor for their reproductive success. Owing to the traits and floral resources of *M. armata*, the presence of pollinators is essential to guarantee its reproductive success. The groups sampled in this study are common pollinators of several palm species (Henderson 1986; Balick 1986; Campbell *et al.* 2018; Dumont & Michel, 2018), predominantly performed by beetles, bees, and flies, which have already been recorded in approximately 60% of the palm species (Barfod *et al.*, 2011; Barbosa *et al.*, 2021). The attributes of *M. armata* represent attractions for generalist pollinators, guaranteeing a high frequency of visits and possibly ensuring pollen transport between individuals (Weiblen *et al.* 2000; Núñez-Avellaneda & Carreño-Barrera, 2013). In previous studies, pollination by small insects, considered generalists, was more common in the canopy and less common in the subcanopy and understory (Kress & Beach 1994). *Mauritiella armata* is one of the species that compose the canopy in areas of *veredas*; therefore, the height of this plant may be one of the traits that could influence the presence of these groups of pollinators in this palm tree.

These pollinators and individuals of *M. armata* formed modules that were not related to the different groups of pollinators, nor to the sex and location of the individuals in the different populations sampled. Notably, some modules were formed by individuals from the three sampled populations along the different *veredas*. This can reflect that the variation of these traits in the individuals (e.g., number of inflorescences, CAP, and neighborhood) may be more influential in the formation of these modules than the fact that these individuals are present in the same population or in greater proximity, because even sampling different populations of *M. armata*, the species shared the same groups of pollinators. Furthermore, it is possible to notice that male and female individuals were distributed among the five modules. Thus, variation in the attributes of individuals can cause changes in their pollination niche owing to the different preferences of pollinator species. This tends to dilute the effects of the proximity and sex of these individuals, leading to the formation of spatially and sexually heterogeneous modules (Gómez *et al.* 2014).

In relation to the role of *M. armata* individuals in the network, as the individuals increased in size, the number of partners that interacted with these individuals decreased. Individuals with a greater number of inflorescences presented a higher degree, which may be related to greater visibility of the floral display and greater availability of resources, attracting more pollinators in search of resources and influencing the establishment of interactions (Gómez *et al.* 2014; Arroyo-Correa *et al.* 2021). When considering the degree and strength of the individual in relation to the neighborhood, individuals with a greater number of species flowering in their neighborhood had a lower number of partners and lower interaction strength. The proximity of plants and aggregation of individuals or species can influence the number of pollinators (Dupont *et al.* 2011). The overlap of flowering between individuals increases the abundance of flowers, increasing the attractiveness to pollinators and the availability of partners, which can

lead to increased competition between plant species in search of pollinators (Rathcke 1983; Soares *et al.* 2021). These interactions are described as negative – generating competition, and if different species of flowering plants share pollinators, they can lead to competition for pollination services, which is often detrimental to one or more species (Mitchell *et al.* 2009; Braun & Lortie, 2019; Ashman *et al.* 2020). Competition can decrease patterns diversity and affect reproductive performance by reducing the amount of pollen on the stigmas. Therefore, the effects of competition will probably be more influential in species that completely depend on pollinators for fertilization, as is the case with dioecious species (Mitchell *et al.* 2009; Ashman *et al.* 2020). Thus, the increase in species flowering in the neighborhood caused a reduction in visits to *M. armata*, which may be related to a tendency for competition between *M. armata* individuals and their neighborhood in search of pollinators, supported by the negative density-dependence (NDD) (see Bergamo *et al.* 2020). It is expected that extrinsic characteristics, such as close species flowering, may be especially relevant to plants, as they are non-mobile organisms, conditioned to experience local environmental conditions. The neighborhood effect shapes the importance of individuals in the ecological network (degree and strength of the individual) and promotes spatially heterogeneous interactions within populations (Arroyo-Correa *et al.* 2021; Friedemann *et al.* 2022).

In this study, no differences were found in the roles of male and female individuals in the interaction network, except for the frequency of visits, which was higher for female individuals. Morphoanatomical sections and histochemical tests on female flowers of *M. armata* showed the presence of terpenoids in the flower regions (petals, trichomes, and microspores), which may be related to the pollinators attraction. The petals and anthers in palm flowers have an affinity for lipophilic compounds, which may contribute to the anchoring of pollen grains (Mazzottini-dos-Santos *et al.* 2015). During the flowering period, pollinators visit

female flowers, probably because of the similarity in olfactory signals released by male and female inflorescences. Furthermore, anthers of staminodes have microspores that can act as a different type of resource for pollinators in female inflorescences. These structures are present in the epidermis and secretory tapetum of the flowers. However, there is the presence of trichomes with thick lignified walls that can make it difficult for insects to access the microspores. The efficiency of this strategy could be increased by synchronizing the flowering period with male inflorescences and insects (Auffray *et al.* 2017).

CONCLUSIONS

Limiting the scale of network analysis to the individual level can contribute to the understanding of the mechanisms of ecosystem services as well as plant population dynamics. When data are used to describe interactions at the species level, intrapopulation variations in interactions can be neglected (Vissoto *et al.* 2022). Thus, the results found here can contribute to the understanding of intraspecific variations in individuals of a keystone palm tree, helping to identify the patterns found in the formation of the network between individuals and their pollinators and in the processes involving their dynamics. The network of interactions between *M. armata* individuals and their pollinators presented a specialized and modular structure, with different groups of small pollinators involved in the interactions, with bees, wasps, and beetles being the most frequent, highlighting the importance of these groups in the pollination of *M. armata*. There were no differences in the frequency of visits between individuals in the sampled *veredas*, but female individuals had a higher frequency of visits, which may be related strategy associated with the presence of microspores in floral parts. Bees had higher degree and strength, whereas individuals with a greater number of inflorescences and fewer species flowering in their neighborhood had higher degree and strength. This highlights the importance of

intraspecific variation in *M. armata* individuals, their role in the network construction, and the connection between individuals and their pollinators. Variations in individual plant characteristics can influence the attraction and pollination of these plants. Furthermore, understanding the role of individuals in network formation is essential for understanding ecosystem services in natural environments, mainly considering dioecious species.

FUNDING

This research was supported by the Long-term Ecological Research Network (PELD-VERE) of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 441440/2016-9; 441583/2020-2; 308877/2019-5), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES 88887.136273/2017-00), and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG APQ-02166-21, APQ-04816-17; CRAPPM- 00539-18; APQ-02166-21). We also thanks FAPEMIG (FAPEMIG/RED-00253-16) for the support and for the last author scholarship.

ACKNOWLEDGEMENTS

Postgraduate Program in Applied Botany, to the field assistance of the Plant Ecology Laboratory (Universidade Estadual de Montes Claros), support from RESA (Rede de Serviços Ambientais) and logistical support from the Instituto Estadual de Florestas, in the Minas Gerais State.

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Legends list

Fig. 1 Location of individuals of *Mauritiella armata* sampled in *veredas* in the north of the state of Minas Gerais, southeastern Brazil.

Fig. 2 Female individual of *Mauritiella armata*. In detail, the palmate leaves and the stipe with the presence of rigid thorns (A-C), inflorescences (B) and infructescences (D).

Fig. 3 Morphology and histochemistry of staminate and pistillate flowers of *Mauritiella armata*. (C-F, I -L - longitudinal sections. (J, K - cross sections). (A) Sessile, trimerous staminate flowers, greenish-yellow petals. (B) Lipophilic compounds (red) in sepals, fillets and anthers (arrowheads). (C) Terpenoids (purple) in the cuticle and subepidermal layers of the petals (arrowheads). (D) Pollen grains rich in mucilage (purple), (E) starch (black) and (F) essential oils (blue) (arrowheads). (G) Pistillate, sessile, trimerous flowers, with green sepals and petals and six staminodes. (H) Lipophilic compounds (red) in the petals and anthers of staminodes (arrowheads). (I) Terpenoids (purple) in the cuticle, epidermis, subepidermal layers and in trichomes (highlighted) of the petals (arrowheads). (J) Staminode anthers have spores rich in callose (blue) and mucilage (purple), (K) proteins (red) and terpenoids (purple) (arrowheads). **at** - anther; **cu** - cuticle; **en** - endothecium; **ep** - epidermis; **et** - staminode; **ft** - fillet; **gc** - generative cell; **ml** - middle layer; **ms** - microspores; **pi** - phenolic idioblast; **pt** - petal; **se** - sepal; **st** - stigma; **ta** - carpet; **tr** - trichome; **vn** - vegetative cell nucleus.

Fig. 4 Network of interactions between pollinators and different individuals of *Mauritiella armata* sampled in the *veredas* studied in September 2022. Male and female individuals and the different groups of pollinators sampled are highlighted in the network. The graphs below show the occurrence of different groups of pollinators in the different modules and the *vereda* of origin of each individual of *M. armata* sampled.

Fig. 5 A) Frequency of pollinator species interactions in relation to the location of the *Mauritiella armata* individuals sampled. B) Frequency of interactions between pollinator species in relation to the sex of the *Mauritiella armata* individuals sampled. C) Difference in degree between the different groups of pollinators sampled in individuals of *Mauritiella armata*. D) Difference in the species strength between the different groups of pollinators sampled in individuals of *Mauritiella armata*.

Fig. 6 Degree in relation to the size of the individuals – CAP (A), number of flowering species in the neighborhood (B) and number of inflorescences produced by the individuals of *Mauritiella armata* sampled (C). Species strength

of the individual in relation to the number of flowering species in the neighborhood of the *Mauritiella armata* individuals sampled.

Table 1 Correlation of the degree and species strength of the individual in relation to the attributes and spatial context of the different individuals of *Mauritiella armata* sampled in the *veredas* studied in September 2022.

Supplementar material

Fig. S1 Graph and correlation table of the evaluated attributes of the different individuals of *Mauritiella armata* sampled in the *veredas* studied in September 2022. Correlation values greater than 0.50, only one of the attributes in the models was considered.

Fig. S2 Rarefaction and extrapolation curve for the network of *Mauritiella armata* individuals sampled.

Table S1. List of individuals of *Mauritiella armata* sampled and their pollinators, functional group, sex and sampling location (*vereda*).

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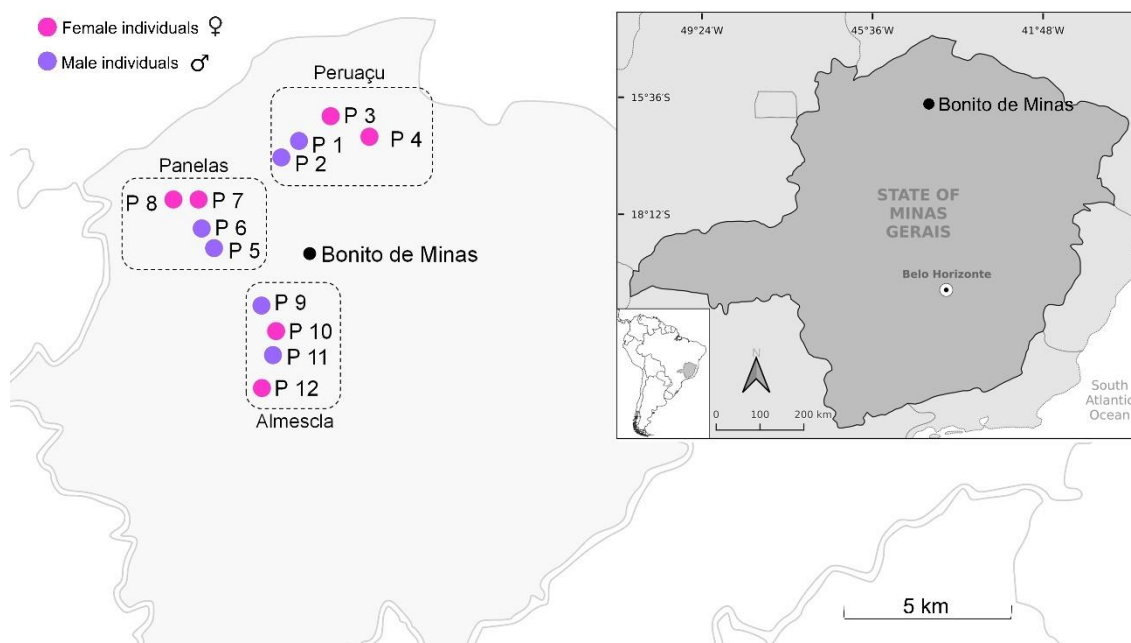


Fig. 1

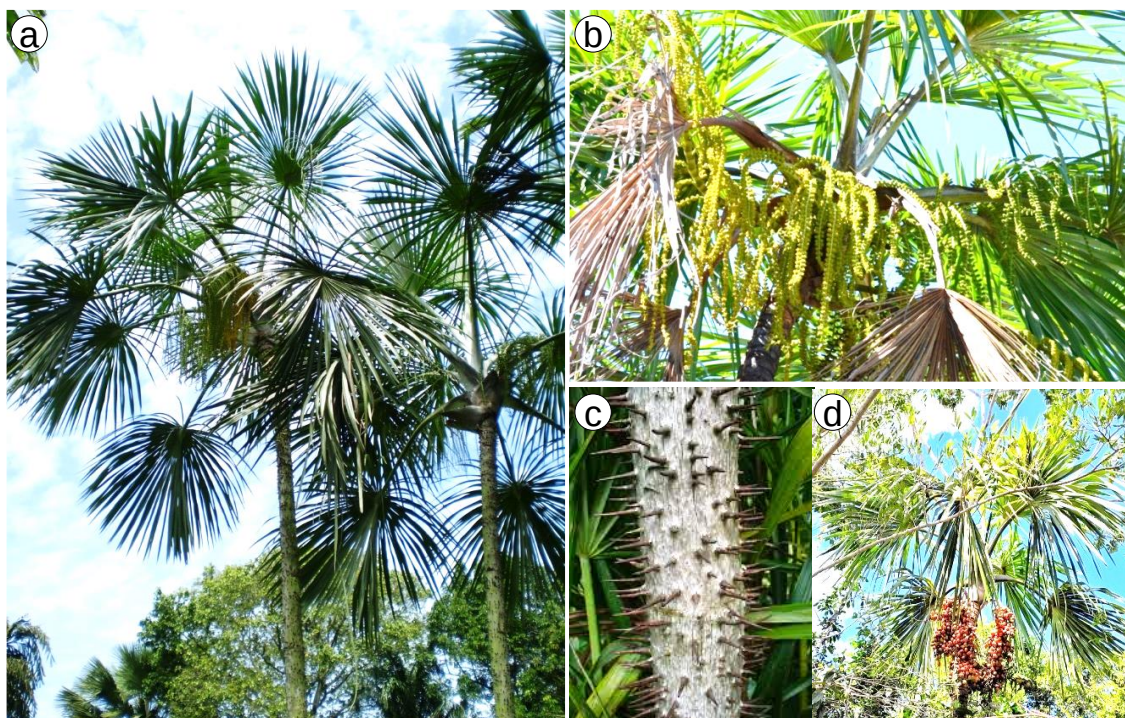


Fig. 2

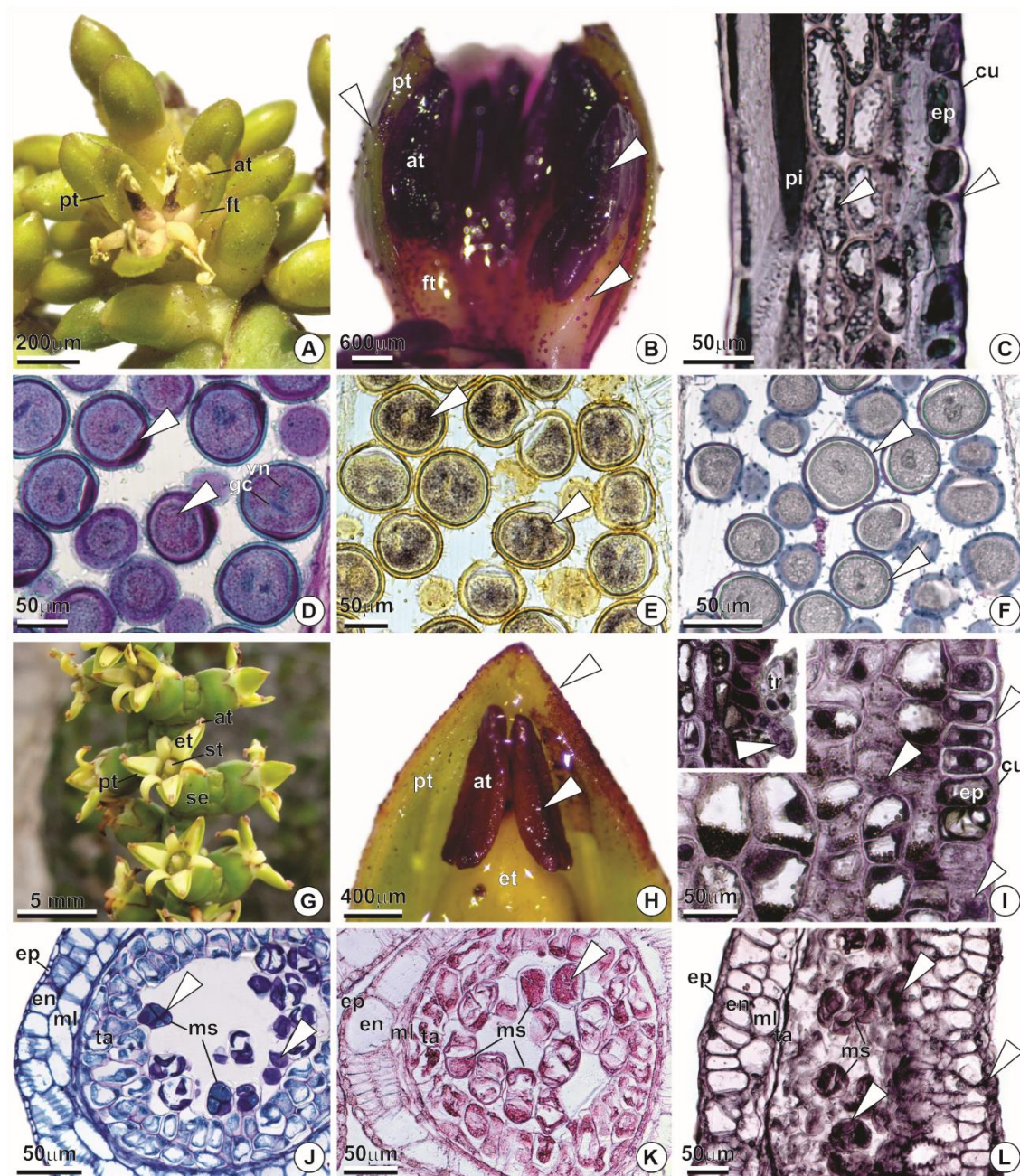


Fig. 3

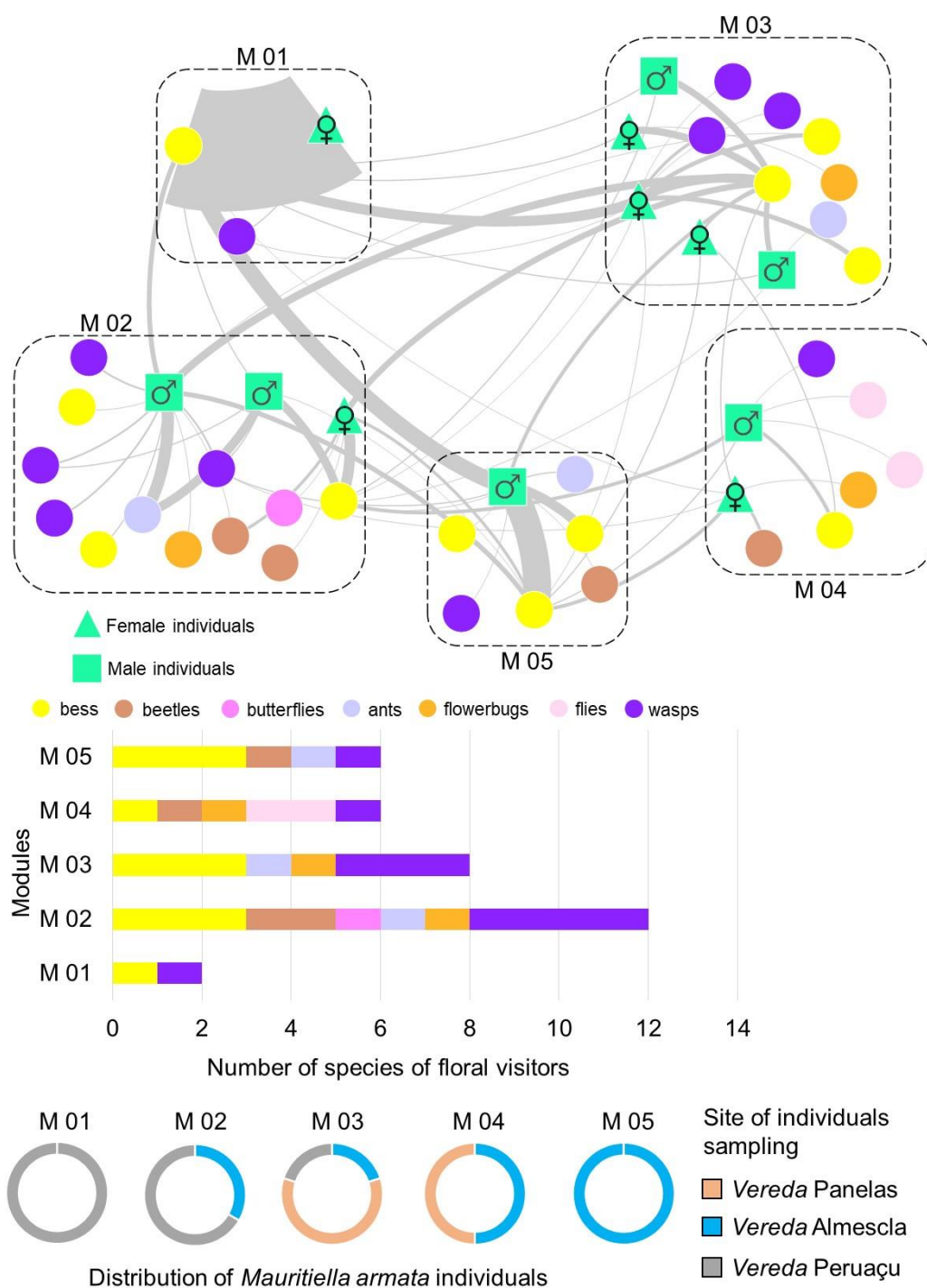


Fig. 4

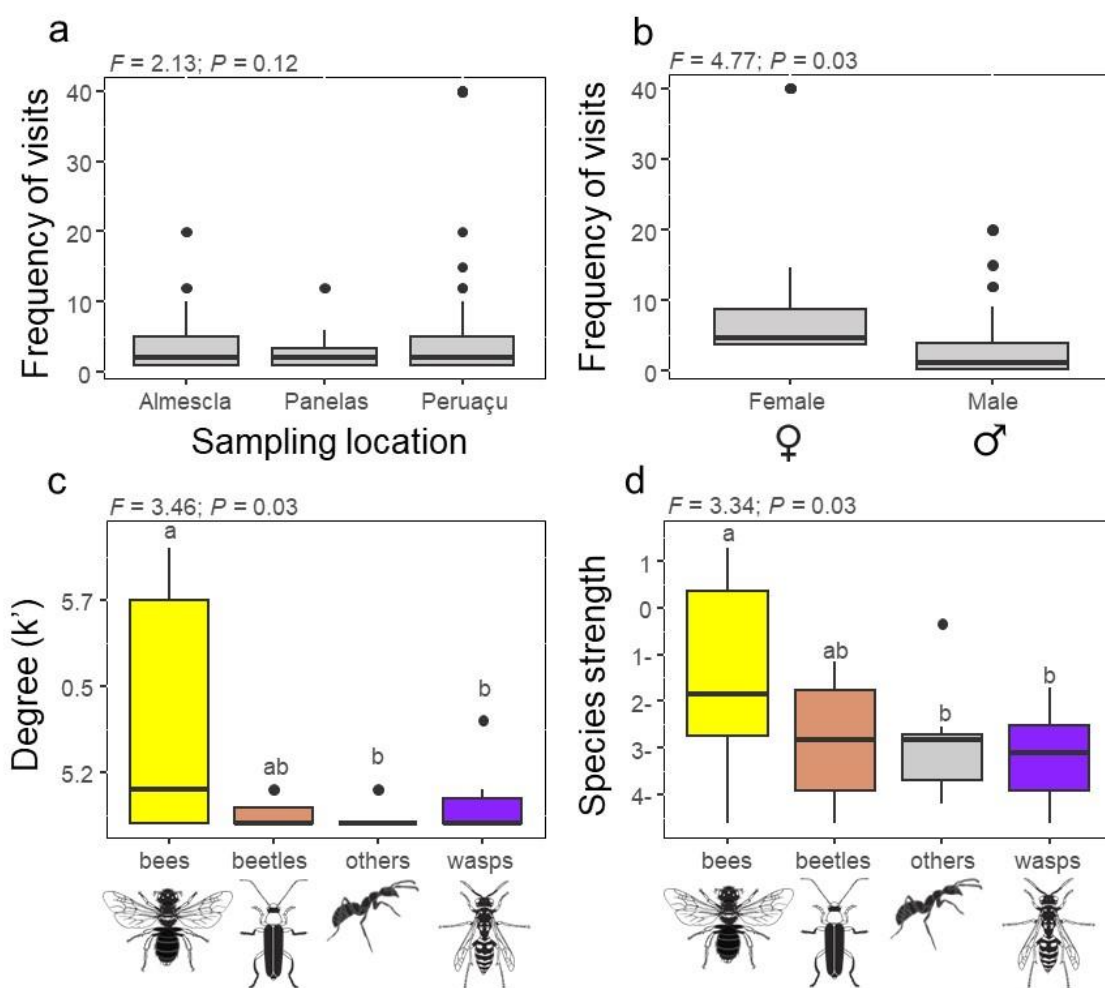


Fig. 5

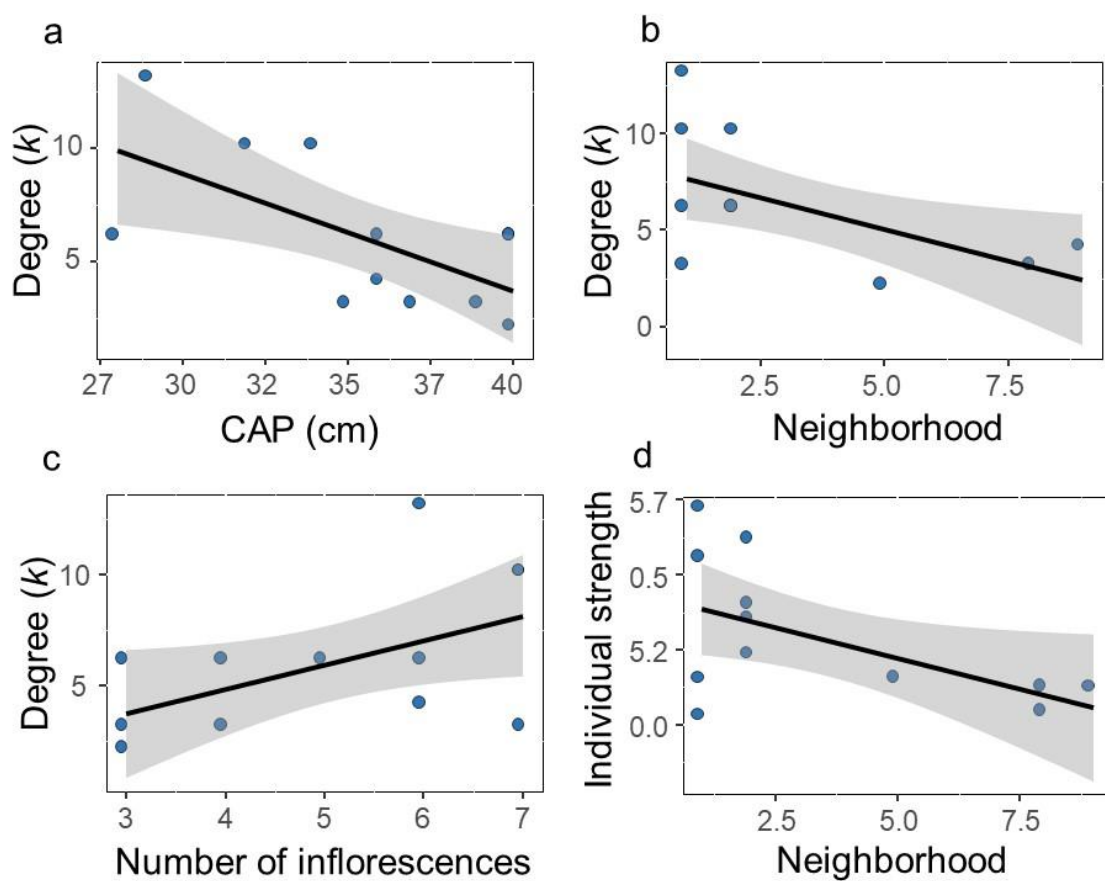


Fig. 6

Table 1

Metrics		<i>F</i>	Residual standard error	<i>df</i>	<i>R</i> ²	<i>P</i> value
Habitat	Degree (k)	3.11	3.12	10	0.16	0.11
	Individual strength	2.54	2.21	10	0.12	0.14
Sex	Degree (k)	1.03	3.41	10	0.00	0.33
	Individual strength	0.48	2.41	10	0.04	0.50
CAP	Degree (k)	6.58	2.78	10	0.34	0.02
	Individual strength	2.75	2.19	10	0.14	0.13
Number of inflorescences	Degree (k)	3.83	3.04	10	0.21	0.04
	Individual strength	2.60	2.20	10	0.13	0.14
Neighborhood	Degree (k)	5.57	2.87	10	0.30	0.03
	Individual strength	4.23	2.07	10	0.23	0.05

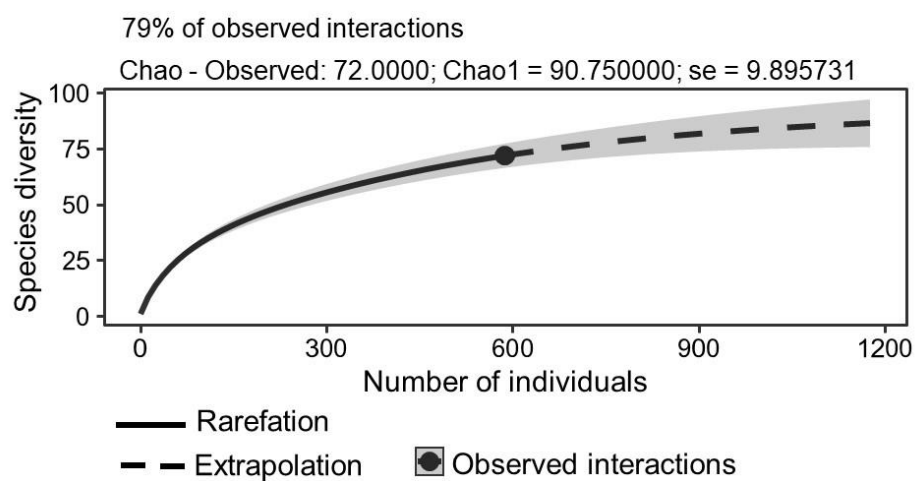


Fig. S1

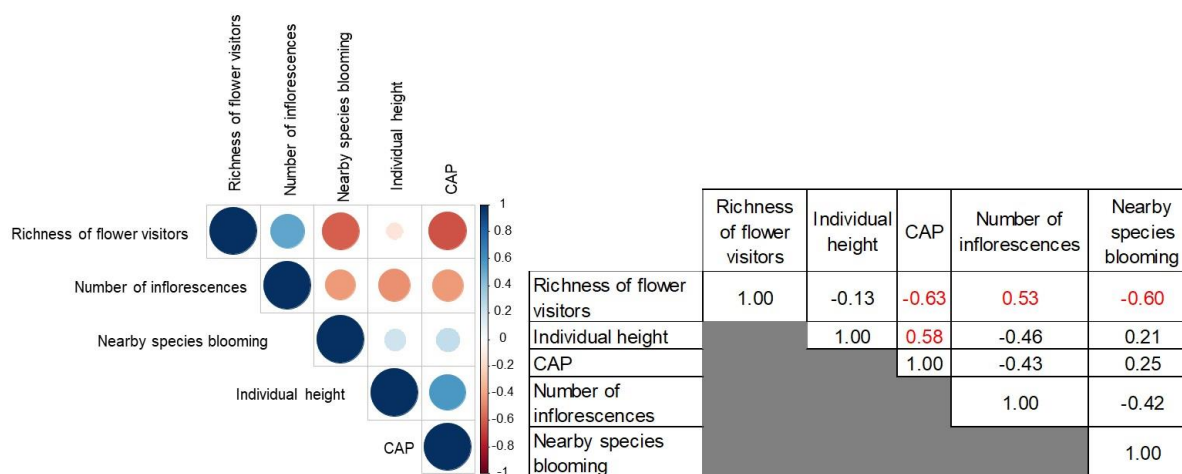


Fig. S2

Table S1.

Individual	Identification	Group	Frequency	Sex	Vereda
P1	<i>Trigona spinipes</i>	bee	5	male	peruacu
P1	<i>Trigona spinipes</i>	bee	1	male	peruacu
P1	Formicidae sp. 2	ant	15	male	peruacu
P1	<i>Brachygastra</i> sp.	wasp	2	male	peruacu
P1	<i>Apis mellifera</i>	bee	2	male	peruacu
P1	Vespidae sp. 3	wasp	2	male	peruacu
P1	<i>Trigona spinipes</i>	bee	5	male	peruacu
P1	<i>Trigona spinipes</i>	bee	3	male	peruacu
P1	<i>Tetragonisca angustula</i>	bee	1	male	peruacu
P2	<i>Trigona</i> sp.	bee	12	male	peruacu
P2	Vespidae sp. 2	wasp	3	male	peruacu
P2	Curculionidae sp. 1	beetle	1	male	peruacu
P2	<i>Augochlora</i> sp.	bee	1	male	peruacu
P2	Vespidae sp. 3	wasp	3	male	peruacu
P2	<i>Brachygastra</i> sp.	wasp	3	male	peruacu
P2	Formicidae sp. 2	ant	20	male	peruacu
P2	<i>Tetragonisca angustula</i>	bee	4	male	peruacu
P2	<i>Tetragonisca angustula</i>	bee	1	male	peruacu
P2	Megachilidae sp.	bee	2	male	peruacu
P2	<i>Tetragonisca angustula</i>	bee	1	male	peruacu
P2	<i>Apis mellifera</i>	bee	4	male	peruacu
P2	Vespidae sp. 8	wasp	3	male	peruacu
P2	<i>Trigona</i> sp.	bee	1	male	peruacu
P2	<i>Tetragonisca angustula</i>	bee	2	male	peruacu
P2	Apidae sp.	bee	1	male	peruacu
P2	<i>Apis mellifera</i>	bee	4	male	peruacu
P2	Hemiptera sp. 2	flowerbug	1	male	peruacu
P3	<i>Apis mellifera</i>	bee	10	female	peruacu
P3	Vespidae sp. 4	wasp	1	female	peruacu
P3	Vespidae sp. 6	wasp	1	female	peruacu
P3	<i>Trigona</i> sp.	bee	1	female	peruacu
P3	<i>Apis mellifera</i>	bee	1	female	peruacu
P3	<i>Tetragonisca angustula</i>	bee	1	female	peruacu
P3	<i>Trigona spinipes</i>	bee	1	female	peruacu
P3	<i>Apis mellifera</i>	bee	1	female	peruacu
P3	<i>Apis mellifera</i>	bee	2	female	peruacu

P3	<i>Apis mellifera</i>	bee	3	female	peruacu
P3	<i>Apidae</i> sp. 3	bee	8	female	peruacu
P3	<i>Trigona</i> sp.	bee	1	female	peruacu
P3	<i>Trigona</i> sp.	bee	12	female	peruacu
P3	<i>Vespidae</i> sp. 5	wasp	1	female	peruacu
P3	<i>Apidae</i> sp.	bee	7	female	peruacu
P3	<i>Vespidae</i> sp. 1	wasp	5	female	peruacu
P4	<i>Vespidae</i> sp. 4	wasp	2	female	peruacu
P4	<i>Apis mellifera</i>	bee	40	female	peruacu
P4	<i>Apis mellifera</i>	bee	40	female	peruacu
P4	<i>Apis mellifera</i>	bee	40	female	peruacu
P4	<i>Apis mellifera</i>	bee	40	female	peruacu
P4	<i>Apis mellifera</i>	bee	40	female	peruacu
P5	<i>Diptera</i> sp.	fly	1	male	panelas
P5	<i>Vespidae</i> sp. 7	wasp	1	male	panelas
P5	<i>Diptera</i> sp. 2	fly	1	male	panelas
P5	<i>Trigona spinipes</i>	bee	1	male	panelas
P5	<i>Trigona spinipes</i>	bee	1	male	panelas
P5	<i>Trigona spinipes</i>	bee	3	male	panelas
P5	<i>Tetragonisca</i> sp.	bee	1	male	panelas
P5	<i>Tetragonisca</i> sp.	bee	5	male	panelas
P5	<i>Tetragonisca angustula</i>	bee	2	male	panelas
P5	<i>Trigona spinipes</i>	bee	1	male	panelas
P6	<i>Trigona</i> sp.	bee	5	male	panelas
P6	<i>Trigona spinipes</i>	bee	2	male	panelas
P6	<i>Apis mellifera</i>	bee	2	male	panelas
P6	<i>Trigona</i> sp.	bee	6	male	panelas
P7	<i>Hemiptera</i> sp. 1	flowerbug	1	female	panelas
P7	<i>Trigona</i> sp.	bee	12	female	panelas
P7	<i>Apis mellifera</i>	bee	2	female	panelas
P8	<i>Trigona</i> sp.	bee	4	female	panelas
P8	<i>Tetragonisca</i> sp.	bee	2	female	panelas
P8	<i>Tetragonisca angustula</i>	bee	2	female	panelas
P9	<i>Formicidae</i> sp. 3	ant	1	male	almescla
P9	<i>Trigona</i> sp.	bee	5	male	almescla
P9	<i>Apis mellifera</i>	bee	2	male	almescla
P9	<i>Trigona</i> sp.	bee	2	male	almescla
P9	<i>Trigona</i> sp.	bee	1	male	almescla
P9	<i>Trigona</i> sp.	bee	1	male	almescla
P9	<i>Trigona spinipes</i>	bee	1	male	almescla
P10	<i>Trigona</i> sp.	bee	1	female	almescla
P10	<i>Hemiptera</i> sp. 3	flowerbug	1	female	almescla
P10	<i>Curculionidae</i> sp. 2	beetle	5	female	almescla
P10	<i>Tetragonisca angustula</i>	bee	2	female	almescla
P10	<i>Trigona</i> sp.	bee	1	female	almescla
P10	<i>Brachygastra</i> sp.	wasp	1	female	almescla

P10	<i>Apis mellifera</i>	bee	1	female	almescla
P10	<i>Tetragonisca angustula</i>	bee	4	female	almescla
P11	<i>Apis mellifera</i>	bee	3	male	almescla
P11	<i>Trigona</i> sp.	bee	5	male	almescla
P11	Ceratopogonidae sp.	fly	1	male	almescla
P11	Apidae sp. 2	bee	1	male	almescla
P11	<i>Apis mellifera</i>	bee	10	male	almescla
P11	<i>Paratrigona lineata</i>	bee	1	male	almescla
P11	<i>Paratrigona lineata</i>	bee	1	male	almescla
P11	<i>Paratrigona lineata</i>	bee	1	male	almescla
P11	Formicidae sp. 1	ant	2	male	almescla
P11	<i>Trigona</i> sp.	bee	1	male	almescla
P11	<i>Trigona spinipes</i>	bee	1	male	almescla
P11	<i>Tetragonisca angustula</i>	bee	20	male	almescla
P11	<i>Apis mellifera</i>	bee	10	male	almescla
P11	<i>Paratrigona lineata</i>	bee	5	male	almescla
P11	<i>Paratrigona lineata</i>	bee	8	male	almescla
P11	<i>Tetragonisca angustula</i>	bee	12	male	almescla
P11	Vespidae sp. 9	wasp	1	male	almescla
P11	<i>Tetragonisca angustula</i>	bee	1	male	almescla
P11	<i>Brachygastra</i> sp.	wasp	2	male	almescla
P11	<i>Tetragonisca angustula</i>	bee	7	male	almescla
P11	<i>Tetragonisca angustula</i>	bee	6	male	almescla
P11	<i>Apis mellifera</i>	bee	4	male	almescla
P12	<i>Tetragonisca angustula</i>	bee	2	female	almescla
P12	Curculionidae sp. 1	beetle	4	female	almescla
P12	<i>Trigona spinipes</i>	bee	6	female	almescla
P12	<i>Tetragonisca angustula</i>	bee	3	female	almescla
P12	<i>Trigona spinipes</i>	bee	5	female	almescla
P12	<i>Trigona</i> sp.	bee	2	female	almescla
P12	<i>Trigona spinipes</i>	bee	6	female	almescla
P12	<i>Trigona</i> sp.	bee	6	female	almescla
P12	<i>Trigona</i> sp.	bee	2	female	almescla
P12	<i>Trigona spinipes</i>	bee	1	female	almescla
P12	Curculionidae sp. 1	beetle	1	female	almescla
P12	Curculionidae sp. 3	beetle	1	female	almescla
P12	Lepidoptera	butterfly	1	female	almescla

ANEXO 2

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Abbreviation: List with abbreviations where appropriate.

Abstract: The abstract must be usable as a stand-alone document and must not exceed 250 words. For all papers submitted from 2016 onwards, a structured abstract is required using four bullet points to indicate (1) the research conducted including its rationale, (2) central methods applied, (3) key results, and (4) main conclusions including key points of discussion. It should not contain citations of other papers. For reviews, bullet points do not apply.

The following sections cover the usual contents: Introduction, Materials and Methods, Results, Discussion, Acknowledgements, References (see below), Tables (see below), Figure legends (see below), Illustrations (see below).

In Materials and Methods, Results and Discussion subheadings are possible. If an author chooses to combine sections Results and Discussion, an additional section Conclusions can be added, but this must be brief.

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Choose subheadings as appropriate but do not use a numbering system. Title page, Key words, Abstract and other items as for full length papers.

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Electronic artwork

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If you should encounter difficulties upon submitting figures and graphics, please contact the editorial office by e-mail under annette.schlierenkamp@ctp.uni-freiburg.de or by telephone under ++ 49/(0)761/203-8300.

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Gage J.D., Tyler P.A. (1991) *Deep-sea Biology: A Natural History of Organisms at the Deep-sea Floor*. Cambridge University Press, Cambridge, UK: 504 pp.
Lester R.N., Hasan S.M.Z. (1991) Origin and domestication of the brinjal eggplant, *Solanum melongena*, from *S. incanum*, in Africa and Asia. In: Hawkes J.G., Lester R.N., Nee M., Estrada N. (Eds), *Solanaceae III: Taxonomy, Chemistry, Evolution*. Royal Botanic Gardens, Kew; London, UK: 369-387.

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Immediately after acceptance of a manuscript, the authors should:

- prepare a .doc file which includes:

- the article title;
 - the authors' names (corresponding author indicated by an asterisk); and
 - a 1-sentence summary (maximum 200 characters) summarizing the key findings presented in the paper.
- Submit a figure that:
 - best represents the scope of the paper;
 - o is in .tiff or .eps file formats;
 - o is within the dimensions of 50mm x 60mm; and
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Note that common abbreviations can be used without explanation. Others must be explained. In case of doubt always give an explanation. Use FW = fresh weight and DW = dry weight.

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Scientific names should be cited in their complete form when first mentioned with genus - species - authority - cultivar (cv.) or subspecies (ssp.) where appropriate. Latin names should be underlined or typed in italics. Subsequently the generic names should be abbreviated, but avoid confusion: e.g. use *A. comosus* if the only genus with a first letter A in your paper is *Ananas*; but use unambiguous abbreviations if you have more than one genus with the same first letter, e.g. *Ananas comosus*, *Aechmea nudicaulis* = *A. comosus*, *Ae. nudicaulis*, etc. Common names of organisms must be accompanied by the correct scientific name when first mentioned. For rare or exotic genera it may be useful to give the name of the family and/or higher taxon in brackets when first mentioned.

CAPÍTULO 3

Artigo formatado de acordo com a Revista *Plant Biology*

Interações entre *Mauritia flexuosa* L.f (Arecaceae) e seus polinizadores: caracterização da rede de indivíduos de palmeira-chave em ambiente de veredas

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Título curto para cabeçalho: Polinização em espécie-chave no Cerrado brasileiro

Palavras-chave: baixa especialização; polinização em palmeiras; entomofilia

RESUMO

- *Mauritia flexuosa* (Buriti) é uma palmeira dioica, espécie-chave e dependente de polinizadores, apresentando distintos agentes em diferentes locais, variando de anemofilia a entomofilia. O objetivo é identificar os potenciais polinizadores em *M. flexuosa* em ecossistemas de veredas, levando em consideração sua plasticidade fenotípica, capaz de influenciar na diversidade dos agentes polinizadores. Procuramos também descrever a estrutura da rede de interações entre os indivíduos da palmeira e seus polinizadores, analisar os atrativos dos indivíduos de *M. flexuosa* para o maior número de parceiros e força da espécie e apresentar os polinizadores que compartilham flores masculinas e femininas.
- Foram amostrados indivíduos femininos e masculinos de *M. flexuosa* em áreas de veredas, sudeste do Brasil. Nesses indivíduos foi realizada a medição de diferentes atributos dos indivíduos e caracterização dos grupos de polinizadores. Foi montada uma rede de interações de indivíduos para *M. flexuosa* e calculada a especialização e modularidade para toda a rede, com dois índices, em nível de indivíduos para *M. flexuosa* e de espécies para seus polinizadores: grau e força da espécie.
- Insetos como abelhas, vespas, besouros, moscas e hemípteras foram observados nas inflorescências, com 16 espécies de polinizadores coletadas em ambos os sexos florais. A rede de interações não foi significativamente especializada e modular. As inflorescências nos indivíduos masculinos atraíram maior número de polinizadores, sendo as abelhas com maior força de espécie e abelhas, besouros e vespas apresentaram maior grau na rede.
- Através da rede de interações, demonstramos que espécies de abelhas, besouros, vespas e moscas são os potenciais polinizadores de *M. flexuosa* em ecossistema de veredas.

49 Trabalhos como este são fundamentais para compreensão das estratégias e mecanismos
50 reprodutivos de palmeiras, bem como da conservação da espécie e seus polinizadores,
51 a fim de assegurar suas interações.

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68 INTRODUÇÃO

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70 A família Arecaceae possui aproximadamente 2.600 espécies e está amplamente
71 distribuída pelos trópicos (Baker & Dransfield 2016). As palmeiras são consideradas como
72 espécies-chaves por representarem um recurso fundamental para comunidades de polinizadores
73 e frugívoros (Friedemann *et al.* 2022). Apresentam diversos sistemas sexuais, até mesmo flores
74 masculinas e femininas separadas de várias maneiras, no espaço e tempo, para favorecer a
75 polinização cruzada junto aos agentes de polinização (Barfod *et al.* 2011; Nadot *et al.* 2016). A
76 dioícia, onde flores masculinas e femininas nascem em indivíduos diferentes, está presente na
77 família, porém com menos frequência (Renner & Ricklefs 1995; Nadot *et al.* 2016). Espécies
78 que apresentam a dioícia como sistema sexual, são dependentes dos agentes polinizadores, por
79 isso, possuem mecanismos que facilitam a ação dos polinizadores, como atributos florais para
80 atração, recursos disponíveis e grande quantidade de pólen (Silva *et al.* 2022).

81 As pressões seletivas devido às interações dos polinizadores podem influenciar nas
82 características morfológicas das flores de palmeiras, sendo que o tamanho e a quantidade de
83 flores masculinas e femininas tem sido relacionada à atração dos polinizadores (Kriebel 2014;
84 Nadot *et al.* 2016). Em palmeiras dioicas, as flores masculinas são mais abundantes do que as
85 flores femininas e oferecem a maior quantidade de recursos aos visitantes florais, enquanto as
86 flores femininas são descritas como não recompensadoras (Núñez-Avellaneda & Carreño 2016;
87 Auffray *et al.* 2023; Ávila *et al.* 2023). Mudanças na ocorrência de polinizadores, seja pela
88 diversidade, abundância ou fenologia, pode levar a modificações na transferência de pólen entre
89 os sexos, reduzindo o sucesso reprodutivo da planta (Auffray *et al.* 2023).

90 A palmeira *Mauritia flexuosa* L.f (Arecaceae), popularmente conhecida como Buriti,
91 possui alta densidade onde ocorre, sendo considerada de grande importância ecológica nos
92 ecossistemas em que está inserida. Além disso, apresenta alta produção de frutos, que são

essenciais para a conservação da fauna e fonte de renda para as populações tradicionais (Resende *et al.* 2012; Virapongse *et al.* 2017; Ávila *et al.* 2023). O centro de origem da palmeira está ligado a região amazônica, no entanto, a espécie é encontrada em diferentes ecossistemas, com ampla distribuição no Brasil (Resende *et al.* 2012; Leitman *et al.* 2015; Melo *et al.* 2020; Ávila *et al.* 2023). No Cerrado brasileiro, *M. flexuosa* é associada à cursos d'água e áreas úmidas, conhecidas como veredas, com solos hidromórficos e alagados, em que ocorre o afloramento do lençol freático (Nunes *et al.* 2022; Silva *et al.* 2022; Ávila *et al.* 2023).

A espécie possui a dioicia como sistema sexual (Renner & Ricklefs 1995; Ávila *et al.* 2023). Esse tipo de sistema depende da sincronização das flores masculinas e femininas e da produção de recursos florais suficientes para garantir efetivamente a polinização (Bawa 1980; Aizen & Chacoff 2009; Amorim *et al.* 2011; Mendes *et al.* 2017). Os estudos de fenologia de *M. flexuosa* relatam diferenças no período de floração e frutificação, ocorrendo na mesma estação ou em estações diferentes. A sua fenologia responde as variáveis ambientais locais de forma complexa, sendo capaz de mudar de acordo com a localização geográfica e fatores climáticos (Ávila *et al.* 2023). Além disso, *M. flexuosa* apresenta distintos agentes de polinização em diferentes locais, variando de anemofilia a entomofilia, envolvendo diversas espécies de coleópteros, himenópteros e dípteros (Barfod *et al.* 2011; Nuñez-Avellaneda & Carreño-Barrera 2013; Mendes *et al.* 2017). Esta variação reflete a plasticidade fenotípica e baixa especialização da espécie em relação a potenciais polinizadores (Henderson 2002; Barfod *et al.* 2011; Mendes *et al.* 2017). Estudos realizados na região amazônica destacam que *M. flexuosa* depende do vento como principal vetor de pólen, devido a algumas características como quantidade de flores produzidas, grande produção de pólen, altura dos indivíduos, o pequeno tamanho das flores e a floração síncrona entre flores masculinas e femininas, além de demonstrarem que os visitantes florais encontrados não são polinizadores (Khorsand Rosa &

117 Koptur 2013). Diante disso, sua plasticidade fenotípica pode ser capaz de influenciar a maneira
118 como a espécie interage com os polinizadores em diferentes locais, nos levando a investigar as
119 suas interações em nossa área de estudo.

120 As interações entre plantas e polinizadores são parte de redes antagônicas ou
121 mutualísticas, que são complexas e apresentam variação espaço-temporal, principalmente em
122 ecossistemas tropicais (Bascompte *et al.* 2006; Souza *et al.* 2018). As populações de plantas
123 que compartilham polinizadores entre seus indivíduos têm maior probabilidade para que ocorra
124 a transferência do pólen e, conseqüentemente, maior fluxo gênico do que aquelas que
125 compartilham menos polinizadores. Dentro da população, isso pode ser afetado pela variação
126 dos atributos estruturais da planta e do ambiente, o que pode influenciar no sucesso reprodutivo
127 da espécie (Gómez *et al.* 2011; Arroyo-Correa *et al.* 2021). Uma maior diversidade de
128 polinizadores pode influenciar na complementariedade entre os comportamentos de
129 forrageamento dos grupos de polinizadores, gerando maior probabilidade de polinização e
130 resiliência das interações (Tylianakis *et al.* 2010). A maioria das abordagens atuais de redes de
131 interações ecológicas são focadas no nível comunitário (Bascompte *et al.* 2006; Guimarães
132 2020; Souza *et al.* 2018). No entanto, em redes de indivíduos, pequenas mudanças nos padrões
133 estruturais podem ser encontradas em resposta a variações individuais nas características da
134 planta e do ambiente (Dupont *et al.* 2014; Guimarães 2020). Porém, abordagens de redes
135 baseadas em indivíduos, especialmente em relação a plantas com sexos separados espacial ou
136 temporalmente são ainda pouco exploradas (Vizentin-Bugoni *et al.* 2018; Arceo-Gómez *et*
137 *al.* 2020; Arroyo-Correa *et al.* 2021).

138 Apesar das informações apresentadas, não existe nenhum estudo que caracterize a rede
139 de interações entre *M. flexuosa* e seus polinizadores em ambiente de vereda, no Cerrado
140 brasileiro. Portanto, o nosso principal objetivo é identificar os potenciais polinizadores em *M.*

flexuosa em ecossistemas de veredas, no Estado de Minas Gerais, Brasil, visto que a espécie apresenta plasticidade fenotípica e possui diversos agentes polinizadores. Além disso, procuramos: (1) descrever a estrutura da rede de interações (especialização e modularidade) entre os indivíduos da espécie, (2) identificar as espécies de polinizadores presentes em flores dos indivíduos masculinos e femininos através da rede compartilhada e (3) analisar quais atrativos dos indivíduos de *M. flexuosa* (por exemplo, número de inflorescências e tamanho) contribuíram para o maior número de parceiros (grau e força da espécie). É esperado baixa especialização na rede de interações, uma vez que, a espécie apresenta diferentes agentes e mecanismos de polinização relatados na literatura científica. Normalmente em palmeiras as inflorescências masculinas apresentam maior mancha de recurso para os polinizadores, portanto, o maior número de parceiros estaria relacionado aos atrativos apresentados por esses indivíduos, atraindo mais polinizadores e diversos.

MATERIAL E MÉTODOS

Área de estudo

O estudo foi realizado na Área de Proteção Ambiental do Rio Pandeiros (APA Pandeiros), em duas veredas localizadas no município de Bonito de Minas, do Estado de Minas Gerais, sudeste do Brasil. As veredas Almescla (15°20'54,9" S e 44°53'84,5" W) e Riacho Claro (15°18'48.30" S e 44°56'30.26" W) apresentam microhabitats que se diferenciam no nível de saturação da água no solo, refletindo em sua composição florística. No solo saturado com água, a vegetação é mais densa e composta principalmente por espécies arbóreas, com

solos formados a partir de resíduos vegetais em diferentes estágios de decomposição, como Histossolos Mésicos e Gleissolos Háplicos. Enquanto a vegetação em solo mais úmido (menos saturado de água), é composto por espécies herbáceas e arbustivas. A palmeira *M. flexuosa* está presente nos dois ambientes característicos do ecossistema de veredas dessa região (Nunes *et al.* 2022; Ávila *et al.* 2023; Luna *et al.* 2024).

De acordo com a classificação de Köppen, o clima da região é Aw, tropical com inverno seco e verão chuvoso (Alvares *et al.* 2013). O período seco se prolonga por cinco meses (maio a setembro), principalmente durante o inverno, e o período de chuva é definido entre os meses de novembro a janeiro (Azevedo *et al.* 2014). A precipitação média anual na área de estudo é de 920 mm e 26,8°C de temperatura média (Ávila *et al.* 2023).

Espécie estudada

Mauritia flexuosa (Fig. 1) está amplamente distribuída pela América do Sul, desempenhando um papel importante na ecologia, economia e cultura nas áreas onde ocorre (Virapongse *et al.* 2017). Possui uma estimativa de 1,5 bilhão de indivíduos, sendo considerada “hiperdominante” na Bacia Amazônica (Steege *et al.* 2013; Virapongse *et al.* 2017). Além disso, *M. flexuosa* fornece habitat e recursos alimentares essenciais para uma ampla variedade de animais (Brightsmith 2005; Virapongse *et al.* 2017) e os locais onde a palmeira está inserida, armazenam carbono em grandes camadas de matéria orgânica em decomposição, sendo consideradas fontes importantes para o sequestro e troca de carbono (Draper *et al.* 2014; Virapongse *et al.* 2017).

Em ecossistemas de veredas, *M. flexuosa* foi classificada como supra-anual, com eventos de floração e frutificação ocorrendo em intervalos superiores a um ano e apresentou padrão sazonal na fenologia reprodutiva, florescendo principalmente na estação chuvosa e

frutificando na transição da estação seca para a chuvosa (Ávila *et al.* 2023). Por ser uma espécie dioica, apresenta diferenças entre as estruturas reprodutivas dos indivíduos masculino e feminino. As suas inflorescências femininas, apesar de terem uma maior quantidade de ramificações e flores maiores, tem uma estimativa de produção de mais de 5 mil flores. Porém, a quantidade de flores masculinas é significativamente maior, com uma estimativa de mais de 176 mil flores por inflorescência (Ávila *et al.* 2023). A frutificação estimada é de aproximadamente 817 frutos por cacho (Ávila *et al.* 2023).

Rede de interações palmeira-polinizador

Os dados de interação da palmeira *M. flexuosa* e seus potenciais polinizadores foram coletados em fevereiro de 2023, durante o pico de floração da espécie. Para isso, nas duas veredas amostradas, foram selecionados 16 indivíduos, sendo seis femininos e dez masculinos. Com o objetivo de gerar maior variabilidade entre os indivíduos da palmeira, a seleção ocorreu em duas populações diferentes. A escolha dos indivíduos foi realizada principalmente pela produção de flores e acessibilidade para observação das inflorescências, dada a dificuldade de amostrar interações em espécies de palmeiras pela altura. As espécies vegetais em um raio de 10 metros foram contabilizadas e registradas a presença e quantidade de flores. Além disso, foi realizada a medição da altura e CAP (circunferência a altura do peito) de todos os indivíduos amostrados, bem como a quantidade de inflorescências produzidas durante a observação de campo.

Os polinizadores de cada indivíduo de *M. flexuosa* amostrado, foram observados por aproximadamente duas horas em cada etapa, entre 07:00 e 17:00h, alternando entre os períodos da manhã e tarde, totalizando aproximadamente 60 horas de amostragem. Incluímos apenas as interações legítimas, quando o visitante floral entrou em contato com as estruturas reprodutivas

das flores, indicando potencial para polinização. Esses visitantes legítimos foram chamados de “polinizadores”, apesar de não termos avaliado posteriormente o seu papel na produção de frutos para os indivíduos de *M. flexuosa* (ver Souza *et al.*, 2018). Depois que a visita foi registrada, os polinizadores foram capturados, com o auxílio de rede entomológica com extensor e escada, e armazenados em frascos individuais. Os polinizadores foram examinados em lupa para observar a presença de pólen. Para a amostragem do pólen foram utilizados pequenos cubos de gelatina corada com fucsina no corpo dos insetos e, em seguida, a gelatina foi colocada em lâminas microscópicas (Dafni 1992; Bosch *et al.* 2009; Souza *et al.* 2021). Os grãos de pólen amostrados em cada polinizador foram registrados, quanto a presença e ausência do pólen, e diferenciados em pólen hetero e co-específico.

Com os dados coletados foi montada uma rede de interações de indivíduos para *M. flexuosa* (Alcantara *et al.* 2022; Vissoto *et al.* 2022). Essa rede foi construída através de uma matriz, onde nas linhas são os indivíduos de palmeiras amostrados, e nas colunas as espécies de polinizadores observados. O preenchimento da matriz foi baseado na frequência das interações entre cada indivíduo e as espécies de polinizadores. Além disso, foi utilizado o comportamento durante as visitas em indivíduos masculinos e femininos, e a presença do pólen no corpo do polinizador como um *proxy* de potencial polinizador de *M. flexuosa* (Lima *et al.* 2020). Primeiramente para a rede de indivíduos de *M. flexuosa*, foi avaliado o esforço amostral (Chacoff *et al.* 2012; Vizentin-Bugoni *et al.* 2016) para analisar a detecção de todas as possíveis interações entre os indivíduos de palmeiras e seus polinizadores, durante a amostragem. Para este propósito, cada combinação de um indivíduo e uma espécie de polinizador foi considerada como “espécie” e a frequência de cada interação entre os pares da rede representou sua “abundância” (Vizentin-Bugoni *et al.* 2016). Foi estimada a diversidade das interações usando o estimador Chao1 de riqueza de espécies (Chao 1984; Colwell & Coddington 1994), e

calculado o esforço amostral como sendo a razão entre o observado e o estimado em relação a riqueza de interações (Chacoff *et al.* 2012). O estimador Chao 1 foi calculado usando o pacote INEXT (Hsieh *et al.* 2014) no Programa R (R Development Core Team 2022).

Métricas de redes e análises estatísticas

Para a análise da rede de interações, foram calculadas duas métricas no nível de rede para entender como os indivíduos particionam suas interações na comunidade. Foi calculada a especialização para toda a rede utilizando o índice H_2' , que descreve como os indivíduos de palmeiras distribuem suas interações com base na disponibilidade de parceiros em toda a comunidade (Blüthgen *et al.* 2006) e o índice de modularidade que quantifica a prevalência de interações dentro de subconjuntos de indivíduos na rede. O índice de modularidade foi calculado utilizando o algoritmo DIRTLPAbw + (Beckett 2016) usando a função `computeModules` no pacote Bipartite no programa R (Dormann *et al.* 2008).

Como os índices de rede podem ser afetados pelo número de espécies ou indivíduos interagindo na comunidade e o esforço de amostragem (Fründ *et al.* 2016), além dos valores observados obtidos, também foram comparadas as métricas utilizando um modelo nulo. Aqui, foi utilizado o modelo nulo de Vaznull (Vázquez *et al.* 2005), que restringe a conectância, tamanho da rede e número total de interações em cada aleatorização. O intervalo de confiança estimado foi de 95% para cada métrica dos 10.000 valores simulados, e um valor significativo da métrica foi considerado quando maior do que o intervalo de confiança gerado pelas aleatorizações do modelo nulo utilizado.

Além desses dois índices em nível de rede, também foram calculados dois índices à nível de indivíduos para *M. flexuosa* e de espécies para seus polinizadores, que capturam propriedades distintas de um indivíduo ou espécie na rede: 1) grau, expressando o número de

263 parceiros de interação (polinizadores) que cada indivíduo de palmeira interage na rede; 2) força
264 da espécie ou do indivíduo que mede a extensão no qual o conjunto de indivíduos/espécies
265 depende de uma espécie de polinizador ou indivíduo específico (Bascompte *et al.* 2006). Todos
266 os índices de nível de espécie foram quantificados pela função *specieslevel* () no pacote
267 Bipartite em R (Dormann *et al.* 2008).

268 Foram avaliados se os módulos formados na rede de interações correspondem à
269 distribuição dos grupos de polinizadores compartilhados pelos indivíduos de palmeiras, isto é,
270 se os módulos formados na rede estão relacionados com o compartilhamento entre os grupos
271 de polinizadores pelos indivíduos de palmeiras, usando um teste de qui-quadrado. O mesmo
272 teste foi realizado para verificar se os módulos correspondem a distribuição dos indivíduos nas
273 diferentes populações estudadas (veredas Almescla e Riacho Claro). Os índices de grau em
274 relação a CAP dos indivíduos, vizinhança, número de inflorescência, a força da interação em
275 relação a vizinhança para os indivíduos da palmeira foi analisada utilizando modelos lineares.
276 Além disso, avaliamos se a frequência de visitas variou entre indivíduos masculinos e
277 femininos. Realizamos uma análise de correlação entre as variáveis avaliadas e devido à alta
278 correlação de alguns atributos (>0.50 , Fig. S2), utilizamos nos modelos a riqueza de visitantes,
279 CAP, altura, vizinhança e número de inflorescências produzidas.

280 Dessa forma, foram usados os índices dos indivíduos de palmeiras e polinizadores como
281 variável resposta e para indivíduos de *M. flexuosa*, o CAP, sexo do indivíduo, vizinhança e
282 número de inflorescências produzidas como variáveis preditoras nos modelos. Para os
283 polinizadores, foram utilizados grupos de polinizadores como variável preditora. Foram
284 utilizadas as seguintes categorias: abelhas, besouros, vespas, moscas e outros (incluindo grupos
285 com menos de três espécies como formigas e hemípteras). Além disso, foi utilizado a frequência

286 de visita como variável resposta e o sexo como variável preditora. Todas as análises estatísticas
287 foram conduzidas no programa R (R Development Core Team 2022).

288 **Morfoanatomia e histoquímica das flores femininas**

289

290 As flores femininas de *M. flexuosa* foram coletadas em duas fases de desenvolvimento:
291 imatura (flor com todos os verticilos desenvolvidos, antes da antese) e antese. Para detecção de
292 substâncias lipofílicas, as flores em antese foram imersas em solução de vermelho neutro (Kirk
293 1970), por 5 minutos. As características morfológicas foram registradas com câmera digital
294 acoplada em estereomicroscópio (Zeiss Stemi 305, Axion Cam ICC 3, Jena, Alemanha). Para
295 as avaliações anatômicas e histoquímicas, amostras de pétalas e estaminódios foram fixadas em
296 solução de Karnovsky (Karnovsky 1965), por 24 horas, desidratados em série etanólica e
297 incluídas em resina 2-hidroxi-etil-metacrilato (Leica Microsystems, Heidelberg, Alemanha)
298 (Paiva *et al.* 2011). Secções transversais e longitudinais, de 5 µm de espessura, foram obtidas
299 em micrótomo rotativo (Histocore Autocut, Leica Biosystems, Heidelberg, Alemanha). Foram
300 realizados testes com reagente de Lugol (Johansen 1940), para amido; xylidine-ponceau (Vidal
301 1970), para proteínas; reagente de Nadi (David & Carde 1964), para terpenoides; azul de
302 toluidina 0,05%, pH 4,7 (O'Brien *et al.* 1964, modificado), cuja metacromasia permite
303 identificar mucilagens e compostos fenólicos. Todas as secções foram analisadas e as imagens
304 obtidas em fotomicroscópio (Zeiss Lab A1, Axion Cam ICC 3, Jena, Alemanha).

305

306 **RESULTADOS**

307

308 Um total de 1739 visitas às flores e 33 espécies de insetos foram observados ou
309 coletados em inflorescências *M. flexuosa*, incluindo abelhas, vespas, besouros, moscas e
310 hemípteras. Os insetos mais frequentes foram as abelhas *Tetragonisca angustula* (com 426

visitas), *Trigona spinipes* (n=403), *Apis mellifera* (n=316), *Plebeia* sp. (n=121), *Trigona hyalinata* (n=70); uma vespa *Polybia* sp. 3 (n=83) e um besouro Coleoptera sp. (n=69). A rede de interações mostrou um esforço de amostragem de 92% (Fig. S1), não sendo significativamente especializada ($H_2' = 0.39$, intervalo de confiança = 0.0906-0.1468) e modular ($Q = 0.34$, intervalo de confiança = 0.097-0.1384; Fig. 2). Apesar dos módulos serem significativamente correlacionados com as características avaliadas ($X^2 = 122.47$; $df = 40$; $p = 2.69e-10$; Fig. S3), apenas o módulo quatro foi fortemente associado a maior riqueza de espécies próximas florescendo.

A presença do pólen de *M. flexuosa* foi verificado em 325 (98,4%) dos 330 polinizadores coletados. Esses insetos foram coletados em indivíduos masculinos e femininos e pertenciam aos diferentes grupos de polinizadores: as abelhas *Apis mellifera*, *Trigona spinipes*, *Tetragonisca angustula*, *Plebeia* sp., *Apidae* sp., *Paratrigona lineata* e *Trigona hyalinata*; as vespas *Polybia* sp., *Polybia* sp. 2, *Polybia* sp. 3, *Vespidae* sp. 2, *Vespidae* sp. 3 e *Vespidae* sp. 5; os besouros Coleoptera sp. 1, Coleoptera sp. 2 e Curculionidae sp. 1; e as moscas *Ornidia obesa* e Diptera sp. 3.

Em relação aos grupos de polinizadores, abelhas tiveram maior força de espécie na rede ($F = 6.3$; $p = 0.0009$; Fig. 3A) e abelhas, besouros e vespas apresentaram maior grau na rede ($F = 5.09$; $p = 0.003$; Fig. 3B) do que outros grupos de polinizadores (moscas, formigas e hemípteras). A riqueza de insetos estava positivamente relacionada ao número de inflorescências e ao CAP e altura do indivíduo, e negativamente relacionada a espécies próximas florescendo (Fig. S2).

As inflorescências nos indivíduos masculinos atraíram um número maior de polinizadores, do que os indivíduos femininos ($F = 3.97$; $p = 0.05$; Fig. 4), enquanto 16 espécies de polinizadores foram coletadas em ambos os sexos florais (Fig. 5). No entanto, para os

atrativos dos indivíduos de *M. flexuosa*, o grau ou número de parceiros na rede não foi significativamente relacionado ao número de inflorescências ($F = 2.78$; $p = 0.11$; $R^2 = 0.16$; Fig. 6A), com o CAP do indivíduo ($F = 1.91$; $p = 0.18$; $R^2 = 0.12$; Fig. 6B) e a riqueza de espécies que formavam a sua vizinhança ($F = 0.30$; $p = 0.58$; $R^2 = 0.021$; Fig. 6C). Da mesma forma, a força do indivíduo na rede não foi influenciada pela riqueza de espécies em sua vizinhança ($F = 0.75$; $p = 0.40$; $R^2 = 0.049$; Fig. 6D).

Morfoanatomia e histoquímica das flores femininas

As ráquulas das inflorescências possuem raquíolas, com cerca de três flores femininas (Fig. 7A, D). As flores são sésseis e trímeras e na fase imatura, possuem sépalas e pétalas de coloração verde (Fig. 7A). As pétalas são adnatas na base do anel estaminoidal, que é constituído por seis estames, com anteras volumosas e de coloração branca (Fig. 7B). As anteras dos estaminódios possuem sacos polínicos com epiderme unisseriada, com células tabulares; endotécio com células volumosas e cuboides; duas camadas médias, com células de contornos irregulares; e tapete secretor conspicuo, com 3-4 camadas de células volumosas; essa fase corresponde ao final da microsporogênese, com formação de tétrades de micrósporos unidos por calose (Fig. 7C). Em antese, as flores femininas possuem sépalas de coloração verde-amarelada e pétalas alaranjadas; as anteras do estaminódio e o estigma do gineceu possuem coloração amarelo-pálida (Fig. 7D). As flores são gamossépalas e gamopétalas, com adnação entre esses dois verticilos (Fig. 7E). As anteras dos estaminódios possuem deformações evidentes nas células da epiderme e do endotécio, que apresentam contornos irregulares; o tapete apresenta-se degenerado, com células colapsadas e as tétrades de micrósporos são completamente absorvidas (Fig. 7F). Não há proteínas e amido nas anteras dos estaminódios. As pétalas e as anteras dos estaminódios apresentaram resultado positivo para compostos

lipofílicos (Fig. 7G). A epiderme da pétala é unisseriada, com cutícula delgada e há tricomas multicelulares com paredes espessadas e lignificadas; terpenoides foram identificados na epiderme e camadas subjacentes (Fig. 7H). Nas anteras, os terpenoides ocorrem no endotécio e remanescentes do conectivo (Fig. 7I, J).

DISCUSSÃO

Nesse trabalho, as abelhas e besouros foram os mais abundantes e frequentes durante as visitas em *M. flexuosa*. Além disso, o pólen da palmeira foi frequentemente encontrado em seus corpos, indicando esse grupo como potenciais polinizadores de *M. flexuosa*. Apesar dos coleópteros serem considerados os principais polinizadores nas palmeiras em geral, sendo considerado também para *M. flexuosa* em trabalhos realizados em outros locais, nas veredas estudadas os himenópteros (mais especificamente abelhas e vespas) foram considerados como os seus principais polinizadores.

A rede de interações dos indivíduos da palmeira *M. flexuosa* com seus polinizadores não apresentou especialização significativa e isso pode estar relacionado a sua plasticidade fenotípica, visto que sua adaptação em outras regiões já foi mencionada e estudada em trabalhos anteriores. Em estudos realizados no Brasil, os coleópteros foram considerados potenciais polinizadores de *M. flexuosa* em Manaus, Amazonas (Storti 1993; Mendes *et al.* 2017). No Equador foram os besouros crisomelídeos (Ervik 1993) e na Colômbia uma espécie de escaravelho e os autores enfatizaram a falta de contribuição na polinização pelo vento (Núñez-Avellaneda & Carreño-Barrera 2013). Porém, em Roraima, os pesquisadores relataram o vento como o principal agente polinizador nos indivíduos de *M. flexuosa*, uma vez que os visitantes florais não carregavam pólen da espécie em seus corpos e eram raros nas flores (Khorsand Rosa

& Koptur 2013). Portanto, existe uma divergência em relação aos agentes polinizadores encontrados para *M. flexuosa*, demonstrando que a espécie apresenta baixo grau de especialização durante o processo de polinização

O grupo das abelhas apresentou maior força de espécie e as abelhas, besouros e moscas maior grau na rede de interações com os indivíduos de *M. flexuosa*. Verificamos que algumas espécies desses grupos de insetos visitaram tanto os indivíduos masculinos quanto os indivíduos femininos de *M. flexuosa*, observados durante a construção da nossa rede compartilhada. Dessa forma, identificamos que *M. flexuosa* em ecossistema de vereda é polinizada por diferentes espécies de abelhas, principalmente por *Apis mellifera*, *Trigona spinipes*, *Tetragonisca angustula*, *Plebeia* sp., *Apidae* sp., *Paratrigona lineata* e *Trigona hyalinata*, mas também por espécies de besouros, vespas e moscas. Abelhas da família Halictidae e da tribo Meliponini se destacam na polinização de palmeiras, sendo encontradas principalmente as espécies do gênero *Trigona* (Barfod *et al.* 2011), justamente as abelhas que se destacaram em grau e força de espécie em nosso estudo.

A visita dos polinizadores em ambos os sexos florais é uma contribuição fundamental para a transferência do pólen em espécies dioicas (Campbell *et al.* 2018). E para que ocorra a polinização, garantido o sucesso reprodutivo da espécie e alta produção de frutos, é necessária uma sincronia na floração entre indivíduos masculinos e femininos (Ávila *et al.* 2022; Ávila *et al.* 2023). O compartilhamento de polinizadores através da maior sincronia de floração de plantas da mesma espécie, pode aumentar as chances de indivíduos receberem pólen de melhor qualidade (Arroyo-Correa *et al.* 2021). Além disso, a sincronia na floração entre indivíduos pode garantir maior disponibilidade de recursos para a fauna local, destacando a importância ecológica de *M. flexuosa* nos ecossistemas de veredas (Ávila *et al.* 2023). É esperado que plantas individuais que apresentem maior sincronia de floração dentro da sua população

partilhem polinizadores com outros indivíduos da mesma espécie. Assim, a maior sincronia de floração pode influenciar no nível de compartilhamento de polinizadores e aumentar a rotatividade intrapopulacional na interação (Weis 2005; Arroyo-Correa *et al.* 2021).

Os nossos resultados demonstram que as interações observadas entre os indivíduos de *M. flexuosa* e seus polinizadores pode ser influenciada por outras variáveis, como a sexualidade dos indivíduos. A variação na composição de polinizadores entre plantas individuais também pode ser influenciada pela sua posição espacial, devido as condições ambientais e a comunidade vegetal em que essas plantas estão expostas (Rodríguez-Rodríguez *et al.* 2017; Arroyo-Correa *et al.* 2021). Dessa forma, plantas que ocupem posições mais centrais podem ser beneficiadas por um maior compartilhamento de polinizadores com outros indivíduos da mesma espécie, aumentando a possibilidade de interação (Arroyo-Correa *et al.* 2021; Soares *et al.* 2021).

Foi possível observar uma maior frequência de visitas nos indivíduos masculinos de *M. flexuosa*, o que já era esperado devido a maior quantidade de flores presentes nas suas inflorescências. A alta produção de recursos florais, principalmente pelas inflorescências masculinas, está relacionada a atração da abundância de polinizadores, sendo considerado um tipo de estratégia apresentado pelas palmeiras (Nunez-Avellaneda 2014; Carreno-Barrera *et al.* 2021), permitindo a manutenção de polinizadores e, conseqüentemente, garantindo o fluxo cruzado de pólen para a reprodução (Núñez Avellaneda 2014; Núñez & Carreño 2016; Carreño-Barrera *et al.* 2020; Carreno-Barrera *et al.* 2021). Enquanto as flores femininas apresentam maior longevidade, pois permanecem de quatro a cinco dias (Mendes *et al.* 2017; Ávila *et al.* 2023). Esse tipo de estratégia oferece grande quantidade de pólen aos potenciais polinizadores, enquanto a longevidade das flores femininas aumenta as chances de transferência de pólen entre as partes reprodutivas entre diferentes indivíduos (Barfod *et al.* 2003; Oliveira *et al.* 2003;

Mendes *et al.* 2017). A proporção das inflorescências masculinas apresenta grande importância no fornecimento de recursos através do pólen produzido (Brieva-Oviedo *et al.* 2020).

M. flexuosa é uma espécie-chave em ecossistema de vereda (Nunes *et al.* 2022; Ávila *et al.* 2022, 2023), fornecendo recursos para muitos polinizadores, demonstrando importante papel ecológico no equilíbrio desse ecossistema (Silva *et al.* 2022). No entanto, se houver uma diminuição populacional dos polinizadores no ambiente, pode afetar principalmente as espécies dioicas (Peng *et al.* 2014; Ramirez & Hokiche 2019; Silva *et al.* 2022) o que torna sua relação com o polinizador ainda mais essencial, deixando o cenário preocupante caso ocorra um declínio populacional nessas populações. Para espécies de palmeiras como *M. flexuosa*, que são economicamente exploráveis, o conhecimento acerca das suas interações planta-polinizador é extremamente importante, pois permitem a compreensão desse tipo de processo ecossistêmico, representando um passo importante em direção às estratégias de conservação. Ao utilizar a abordagem de rede individual, nosso estudo contribui para a compreensão da estruturação das redes de polinização em palmeiras em relação as suas características individuais e do ecossistema.

FINANCIAMENTO

Este trabalho foi apoiado pelo Programa de Pesquisa Ecológica de Longo Duração (PELD-VERE) do Conselho Nacional de Desenvolvimento Científico e Tecnológico [441440/2016-9, 441583/2020-2, 308877/2019-5], Coordenação de Aperfeiçoamento de Pessoal de Nível Superior [88887. 136273/2017-00], e Fundação de Amparo à Pesquisa do Estado de Minas Gerais [APQ-04816-17, CRAPPM- 00539-18, APQ-04816-17, APQ-02166-21]. Agradecemos também à FAPEMIG (FAPEMIG /RED-00253–16) pelo apoio na realização do trabalho.

454 **AGRADECIMENTOS**

455 Ao Programa de Pós-Graduação em Botânica Aplicada, à assistência em campo do Laboratório
456 de Ecologia Vegetal (Universidade Estadual de Montes Claros), ao apoio do RESA (Rede de
457 Serviços Ambientais) e ao apoio logístico do Instituto Estadual de Florestas, no Estado de
458 Minas Gerais.

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732 **Lista de legendas**

733 **Fig. 1.** Indivíduo feminino de *Mauritia flexuosa*. Em detalhe, as folhas palmadas e o estipe e as inflorescências
734 masculinas e femininas
735

736 **Fig. 2.** Rede de interações entre polinizadores e diferentes indivíduos de *Mauritia flexuosa* amostrados nas veredas
737 estudadas em fevereiro de 2023. Na rede são evidenciados indivíduos masculinos e femininos e os diferentes
738 insetos polinizadores amostrados. As diferentes cores mostram os indivíduos de *M. flexuosa* e os polinizadores em
739 cada um dos módulos.
740

741 **Fig. 3.** Força da espécie entre os diferentes grupos de polinizadores (A) e diferença de grau entre os grupos de
742 polinizadores (B) amostrados nos indivíduos de *Mauritia flexuosa*.
743

744 **Fig. 4.** Frequência de interações das espécies de polinizadores em relação ao sexo dos indivíduos de *Mauritia*
745 *flexuosa* amostrados.
746

747 **Fig. 5.** Soma dos insetos polinizadores de inflorescências de *Mauritia flexuosa* nos diferentes sexos florais nas
748 veredas estudadas em fevereiro de 2023. A largura das arestas (cinza) representa a frequência de visitas. Nós
749 vermelhos = polinizadores encontrados em indivíduos femininos. Nós verdes = polinizadores encontrados em
750 indivíduos masculinos. Os nós ao centro da rede representam os polinizadores registrados em ambos os sexos
751 florais.
752

753 **Fig. 6** Grau em relação ao número de inflorescências (A), ao tamanho dos indivíduos (B) e número de espécies
754 florescendo – vizinhança nos indivíduos de *Mauritia flexuosa* amostrados (C). Força do indivíduo em relação ao
755 número de espécies florescendo – vizinhança próximo aos indivíduos de *Mauritia flexuosa* amostrados (D).
756

757 **Fig. 7.** Morfoanatomia e histoquímica de flores pistiladas de *Mauritia flexuosa*. (B, C, E, F, H-J) secções
758 longitudinais. (A) Ráquila com flores imaturas; sépalas e pétalas de coloração verde. (B) Adnação entre pétalas e
759 estaminódio (retângulo pontilhado); anteras são volumosas e ovário gamocarpelar. (C) Antera do estaminódio com
760 tétrades de micrósporos no saco polínico. (D) Ráquila com flores em antese; pétalas alaranjadas, estaminódios e
761 estigma amarelo-pálidos. (E) Adnação entre sépalas e pétalas e estaminódio (retângulo pontilhado); anteras de
762 aspecto flácido. (F) Antera do estaminódio vazia, com sinais de degradação do tapete e absorção das tétrades de
763 micrósporos (pontas de setas pretas). (G) Compostos lipofílicos (vermelho, pontas de setas brancas) nas pétalas e
764 nas anteras dos estaminódios. (H) Terpenoides (púrpura, pontas de setas brancas) na cutícula, epiderme e camadas
765 subepidérmicas das pétalas, e (I, J) nas paredes das anteras dos estaminódios. at, antera; co, conectivo; en,
766 endotécio; ep, epiderme; et, estaminódio; ml, camada média; ms, micrósporos; ol, óvulo; ov, ovário; pt, pétala; ra,
767 ráquila; se, sépala; st, estigma; ta, tapete.

768 **Material suplementar**

769 **Fig. S1.** Curva de rarefação e extrapolação para a rede de indivíduos de *Mauritia flexuosa* amostrados.

770

771 **Fig. S2.** Gráfico de correlação dos atributos avaliados nos diferentes indivíduos de *Mauritia flexuosa* amostrados
772 nas veredas estudadas em fevereiro de 2023. Valores de correlação maiores que 0.50, foi considerado apenas um
773 dos atributos nos modelos.

774 **Fig. S3.** Gráfico de correlação dos atributos avaliados nos módulos dos diferentes indivíduos de *Mauritia flexuosa*
775 amostrados nas veredas estudadas em fevereiro de 2023. Valores de correlação maiores que 0.50, foi considerado
776 apenas um dos atributos nos modelos.

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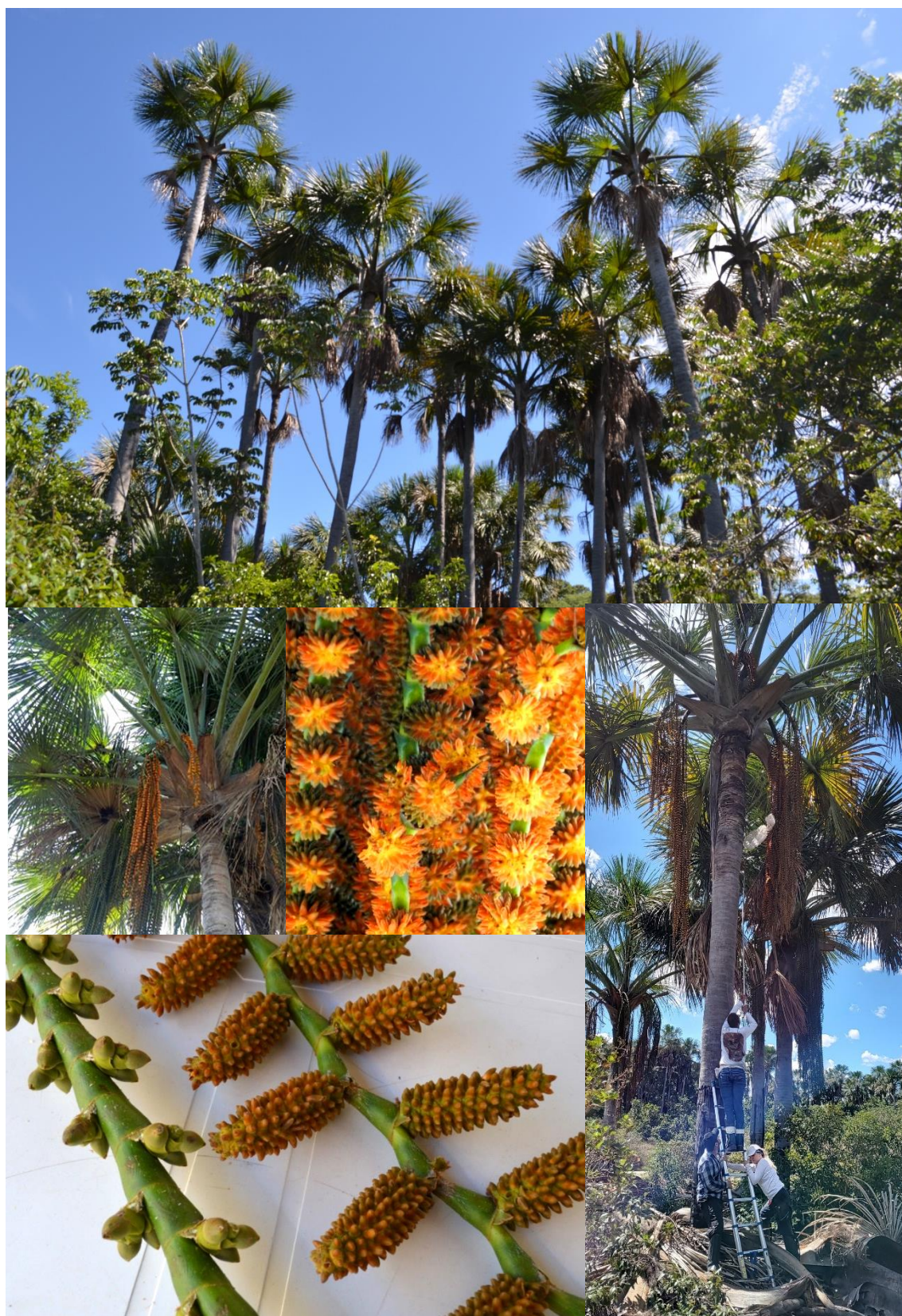


Fig. 1.

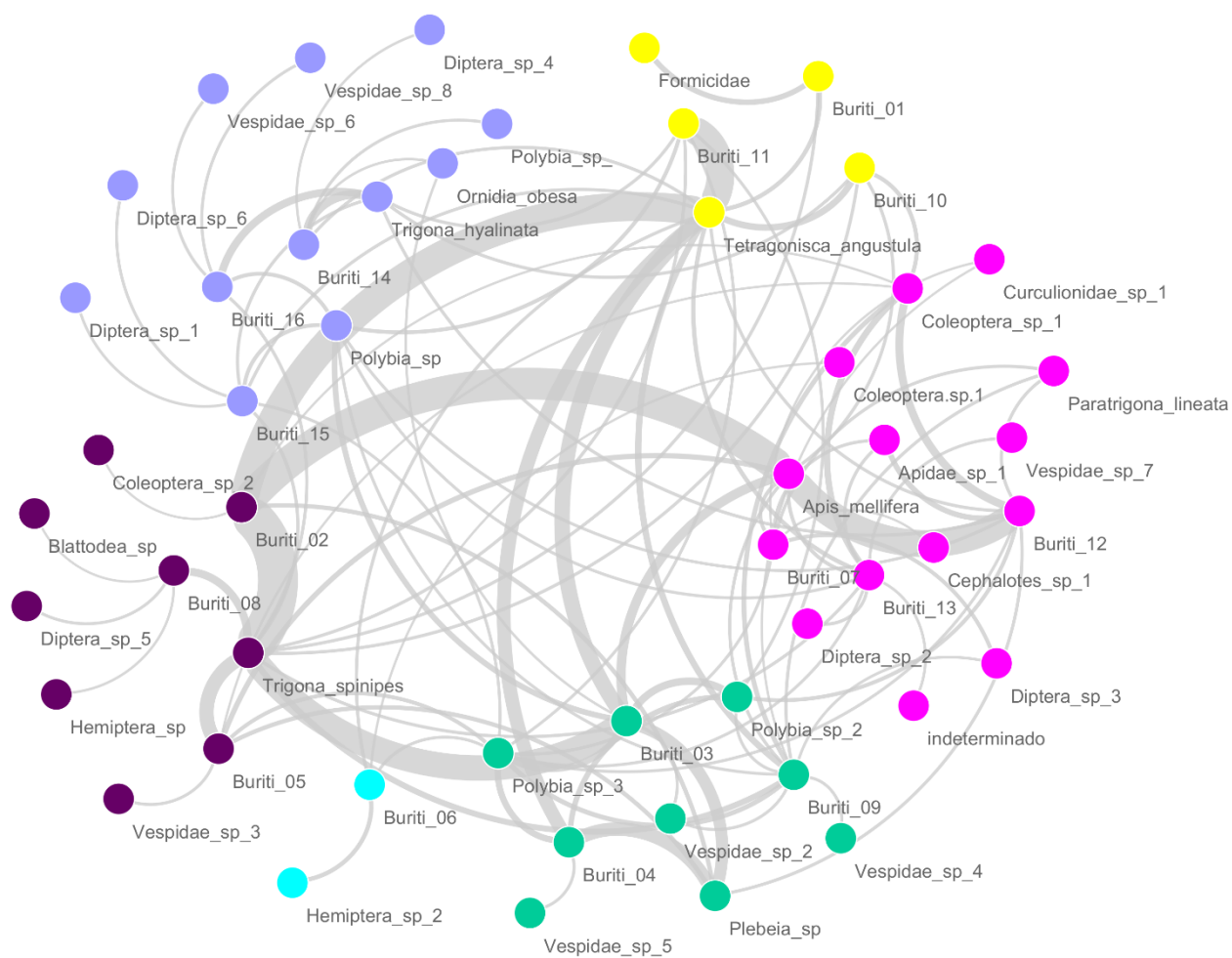


Fig. 2.

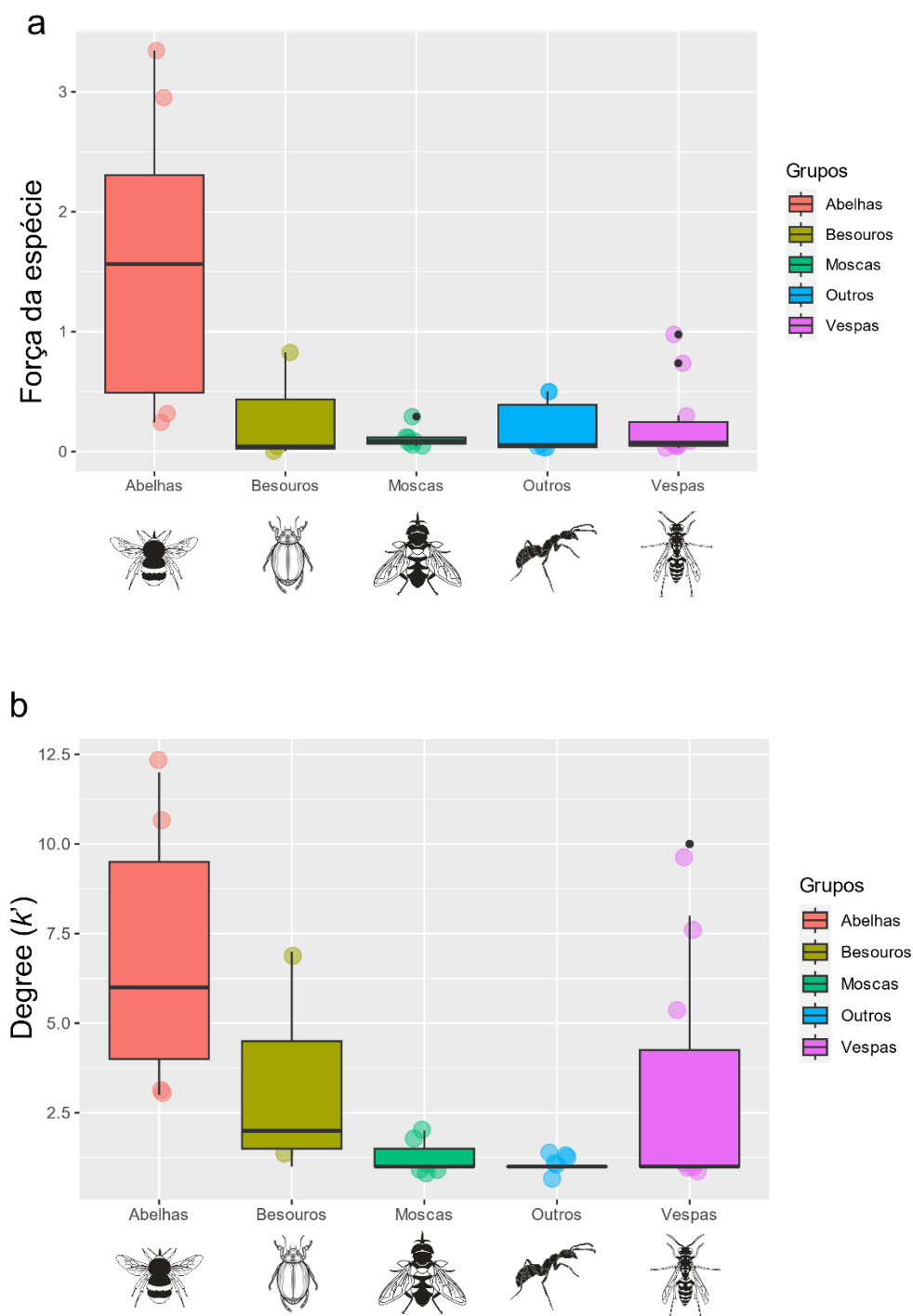


Fig. 3.

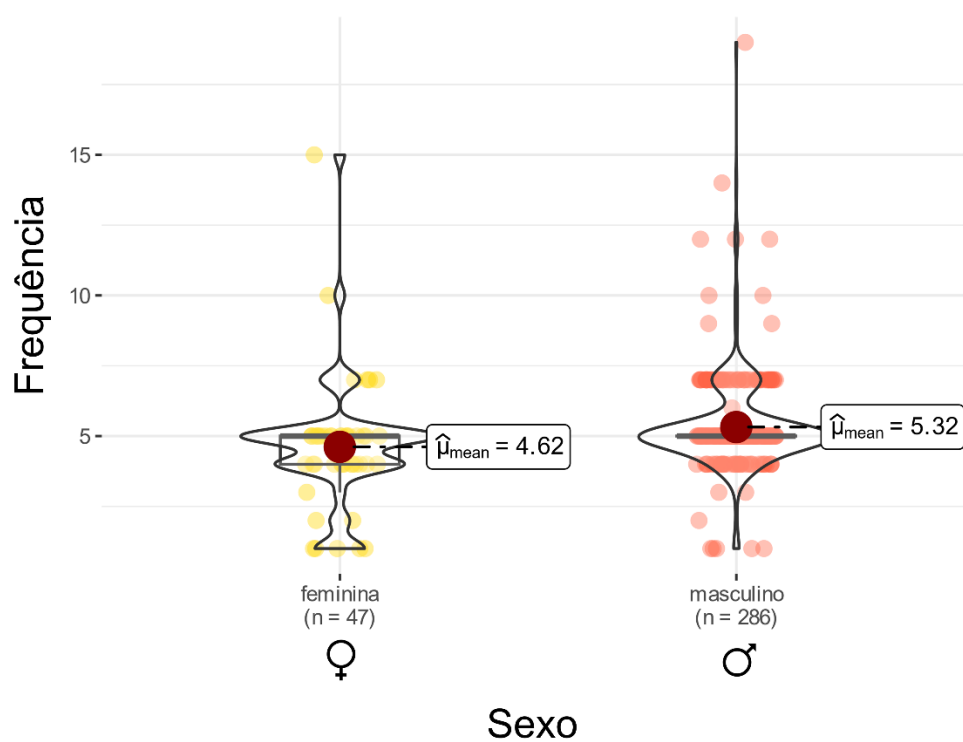


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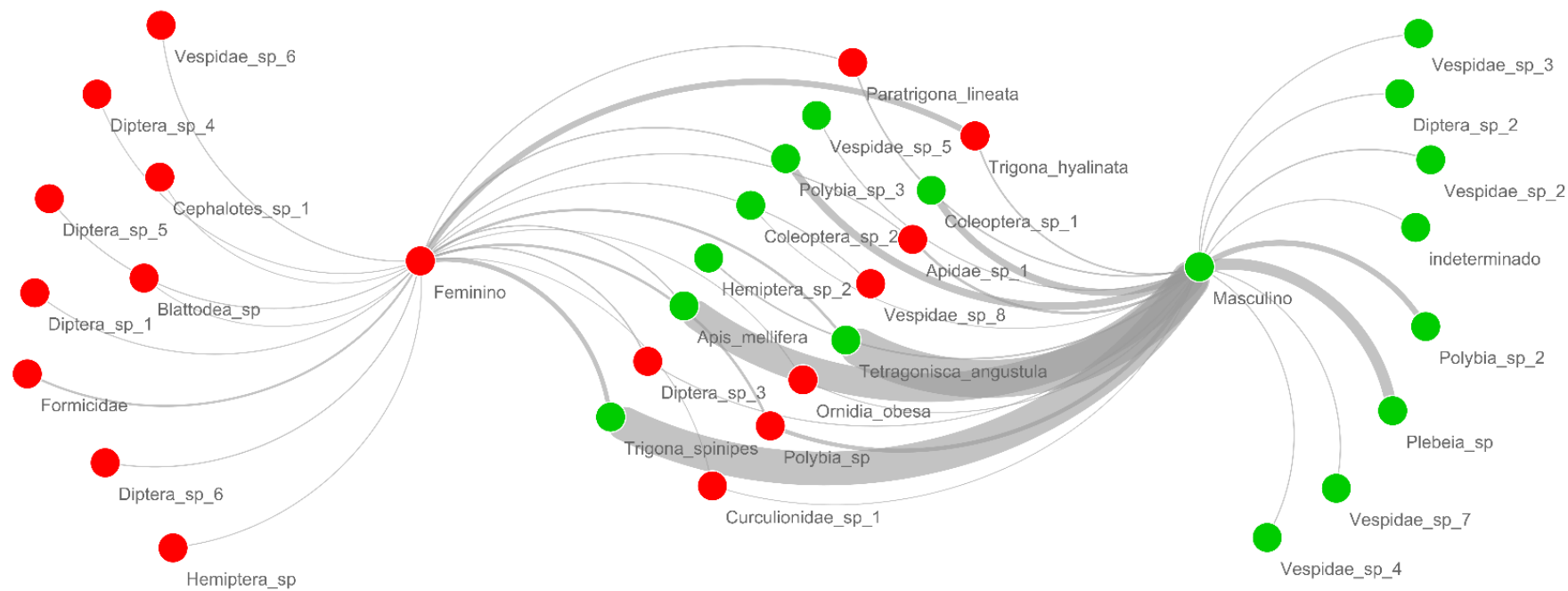


Fig. 5.

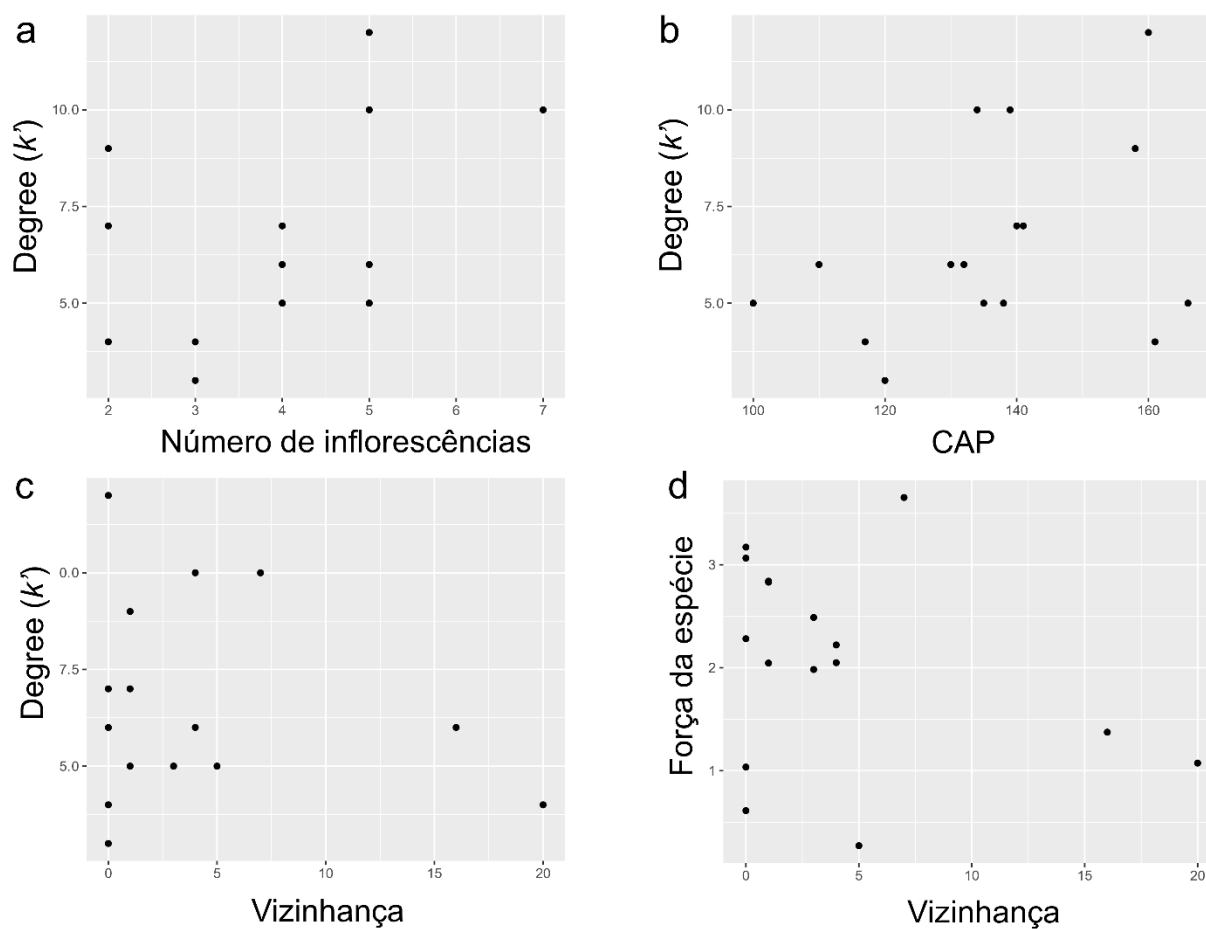


Fig. 6.

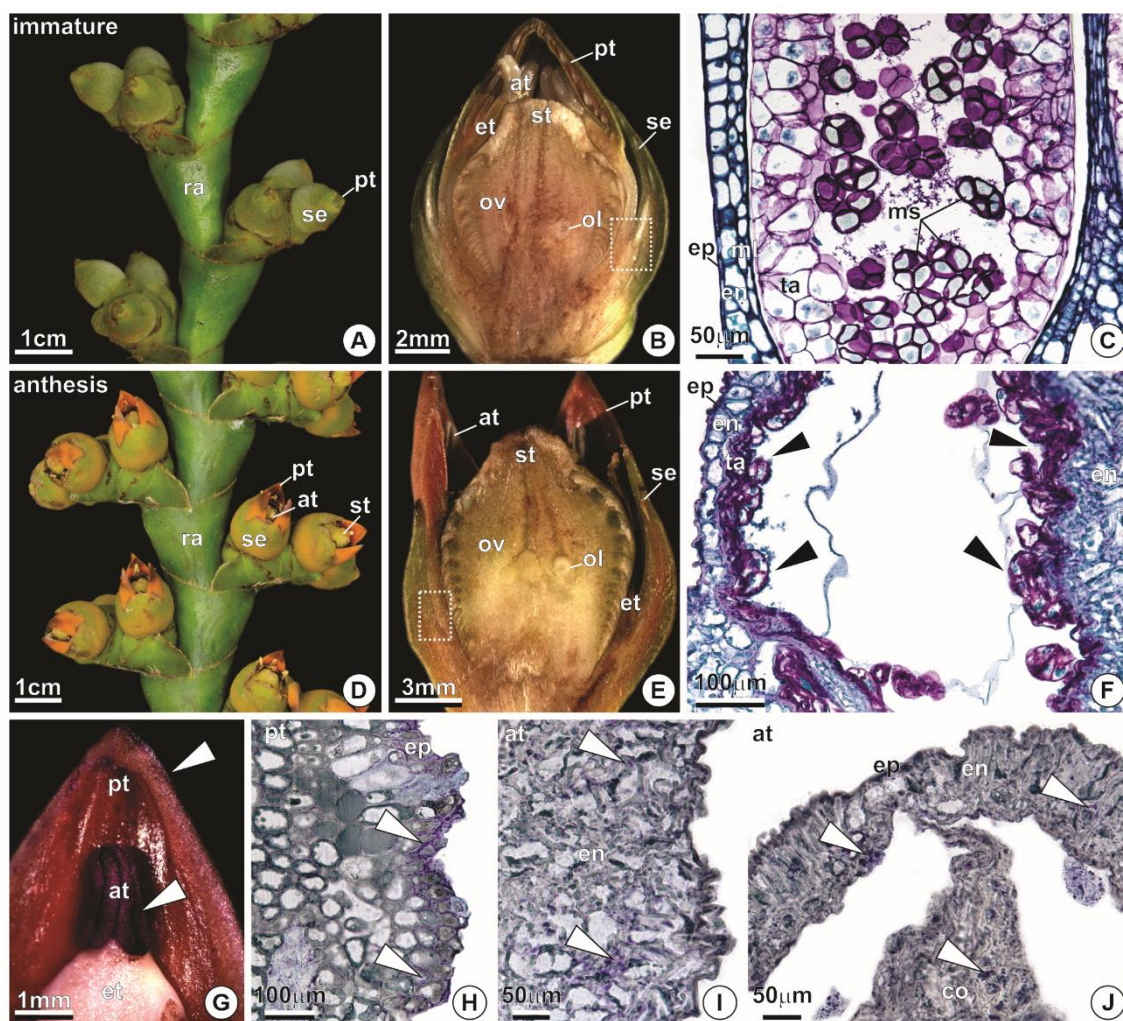


Fig. 7.

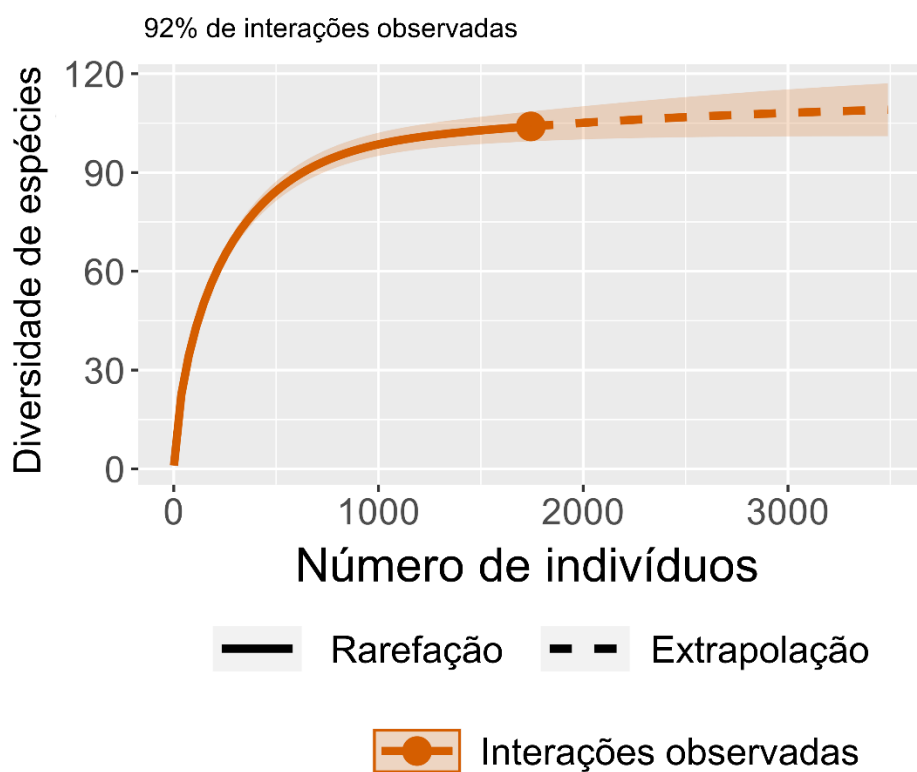


Fig. S1.

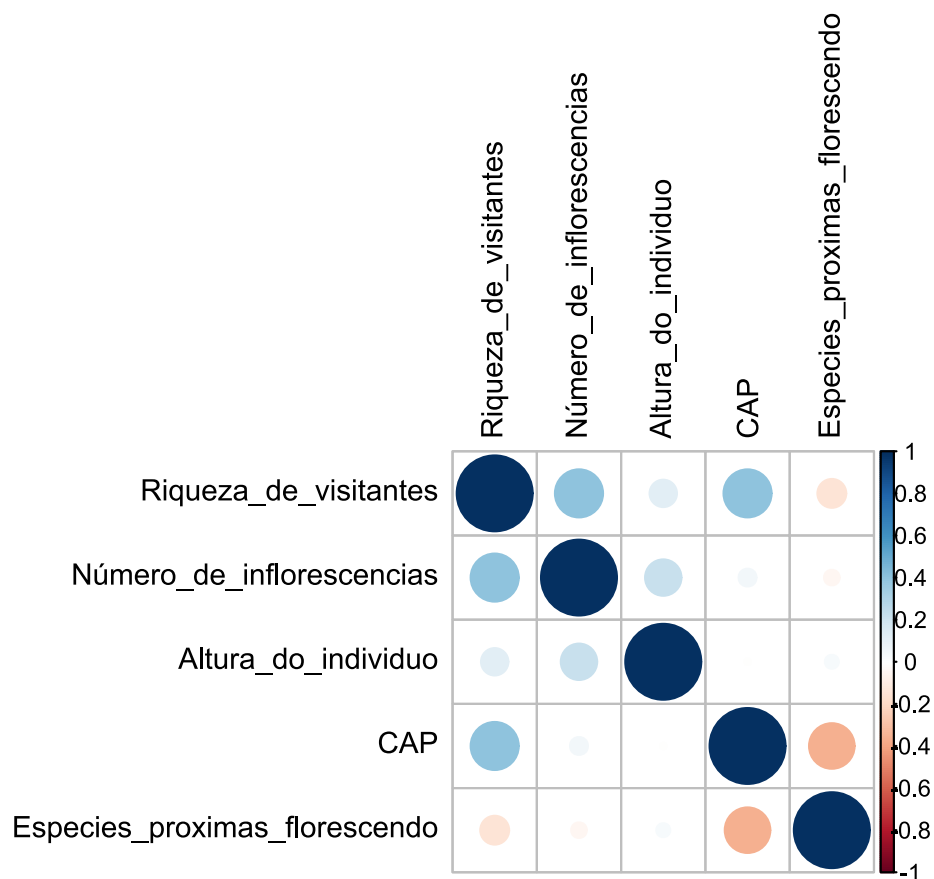


Fig. S2.

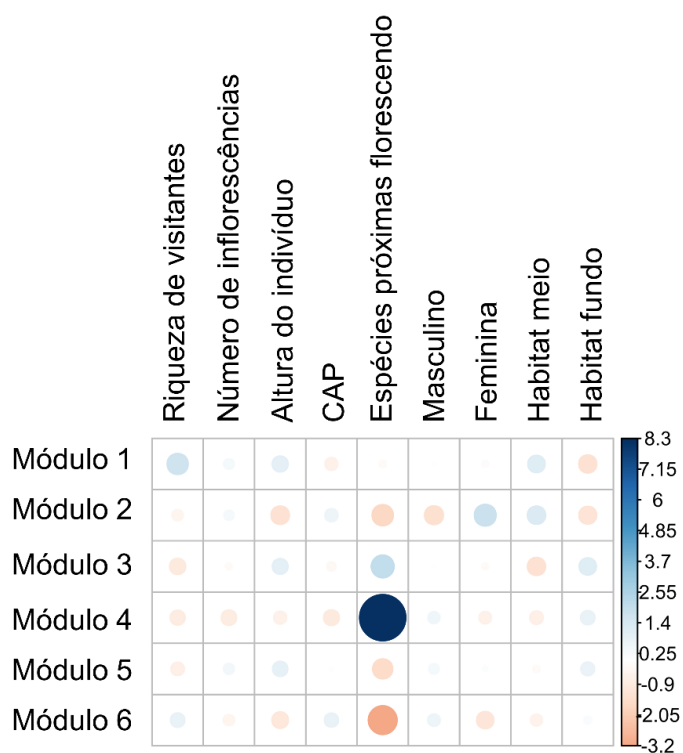


Fig. S3.

ANEXO 3

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Research articles

Title page: The first page of each paper should indicate: The title, the authors' names and affiliations, a short title for use as running head, the name, address, e-mail address, phone and fax number of the corresponding author, 3 to 7 keywords, and a one-sentence summary of the key message of the paper.

Abbreviation: List with abbreviations where appropriate.

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The following sections cover the usual contents: Introduction, Materials and Methods, Results, Discussion, Acknowledgements, References (see below), Tables (see below), Figure legends (see below), Illustrations (see below).

In Materials and Methods, Results and Discussion subheadings are possible. If an author chooses to combine sections Results and Discussion, an additional section Conclusions can be added, but this must be brief.

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Choose subheadings as appropriate but do not use a numbering system. Title page, Key words, Abstract and other items as for full length papers.

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Tables must be serially numbered in Arabic numerals and each must carry a brief descriptive heading. Tables reproduced from other publications must state their precise source. Only signs that can be typeset should be used in the tables and legends. Please provide Tables in Word and include them at the end of the manuscript after the References, each on a separate page. Refrain from using both tables and graphs to demonstrate the same results.

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Electronic artwork

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Please do not embed any tables and/or figures in the text document.

If you should encounter difficulties upon submitting figures and graphics, please contact the editorial office by e-mail under annette.schlierenkamp@ctp.uni-freiburg.de or by telephone under ++ 49/(0)761/203-8300.

References

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Alfano J.R., Collmer A. (2004) Type III secretion system effector proteins: double agents in bacterial disease and plant defence. *Annual Review Phytopathology*, 42, 385–414. Books or other non-serial publications which are quoted in the references must be cited as follows:

Gage J.D., Tyler P.A. (1991) *Deep-sea Biology: A Natural History of Organisms at the Deep-sea Floor*. Cambridge University Press, Cambridge, UK: 504 pp.
Lester R.N., Hasan S.M.Z. (1991) Origin and domestication of the brinjal eggplant, *Solanum melongena*, from *S. incanum*, in Africa and Asia. In: Hawkes J.G., Lester R.N., Nee M., Estrada N. (Eds), *Solanaceae III: Taxonomy, Chemistry, Evolution*. Royal Botanic Gardens, Kew; London, UK: 369-387.

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Data citation is appropriate for data held within institutional, subject focused, or more general data repositories. It is not intended to take the place of community standards such as in-line citation of GenBank accession codes.

When citing or making claims based on data, authors must refer to the data at the relevant place in the manuscript text and in addition provide a formal citation in the reference list. We recommend the format proposed by the Joint Declaration of Data Citation Principles:

[dataset] Authors; Year; Dataset title; Data repository or archive; Version (if any); Persistent identifier (e.g. DOI)

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Immediately after acceptance of a manuscript, the authors should:

- prepare a .doc file which includes:

- the article title;
 - the authors' names (corresponding author indicated by an asterisk); and
 - a 1-sentence summary (maximum 200 characters) summarizing the key findings presented in the paper.
- Submit a figure that:
 - best represents the scope of the paper;
 - o is in .tiff or .eps file formats;
 - o is within the dimensions of 50mm x 60mm; and
 - o has a minimum resolution of 300 dpi.
 - Avoid graphs and other figures with fine detail due to the relatively small size of this image.
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Note that common abbreviations can be used without explanation. Others must be explained. In case of doubt always give an explanation. Use FW = fresh weight and DW = dry weight.

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Scientific names should be cited in their complete form when first mentioned with genus - species - authority - cultivar (cv.) or subspecies (ssp.) where appropriate. Latin names should be underlined or typed in italics. Subsequently the generic names should be abbreviated, but avoid confusion: e.g. use *A. comosus* if the only genus with a first letter A in your paper is *Ananas*; but use unambiguous abbreviations if you have more than one genus with the same first letter, e.g. *Ananas comosus*, *Aechmea nudicaulis* = *A. comosus*, *Ae. nudicaulis*, etc. Common names of organisms must be accompanied by the correct scientific name when first mentioned. For rare or exotic genera it may be useful to give the name of the family and/or higher taxon in brackets when first mentioned.

1 CONCLUSÃO GERAL

2
3 Estudos como estes são importantes para compreender a dinâmica reprodutiva do
4 ecossistema, assegurando a manutenção da biodiversidade. Encontramos resultados
5 interessantes para a comunidade lenhosa da vereda, que demonstram a relevância dessas áreas
6 para a oferta de recursos aos polinizadores no Cerrado. A disponibilidade de recursos contínua
7 é esperada em ambientes silvestres devido a presença de diversas espécies vegetais, no entanto,
8 a complementariedade da disponibilidade de recursos florais aos polinizadores, encontrada
9 entre os habitats da vereda, validam a dinâmica reprodutiva e funcional do ecossistema,
10 sustentando a necessidade de conservação da biodiversidade. Levando em consideração as
11 alterações que as veredas vêm sofrendo devido a fatores antrópicos resultando em modificações
12 na composição de espécies vegetais, informações de estudos como este reforçam a importância
13 dessas áreas para fortalecer e auxiliar nas práticas de manejo sustentável, que promovam a
14 conservação dos polinizadores nas áreas de Cerrado.

15 Para o estudo das redes de interações entre palmeiras e polinizadores, reduzimos a escala
16 da análise para o nível individual. Encontramos resultados que contribuem para a compreensão
17 das variações intraespecíficas dos indivíduos vegetais, auxiliando no entendimento da estrutura
18 e dos padrões na formação da rede entre indivíduos e seus polinizadores. Também adicionamos
19 informações relacionadas as interações para duas palmeiras, consideradas espécies-chave para
20 o ecossistema em que está presente. As variações nas características individuais são capazes de
21 influenciar na atração e polinização dessas plantas.

22 Em cada ecossistema, o florescimento agregado de espécies vegetais pode levar a
23 facilitação ou competição entre as plantas e os polinizadores. Apresentamos como a floração
24 das palmeiras, juntamente as diferentes espécies vegetais, afetam as interações com os
25 polinizadores (efeito de vizinhança) e as possíveis consequências resultantes. Descrevemos a

estrutura da rede de interações entre os indivíduos de *M. armata* e *M. flexuosa*, abordamos os principais grupos de polinizadores presentes durante a polinização e relatamos o tipo de estratégia que as duas espécies de palmeiras podem estar utilizando para atrair os polinizadores a realizar a polinização cruzada. A falta de informações sobre *M. armata* nos levou a investigar o seu sistema de polinização, no entanto, a espécie ainda carece de estudos pois é considerada com fundamental relevância ecológica e social. Estudos como estes comprovam a importância das interações entre plantas e polinizadores e contribuem para o entendimento dos serviços ecossistêmicos em ambientes naturais.

Durante a revisão na literatura dos estudos relacionados a *M. flexuosa* encontramos diversos agentes polinizadores relacionados a sua polinização. Recentemente, o estudo de Ávila et al. 2023 elucidou a plasticidade fenotípica da espécie, assumindo diferentes épocas de floração e frutificação, sendo um tipo de estratégia para adaptação a diferentes condições ambientais e, consequentemente, perpetuação da espécie. Essa estratégia aliada aos diferentes mecanismos de polinização encontrados demonstra a sua baixa especialização, também descrita em nosso trabalho. Dessa forma, contribuimos com mais informações a respeito dos mecanismos de polinização apresentamos pela espécie em nossa região, colaborando para quaisquer práticas de manejo que visam melhorar os serviços de polinização e conservação da espécie, levando em consideração que ela é uma palmeira economicamente explorável.

Nossos resultados elevam o papel ecológico fundamental das espécies presentes no ecossistema de veredas, como principal recurso para uma grande diversidade de polinizadores, representando um passo importante em direção às estratégias de conservação nessas formações, caracterizado como ambientes pouco resiliente e com constantes problemas com atividades antrópicas. Além disso, nossos estudos permitem compreender melhor como as redes ecológicas complexas são configuradas no nível individual, utilizando fatores interno e externos

50 no contexto das interações, ajudando a avançar a compreensão a respeito da dinâmica
51 reprodutiva, ao mesmo tempo em que contribuímos para os estudos em espécies de palmeiras.

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