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**EFEITOS DA VIZINHANÇA NA POLINIZAÇÃO: análise em múltiplos contextos de
comunidade**

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Marsal Danrlei de Amorim

EFEITOS DA VIZINHANÇA NA POLINIZAÇÃO: análise em múltiplos contextos de comunidade

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Orientador: Pedro Joaquim Bergamo

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No dia 28 de abril de 2025, às 08:30 horas, por vídeo conferência, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) Marsal Danrlei de Amorim, orientando(a) do Professor Pietro Kiyoshi Maruyama Mendonça, intitulada: **“Efeitos das vizinhanças na polinização: análise em múltiplos contextos de comunidade”**. Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) Pietro Kiyoshi Maruyama Mendonça, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Leonor Patrícia Cerdeira Morellato (UNESP), Tatiana Garabini Cornelissen (UFMG), Gudryan Jackson Barônio (USP), Renata Trevizan (UFMG) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

(X) Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;

() Reprovação da tese (marcar se é a primeira ou segunda reprovação): () *primeira reprovação () segunda reprovação

*Conforme o disposto no Artigo 80 da Resolução Complementar do CEPE/UFMG Nº 02/2017, de 04 de julho de 2017, caso seja a primeira reprovação, poderá ser concedido, a critério do Colegiado de Curso, um prazo para a realização de nova defesa de tese.

A banca indica esta tese aos Prêmios CAPES e UFMG de teses? (X) SIM () NÃO

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 28 de abril de 2025.

Assinaturas dos Membros da Banca Examinadora



30/04/2025, às 12:06, conforme horário oficial de Brasília, com fundamento no art. 5º do [Decreto nº 10.543, de 13 de novembro de 2020](#).



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RESUMO

Nesta tese foram utilizadas as características da comunidade de plantas, como quantidade de flores e a morfologia das plantas para compreender as relações indiretas mediadas por polinizadores entre as plantas no Campo Rupestre brasileiro em três contextos de comunidade diferentes: comunidade como um todo, a curta distância na vizinhança e em espécies focais. Para isso foram utilizados dados de visitação, deposição de pólen e produção de sementes para representar medidas de sucesso reprodutivo das plantas. A tese foi dividida em três capítulos que analisam as relações nesses três contextos de comunidade. No primeiro capítulo, foi avaliado o efeito na comunidade como um todo para cada espécie de planta. Os resultados mostraram que as plantas com morfologia mais similar dentro da comunidade têm maior sucesso reprodutivo demonstrando facilitação entre as plantas. Enquanto a maior abundância floral gerou competição intraespecífica ao reduzir a taxa de visitas e a deposição de pólen coespecífico, apesar de não afetar a produção de sementes. No segundo capítulo, foi avaliado o efeito da vizinhança próxima (2,5 m²) na reprodução das plantas em geral e de duas espécies com diferentes morfologias florais: *Piptolepis imbricata* (Gardner) Sch.Bip. (Asteraceae) e *Cuphea disperma* Koehne (Lythraceae). Com essas duas abordagens, vizinhança e espécies, foi possível diferenciar o efeito da vizinhança (traços florais, abundância e riqueza de plantas) na própria comunidade e para as espécies que estão inseridas nela. Os resultados mostram que flores diferentes na comunidade recebem maiores cargas tanto de pólen coespecífico quanto heteroespecífico. No entanto, não foi encontrado efeito no sucesso reprodutivo, quantificado como formação de sementes. Essa ausência de relação pode ser explicada pelo balanço dos efeitos positivos e negativos da similaridade floral que difere no nível das espécies, pois *C. disperma* aumentou o sucesso reprodutivo quando circundada por plantas similares e *P. imbricata* não apresentou relação do sucesso reprodutivo com a comunidade no entorno. No terceiro capítulo, foi avaliada a biologia reprodutiva da *Lantana hypoleuca* Briq. e a relação dessa espécie com as plantas vizinhas. Os resultados mostraram que o sucesso reprodutivo dessa espécie é maior nos locais onde há maior riqueza de espécies e menor nos locais onde há maior abundância de flores da mesma espécie, sugerindo facilitação interespecífica e competição intraespecífica. De forma geral, a abundância floral foi um importante fator para a visitação, porém o sucesso reprodutivo está mais relacionado à comunidade de plantas vizinhas e à morfologia floral. Conclui-se que, em todos os contextos de comunidade, ocorreu competição e facilitação e a abundância e similaridade floral estavam mediando as relações entre as plantas. Portanto, a comunidade de plantas do campo rupestre parece ser estruturada

por competição intraespecífica e facilitação através da abundância e similaridade morfológica das flores, independente do contexto de comunidade.

Palavras-chave: Contexto de comunidade; Diversidade Floral; Reprodução das plantas; Deposição de pólen; Compartilhamento de polinizadores; Abundância floral.

ABSTRACT

In this thesis, characteristics of the plant community, such as flower abundance and plant morphology, were used to understand indirect relationships mediated by pollinators among plants in the Brazilian *Campo Rupestre* across three different community contexts: the entire community, short-distance neighborhood, and focal species. For this, data on visitation, pollen deposition, and seed production were used to represent measures of plant reproductive success. The thesis is divided into three chapters that analyze these relationships in the three community contexts. In the first chapter, the effects on the entire community were assessed for each plant species. The results showed that plants with more similar morphology within the community had higher reproductive success, demonstrating facilitation among plants. Meanwhile, higher floral abundance led to intraspecific competition by reducing the rate of visits and conspecific pollen deposition, although it did not affect seed production. In the second chapter, the effect of the nearby neighborhood (2.5 m²) on the reproduction of plants in general and of two species with different floral morphologies—*Piptolepis imbricata* (Gardner) Sch.Bip. (Asteraceae) and *Cuphea disperma* Koehne (Lythraceae)—was evaluated. With these two approaches—neighborhood and species—it was possible to differentiate the effect of neighborhood (floral traits, plant abundance, and richness) on the community itself and on the species within it. The results show that different flowers in the community receive higher loads of both conspecific and heterospecific pollen. However, no effect was found on reproductive success, quantified as seed formation. This lack of relationship can be explained by a balance between the positive and negative effects of floral similarity, which varies at the species level, since *C. disperma* increased reproductive success when surrounded by similar plants, while *P. imbricata* showed no relationship between reproductive success and the surrounding community. In the third chapter, the reproductive biology of *Lantana hypoleuca* Briq. and its relationship with neighboring plants were assessed. The results showed that the reproductive success of this species is higher in areas with greater species richness and lower in areas with greater abundance of flowers of the same species, suggesting interspecific facilitation and intraspecific competition. Overall, floral abundance was an important factor for visitation, but reproductive success was more closely related to the neighboring plant community and floral morphology. It is concluded that in all community contexts, both competition and facilitation occurred, and floral abundance and similarity mediated the relationships among plants. Therefore, the *Campo Rupestre* plant community appears to be

structured by intraspecific competition and facilitation through floral abundance and morphological similarity, regardless of the community context.

Keywords: Community context; Floral diversity; Plant reproduction; Pollen deposition; Pollinator sharing; Floral abundance.

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INTRODUÇÃO GERAL

Biologia da polinização

As plantas com flores são organismos sésseis, ou seja, não se movimentam. Portanto, para se reproduzirem, elas precisam transferir o pólen (micrósporo, que contém o gametófito masculino) presente nos estames, estrutura da flor onde o pólen está presente, com o óvulo (megásporo, que contém o gametófito feminino) e está localizado no pistilo da flor. Esse processo é chamado polinização. Estima-se que cerca de 90% das espécies de plantas com flores (Angiospermas), necessitam de animais como abelhas, beija-flores, mariposas, moscas, entre outros para realizar a polinização (Ollerton et al. 2011; Rodger et al. 2021; Tong et al. 2023). Em troca desse serviço, as plantas costumam ofertar recursos, por exemplo, o néctar, óleo ou mesmo pólen para atrair esses animais polinizadores (Rech et al. 2014; Ballarin et al. 2024). Esse processo é fundamental para a reprodução e manutenção das populações de plantas. Portanto, as diferentes flores que conhecemos, como rosas, flores de maracujá, ipê, são formas das plantas de se destacar da paisagem e atrair os animais (Rech et al. 2014; Camargo et al. 2019). O estudo desses aspectos da reprodução das plantas, desde a atração dos animais, recursos ofertados, até a produção das sementes está dentro da disciplina de estudo que chamamos de Biologia da Polinização.

Morfologia (forma) das flores

Existem muitas morfologias (formas) de flores. Por exemplo, tem flores de maracujá com coloração branca e com uma coroa de estames coloridos. Ou então uma flor de Ipê que pode ter várias cores, como rosa, amarela, branca, mas na qual os estames estão escondidos no tubo floral em forma de sino. Essas diferenças na forma das flores, odor, cor e recursos são importantes para diferenciar os animais mais “adequados” para polinizar as flores. O conjunto de características, que tanto atraem, como também podem restringir a visita de algum visitante floral, são englobadas no que chamamos de síndromes de polinização (Faegri e Van Der Pijl 1979; Castellanos et al. 2004; Dudash et al. 2011). Essas funções de atração e de restrição de polinizadores, se dão por exemplo, quando a corola (conjunto de pétalas) das flores são estreitas e longas demais para uma abelha alcançar o recurso, mas onde um beija-flor é capaz de acessar o néctar (Aigner, 2004). Nesse caso, nós temos uma planta especializada em beija-flores, que podem se chamar de ornitófilas. Portanto, quando dizemos que uma planta é

especializada, queremos dizer que ela depende exclusivamente, ou fortemente, de um grupo de polinizadores e que as flores desta planta apresentam uma morfologia que favoreça esses visitantes.

No entanto, em um outro extremo, temos plantas generalistas. Essas plantas tendem a ter uma morfologia floral menos restritiva para algum grupo de visitantes, geralmente com as partes reprodutivas expostas, por exemplo, as flores de girassol (Waser et al. 1996). Os polinizadores das plantas especializadas tendem a ser eficientes na polinização, por exemplo, com uma visita sendo suficiente para a polinização ocorrer, enquanto em plantas generalistas, os polinizadores seriam menos eficientes, por exemplo, depositando menos pólen do que a planta necessita para gerar sementes (Aigner, 2001; Ohashi et al. 2021). Dessa maneira, flores generalistas podem precisar de mais visitas para serem polinizadas de maneira eficiente, pois a morfologia da flor não é ajustada à morfologia do animal (Bustos et al. 2023). Por outro lado, as plantas generalistas têm a garantia de que vão receber visita de algum grupo capaz de polinizar, pois qualquer grupo pode acessar os recursos. Portanto, a generalização, pode ser importante quando as plantas estão num ambiente onde há baixa abundância ou variação na disponibilidade de animais polinizadores (Tur et al. 2013; Watts et al. 2016; Lázaro et al. 2020). Logo, a estratégia de ser generalista, pode ser importante para lidar com a flutuação dos polinizadores ao longo do tempo (Waser et al. 1996). Porém, é importante ter em mente que, na natureza, estratégias especialistas e generalistas geralmente formam um contínuo, e a maioria das espécies de plantas têm flores que podem ser polinizadas por mais de um grupo de visitantes, mas que ainda restringe outros (Waser et al. 1996; Chmel et al. 2021; Ohashi et al. 2021).

Competição e Facilitação

Além de ser especialista ou generalista, as plantas também lidam com a relação indireta com outras plantas que estão florindo ao mesmo tempo e que podem atrair/compartilhar os mesmos polinizadores. De modo geral, a maioria das plantas sobrepõe à sua floração com outras espécies e são polinizadas por visitantes compartilhados (Arroyo-Correa et al. 2024). Nesses casos, as espécies de plantas podem competir umas com as outras para atrair mais polinizadores para si, processo chamado de competição. Por exemplo, uma espécie de planta com flores maiores e com mais néctar, pode atrair mais polinizadores, reduzindo as visitas de polinizadores das espécies de plantas que estão em volta e gerando um efeito negativo (Ashman et al. 2020; Tur et al. 2016). Por outro lado,

compartilhar polinizadores também pode ser vantajoso para as plantas. Por exemplo, se há espécies de planta florescendo próximas e ao mesmo tempo, elas atraem mais visitantes do que floridas sozinhas, levando a um processo conhecido como facilitação (Carvalheiro et al. 2014; Bergamo et al. 2020a; Arrowsmith et al. 2023). Assim como generalização e especialização, esses dois processos também representam as extremidades de um processo contínuo que ocorre constantemente em uma comunidade de plantas (Al-Namazi et al. 2021; Losapio et al. 2021; Arroyo-Correa et al. 2024) e são importantes para a sobrevivência das espécies, ou seja, servem de suporte para a biodiversidade (Losapio et al. 2021; Wei et al. 2021). Para estarem competindo ou facilitando, as plantas precisam em algum grau compartilhar os mesmos polinizadores (Coetzee et al. 2021; Wei et al. 2021; Albor et al. 2022). Assim, se uma planta é polinizada exclusivamente por beija-flor e outra é polinizada por abelhas, por exemplo, mesmo que ambas estejam no mesmo local e florindo ao mesmo tempo, essas plantas não têm uma interação indireta. Portanto, incorporar o contexto da comunidade é importante para entender o sucesso reprodutivo das plantas porque auxilia na compreensão e as consequências das relações diretas com os polinizadores e indiretas entre as plantas.

Dependência do contexto da comunidade

O efeito que as plantas têm umas sobre as outras varia de acordo com o foco, ou o contexto da comunidade que estamos avaliando. Por exemplo, em um contexto mais amplo, olhando toda a comunidade, com diferentes morfologias florais, tende a atrair mais grupos/espécies de polinizadores (Ghazoul, 2006; Lázaro et al. 2009; Fornoff et al. 2017). Isso ocorre porque ao aumentar a diversidade e a quantidade de recursos que uma comunidade de plantas oferece, mais grupos de polinizadores são atraídos, pois essa diversidade de recursos complementam as necessidades de diferentes grupos (Lázzaro et al. 2009; Fründ et al. 2013). Essas funções de complementaridade que a comunidade de plantas apresenta é importante para a manutenção do ecossistema (Fründ et al. 2013; Schleuning et al. 2015). No entanto, em alguns casos, onde por exemplo, os polinizadores são mais escassos como em ambientes de alta altitude onde o frio reduz a presença de insetos (Brito e Sazima, 2012; Lehmann et al. 2019), uma comunidade de plantas menos diversa em termos de morfologia, ou redundância funcional, teria uma vantagem em aumentar a atratividade dos mesmos polinizadores compartilhados, levando a comunidades estruturadas pela facilitação (Tur et al. 2016; Bergamo et al. 2020; Lopes et al. 2021).

Quando se foca em uma espécie de planta, os padrões de interações vão depender da estratégia generalista ou especialista. Plantas generalistas recebem a maioria das visitas e compartilham visitantes florais com as plantas mais especializadas, levando a uma estrutura aninhada para as interações entre plantas e polinizadores (Bascompte et al. 2003; Olesen et al. 2008). Essa estrutura é importante pois é flexível a alterações, o que torna as interações mais resistentes às extinções (CaraDonna et al. 2017). No geral, podemos esperar que essas espécies generalistas sejam dominantes, com maior período de floração e maior quantidade de flores (Pauw, 2007; Biella et al. 2019; Resasco et al. 2021). Por concentrarem mais interações com os polinizadores, essas plantas costumam ter maiores taxas de sucesso reprodutivo em um efeito de competição com as plantas menos abundantes (Biella et al. 2019; Lázaro et al. 2020). Por outro lado, uma planta rara florindo próxima de uma planta abundante, com uma morfologia similar, pode se beneficiar da planta mais abundante compartilhando os polinizadores. Ou mesmo, as plantas raras poderiam se beneficiar de atraírem os mesmos visitantes entre si para se tornarem mais atrativas. Em ambas as situações, a facilitação através dos polinizadores levaria a persistência das espécies raras na comunidade (Bergamo et al. 2020; Wei et al. 2021).

Essas mudanças nos processos que mediam o efeito das interações para a comunidade e para as espécies, também ocorrem entre indivíduos de uma mesma espécie (Arroyo-Correa et al. 2024). No nível individual, as plantas da mesma espécie não necessariamente vão compartilhar os mesmos visitantes, isso ocorre pelas características das flores próximas a ela. Por exemplo, uma planta rodeada por uma maior diversidade de flores, com morfologias diferentes atrairia uma maior gama de grupos de polinizadores de onde poderia receber visitas. Isso acontece porque o compartilhamento de visitantes florais e o efeito desse compartilhamento depende da sincronia de floração e abundância de flores e das características dessas flores (Jakobsson et al. 2009; Arroyo-Correa et al. 2024). Assim, indivíduos de plantas que florescem ao mesmo tempo, tendem a aumentar o compartilhamento de polinizadores, sejam plantas da mesma espécie ou não (Arroyo-Correa et al. 2023; Arroyo-Correa et al. 2024). Esse mecanismo pode ser especialmente importante para indivíduos que produzem poucas flores, onde compartilhar visitantes pode aumentar a aptidão (Arroyo-Correa et al. 2024). Então, quando estamos tentando compreender os processos ecológicos que estruturam as comunidades, também é importante levar em conta os processos a nível individual (Streher et al. 2024). Portanto, imaginamos que os processos ecológicos a nível de comunidade dependem dos processos ecológicos no nível da espécie/populações que dependem dos processos ecológicos no nível do indivíduo.

Campo Rupestre

O Campo Rupestre no Brasil pertence ao domínio de savana neotropical (Cerrado) e ocorre em altitudes acima de 900 m ao longo da Serra do Espinhaço nos Estados da Bahia e Minas Gerais, caracterizado por alto endemismo e diversidade de plantas. Embora cubra menos de 1% do território brasileiro, o Campo Rupestre contém mais de 10% da diversidade vegetal do país (Silveira et al. 2016). A diversidade de paisagens do campo rupestre, com muitos afloramentos rochosos, faz com que muitas espécies de plantas tenham distribuição restrita a pequenas manchas (Silveira et al. 2016). Mesmo sendo um ambiente de altas altitudes, as abelhas são as principais polinizadoras, ainda que ocorra uma maior proporção de os sistemas de polinização por vento e moscas ao longo do gradiente altitudinal do Campo Rupestre (Monteiro et al. 2021). Além disso, a distribuição em pequenas populações disjuntas, por conta da distribuição restrita causadas pela paisagem do Campo Rupestre torna fundamental a existência de polinizadores de longa distância, como abelhas grandes e beija-flores, para conectar populações isoladas (Rodrigues et al. 2011; Monteiro et al. 2021). Apesar de ser um lugar único no mundo, vem sendo ameaçado por atividades humanas, como a mineração, queimadas, extração de madeira e espécies invasoras (Silveira et al. 2016). Portanto é importante estudar como as comunidades de plantas desse ambiente são estruturadas para podermos criar estratégias de conservação eficientes para todo o ambiente. Alguns estudos sobre o Campo Rupestre já demonstraram que a comunidade parece ser estruturada pela facilitação na polinização, ainda que a competição também exerça um papel importante para a comunidade (Lopes et al. 2021; Amorim et al. 2022; Lopes et al. 2023; Camargo et al. 2023). Por exemplo, plantas com cores de flores similares tendem a se segregar na floração, sugerindo um mecanismo que evita a competição entre espécies ao mesmo tempo que pode manter a estabilidade de recursos florais aos visitantes ao longo do ano (Camargo et al. 2023). Enquanto a rede de interações com os polinizadores apresenta uma estrutura modular, favorecendo morfologias relacionadas a sistemas de polinizadores, ou especializadas (Carstensen et al. 2016). Ainda que, no geral, as interações parecem ser relacionadas ao oportunismo (Carstensen et al. 2014; Monteiro et al. 2021) favorecendo plantas com morfologias florais generalistas, ou pelo menos, com morfologias similares, favorecendo o compartilhamento de polinizadores entre as plantas, levando a um efeito positivo da comunidade no sucesso reprodutivo dessas plantas, ou seja, facilitação (Lopes et al. 2021; Lopes et al. 2023). Portanto, para essas plantas, a comunidade no entorno pode ser um fator especialmente importante para o sucesso reprodutivo.

OBJETIVOS

Para compreender o efeito da vizinhança na reprodução das plantas nos Campos Rupestre, os estudos apresentados nesta tese avaliaram o efeito da vizinhança em três contextos: da comunidade; da vizinhança próxima; e espécies focais. Para unir esses aspectos, a tese foi dividida em três capítulos:

No primeiro capítulo, *Efeito da vizinhança na comunidade nas plantas*, foi abordado o efeito da diversidade de traços florais, abundância e riqueza de plantas e a sobreposição da fenologia, para compreender como as plantas estão interagindo indiretamente via polinizadores e como essa interação indireta afeta as taxas de visitação, deposição de pólen e produção de sementes ao nível da comunidade. Esse capítulo utilizou uma abordagem de redes de interação, para compreender a direção das interações, ou seja, quais espécies de plantas estavam causando efeitos indiretos via visitantes florais (*acting degree*) e quais eram as espécies que estavam recebendo estes efeitos indiretos (*target degree*) (Bergamo et al. 2021).

No segundo capítulo, *Efeito da vizinhança próxima*, o objetivo foi entender o efeito da vizinhança próxima na reprodução das plantas, considerando as variáveis de visitação, deposição de pólen e produção de sementes. Como uma abordagem complementar, foi observado o efeito da vizinhança próxima em duas espécies de plantas com diferentes morfologias florais: *Piptolepis imbricata* (Gardner) Sch.Bip. (Asteraceae) e *Cuphea disperma* Koehne (Lythraceae) (Figura 1a e 1b). Com essas duas abordagens foi possível diferenciar o efeito da vizinhança (traços florais, abundância e riqueza de plantas) na própria vizinhança e para as espécies que estão inseridas nela.

Por fim, no terceiro capítulo, *Efeito da vizinhança na reprodução da Lantana hypoleuca*, testamos o efeito da vizinhança na reprodução da *Lantana hypoleuca* Briq. (Figura 1c). Neste capítulo, buscamos entender como o sucesso reprodutivo de *L. hypoleuca* é influenciada pela comunidade de plantas no entorno, ou plantas vizinhas, e como essa influência é afetada por fatores como morfologia, abundância e diversidade de plantas.



Figura 1. A figura apresenta as espécies de planta estudadas no nível individual no Campo Rupestre de Diamantina, MG, Brasil. a) *Piptolepis imbricata*; b) *Cuphea disperma*; c) *Lantana hypoleuca*.

METODOLOGIA GERAL

Área de estudo

Os dados dos três capítulos da tese foram coletados em uma área de Campo Rupestre dentro da Universidade Federal dos Vales do Jequitinhonha e Mucuri, Diamantina, Brasil (18°11'48"S, 43°34'8"W). A área está situada a 1300 metros de altitude em relação ao nível do mar, e o clima local é caracterizado por uma estação seca e outra chuvosa (Alvares et al, 2013). A coleta de dados foi realizada entre os anos de 2021 e 2023, durante a estação chuvosa, que ocorreu entre os meses de Outubro e Abril (INMET, 2020). Esse período foi escolhido por representar a época do ano em que há maior diversidade de flores florindo ao mesmo tempo (Monteiro et al. 2021; Luna et al. 2023).

Para responder às perguntas abordadas nos capítulos um e dois, foram delimitadas 32 parcelas com 2.5 m². Cada uma dessas parcelas foi amostrada durante 15 dias, com uma semana de intervalo entre as amostragens, esse processo foi repetido nove vezes. Durante os campos, foram contadas a quantidade de flores por indivíduo de todas as espécies que estavam florindo, observados os visitantes florais, coletados os estigmas e os frutos de cada um dessas espécies que estavam florindo. Para cada espécie florindo dentro da parcela, foram medidos os traços florais como o comprimento da pétala, abertura da pétala, altura dos estames e altura do pistilo. Essas espécies de plantas também foram caracterizadas pelos recursos ofertados, como néctar e pólen.

Especificamente para o capítulo três, foram marcados 20 indivíduos da espécie modelo *Lantana hypoleuca*. Depois, foi delimitada uma parcela circular, com raio de 1.5 m, partindo desses indivíduos marcados. Cada um desses indivíduos estava separado por pelo menos 10 m de distância. Dados de visitação dos polinizadores e abundância de flores por espécie dentro das parcelas foi contado em três dias diferentes para cada parcela. Ao final, coletamos os pistilos e frutos dos 20 indivíduos focais para estimar a deposição de pólen e o sucesso reprodutivo.

Efeito da vizinhança na comunidade nas plantas

No capítulo um foi avaliado como as espécies dentro da comunidade são influenciadas pelo contexto da comunidade através de análise de redes de interação. Para isso, foram utilizadas as características das flores (altura dos estames e pistilos, comprimento e abertura da pétala e recurso) para estimar o quanto as flores de cada espécie eram similares entre si. A soma de todas as flores de cada uma das espécies floridas foi usada para estimar a abundância de flores. Esses dados de abundância foram usados para saber o quanto as flores tinham sobreposição de floração, ou quanto da floração de uma espécie ocorreu ao mesmo tempo que outras espécies. Foi estimada uma taxa de visitação utilizando o número de flores de cada espécie que o polinizador visitou, dividido pela quantidade de flores que tinham para ser visitadas e o tempo de observação de visitantes. Também foi estimado o quanto as espécies de plantas estavam sendo visitadas pelos mesmo polinizadores, através de dois valores, um chamado de ‘grau de alvo’ e o outro de ‘grau de atuação’ (Bergamo et al. 2021). Por exemplo, se uma planta A recebe cinco visitas e a planta B recebe duas visitas do mesmo visitante, a planta A é ‘ator’ e a planta B é ‘alvo’. A ideia é que a planta B receberia mais vezes o visitante floral vindo de A em relação a quantidade de vezes que o visitante visitaria A vindo de B. Os grãos de pólen presentes nos pistilos coletados foram separados entre o pólen de

outras espécies (heteroespecífico) e o pólen da mesma espécie (coespecífico). Para o pólen heteroespecífico foi utilizada a média de pólen de outras flores que chegou nos pistilos de cada espécie. Tanto para o pólen coespecífico, quanto para a produção de sementes, foi utilizada uma transformação nos dados, onde a planta que recebeu mais pólen e gerou mais sementes para cada espécie era caracterizada como 1 e a planta que recebeu menos era caracterizada como 0. Portanto, uma flor que teve 0.7 de produção de sementes, teve 70% da quantidade que a planta que produziu mais, o que indica que ela teve uma boa produção relativa de sementes.

Efeito da vizinhança próxima

Para o capítulo dois, foram utilizados os mesmos dados coletados no capítulo um, mas com uma abordagem analítica diferente: separando os dados de produção de sementes, deposição de pólen e visitação e do contexto da comunidade (abundância, riqueza e similaridade morfológica das flores) em cada uma das 32 parcelas e em cada bloco de 15 dias de observação (ou seja, em vizinhanças próximas de 2,5 m²). Ao todo foram nove períodos de observação. Ainda, foram selecionadas duas espécies de plantas que ocorrem com maior frequência. Essas espécies foram *Piptolepis imbricata* - que possui flores roxas com néctar como recurso, e é visitada por abelhas, borboletas, moscas e beija-flores (Queiroz, 2018). A outra espécie foi a *Cuphea disperma* - que possui flores entre rosa e roxo, também oferece néctar como principal recurso e é visitada por abelhas, moscas e beija-flores (Queiroz, 2018).

Efeito da vizinhança na reprodução da *Lantana hypoleuca*

Para avaliar o efeito das plantas vizinhas no sucesso reprodutivo da *Lantana hypoleuca* testamos como a produção de frutos e deposição de pólen foram afetados pela quantidade de espécies de plantas florindo no entorno (riqueza de plantas), abundância de flores da mesma espécie (abundância de flores de *Lantana hypoleuca*) e abundância de flores de outras plantas (abundância de plantas heteroespecíficas). Para esse capítulo também foi mensurada a similaridade das flores, porém usando apenas o comprimento da pétala para cada espécie que estava florindo dentro da parcela. Nesse caso, quanto mais similar o comprimento da pétala de *Lantana hypoleuca* for com todas as plantas floridas, mais similar é a vizinhança dessa parcela com a planta focal.

EFEITO DA VIZINHANÇA NA COMUNIDADE NAS PLANTAS

Floral trait similarity between neighbors increases reproductive success suggesting facilitation through pollinator sharing

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Abstract

The ability of plants to attract pollinators is context-dependent, influenced by floral traits, abundance, and resources from neighboring plants. Indirect interactions through shared pollinators, from competition to facilitation, may lead to varied reproductive outputs in plants, and the mechanisms behind these interactions remain to be fully elucidated in complex ecological communities. We aimed to disentangle the mechanisms by which the floral neighborhood may impact pollinator sharing and plant reproductive success in the highly biodiverse *campos rupestres* from Brazil. To do so, we investigated the relationships among species traits, ecological networks, pollen deposition and reproductive output (seed set) in variable community contexts, using a piecewise structural equation modeling (SEM) approach. Plant species with similar flowers in relation to its neighbors showed higher seed set, indicating facilitation. In contrast, species with high flower abundance showed decreased visitation rates per flower and conspecific pollen deposition, suggesting intraspecific competition. Our study reveals that, while there is an interplay between facilitation and competition, the former had a stronger influence on the reproductive output of plants sharing pollinators in a highly diverse tropical community. These results show that traits and abundance mediate complex indirect interactions in plant-pollinator communities.

Keywords: flower diversity, network analysis, plant-pollinator community; plant reproduction, pollen deposition; seed set.

Introduction

Most flowering plants require biotic pollination to ensure reproduction (Tong et al, 2023). In this context, pollinators constitute an important reproductive resource for plants, which are shared among individuals and species within communities (Pauw 2013). The indirect interactions through shared pollinators influence plant reproductive success, and vary from competition to facilitation (Sargent & Ackerly, 2008). While competition for pollinators among plants in a community causes less attractive plants to receive reduced visitation and decrease their reproductive success (Ha et al., 2021; Johnson et al., 2022), facilitation has the opposite effect, as it increases overall attractiveness and reproductive success (Tur et al., 2016; Bergamo et al., 2024). Understanding the mechanisms driving the relative importance of competition and facilitation in plant-pollinator communities is particularly important because this balance is a key driver of species coexistence and stability in plant communities (Pauw 2013, Benadi, 2015, e.g. Guimaraes et al. 2017, Duchenne et al. 2021).

Plants attract pollinators providing resources such as pollen and nectar, and advertise these resources via floral traits including color and shape (Dudash et al, 2011). Moreover, the abundance of flowers and individuals also influence pollinator attraction (Peuker et al, 2020). For instance, plant species with longer flowering periods and greater floral abundance tend to interact with more pollinators and experience higher reproductive success (Lázaro et al, 2020). However, the success in attracting pollinators is also context-dependent because floral traits, abundance, and the resources provided by neighboring plants also affect the plant's capacity to attract pollinators (Sritongchuay *et al.* 2021; Shibata & Kudo 2020). In situations of low abundance of pollinators and plants, facilitation might predominate leading to greater pollinator attraction and reproductive success for plant species with higher trait similarity and phenological overlap with neighboring plants (Bergamo et al. 2020, Lopes et al. 2022). On the other hand, competition may prevail when plants are abundant and pollinators become scarce (Rathcke 1983, Ye et al. 2014).

Quantifying the role that each plant species plays in the community according to their interaction with pollinators is a challenge, but this may supposedly be accessed by using species-level network metrics, such as specialization and partner diversity, which measure how plants distribute their interactions across multiple partners (Blüthgen et al, 2006; Dormann, 2011). However, these metrics do not directly represent plants' influence on each other by sharing pollinators, *i.e.*, indirect interactions. Therefore, metrics that are based on quantification of pollinator sharing may perform better to explain the influence that one plant

species should have on or receives from others (Lázaro et al, 2020; Bergamo et al, 2022). By linking such metrics with estimates of plants reproductive success, we can assess how plants affect each other's fitness through pollinator sharing (Lázaro et al, 2020; Bergamo et al, 2022). For instance, target and acting degrees are network metrics based on the Müller's index, measuring the potential indirect effects among plant species through shared pollinators (Müller et al, 1999, Bergamo et al, 2022). Bergamo et al. (2021) highlighted that plant species with larger target degree, i.e. that are strongly affected by other plants because their pollinators mainly rely on other plant species, are expected to have greater fitness in facilitation scenarios but lower fitness in competition scenarios. While network metrics have been shown to greatly depend on species abundance and traits (Carvalho et al. 2014, Bergamo et al. 2021, Lázaro et al. 2020), disentangling their effects on plant reproductive success is still less explored.

An important functional consequence of indirect interactions among plant species in a community can be measured by heterospecific pollen deposition (Arceo-Gómez & Ashman, 2014; Thomson et al, 2019). The flow of heterospecific pollen can go multiple ways or be almost unidirectional, when a plant species sends more pollen than it receives (Fang & Huang, 2013, Arceo-Gómez et al, 2020). In this context, deposition of heterospecific pollen mainly causes negative effects on plant reproduction (Ashman & Arceo-Gómez, 2013). However, a few studies have shown indirect positive association between heterospecific pollen and seed set (Streher et al, 2020; Lopes et al, 2022). These positive effects can be related to, generalized and closely related plant species showing higher tolerance to heterospecific pollen deposition (Streher et al, 2020). Teasing apart correlation from causation on the effects of heterospecific pollen deposition is also important (Ashman et al, 2020), since heterospecific pollen may suggest that the plant received a higher number of visits or a greater amount of conspecific pollen deposition concomitant with heterospecific pollen, which in turn increases seed set (Tur et al. 2016; Lopes et al. 2022). However, there are still few studies that link species traits, ecological networks and reproductive output at the community context, which is essential to understand how plant-pollinator interactions may be linked to ecosystem functioning.

The relationship between community patterns and plant reproductive success is particularly significant in habitats with high diversity, such as OCBIL (old, climatically buffered, infertile landscapes) ecosystems (Hopper, 2009; Silveira et al, 2016). Species in these habitats have a long history of adapting to poor soils and limited climatic buffering in small areas (Hopper, 2009; Hopper et al, 2021). Plants in OCBIL habitats often have

restricted distributions and rely on long-distance pollinators, such as large bees and hummingbirds for gene flow between populations (Hopper et al, 2021; Monteiro et al, 2021). Brazil's campos rupestres is one of such OCBIL areas, characterized by high species endemism within a confined region (Monteiro et al, 2021). In campos rupestres, plant individuals may occur in variable floral neighborhoods, from dense conspecific patches to highly diverse co-flowering patches (Loiola et al. 2023). Therefore, we aimed to understand the influence of the floral neighborhood on pollinator sharing and on the reproductive success of plants in this highly biodiverse tropical grassland ecosystem by characterizing the different process involved (Figure 1): (1) the community context, which refers to floral trait similarity, floral abundance, and phenological overlap with neighboring plants; (2) the visitation rates by pollinators and the indirect effect between species quantified by target degree and acting degree; (3) heterospecific and conspecific pollen deposition; (4) the response variable representing plants' reproductive success: seed set. Facilitation and competition are expected to shape different relations between these different components (Figure 1A vs. 1B).

If facilitation will be a predominant process, we expected that species with greater functional similarity and phenological overlap would lead to higher values of both target and acting degree and visitation rate per flower, as higher floral similarity and phenological overlap would mean more shared pollinators (Bergamo et al, 2020; Lázaro et al, 2020). More abundant species are expected to receive more pollinators and, by sharing them with other plants, to show higher acting degree (Carvalho et al, 2014) as well as to receive more conspecific pollen and set more seeds (Carvalho et al, 2014). Conversely, less abundant species are expected to have a higher target degree because they will share more pollinators with other plants (Bergamo et al, 2021). Species with a higher target degree are expected to receive more heterospecific pollen deposition, while species with a higher acting degree are likely to receive less heterospecific pollen (Bergamo et al, 2021). If facilitation will be predominant, the impact of heterospecific pollen deposition is expected to be weak compared to the benefits of sharing pollinators (Streher et al, 2020; Lopes et al, 2022). Therefore, we anticipated a positive indirect relationship between heterospecific pollen and seed set.

On the other hand, if competition predominates, higher plant functional similarity will lead to reduced visitation for each plant species (Albor et al., 2022). In this context, more abundant species are likely to 'hog' interactions, meaning they monopolize pollinators, thus increasing their visitation rate (Albor et al., 2019; Koptur & Barrios, 2020), and acting degree (Bergamo et al, 2021), while less abundant species will mostly receive pollinators shared with other plants, increasing its target degree (Bergamo et al, 2021). Species with greater

phenological overlap are likely to compete more with other species for pollinators, leading to a reduction in the visitation rate and an increase in their role in the network (target and acting degree). Species with a higher visitation rate and acting degree likely experience higher conspecific pollen deposition and less heterospecific pollen deposition, since they would receive most of the visits of their pollinators. Finally, we expect a direct negative effect of heterospecific pollen deposition on seed set due to the interference of heterospecific pollen on reproduction (Ashman & Arceo-Gómez, 2013).

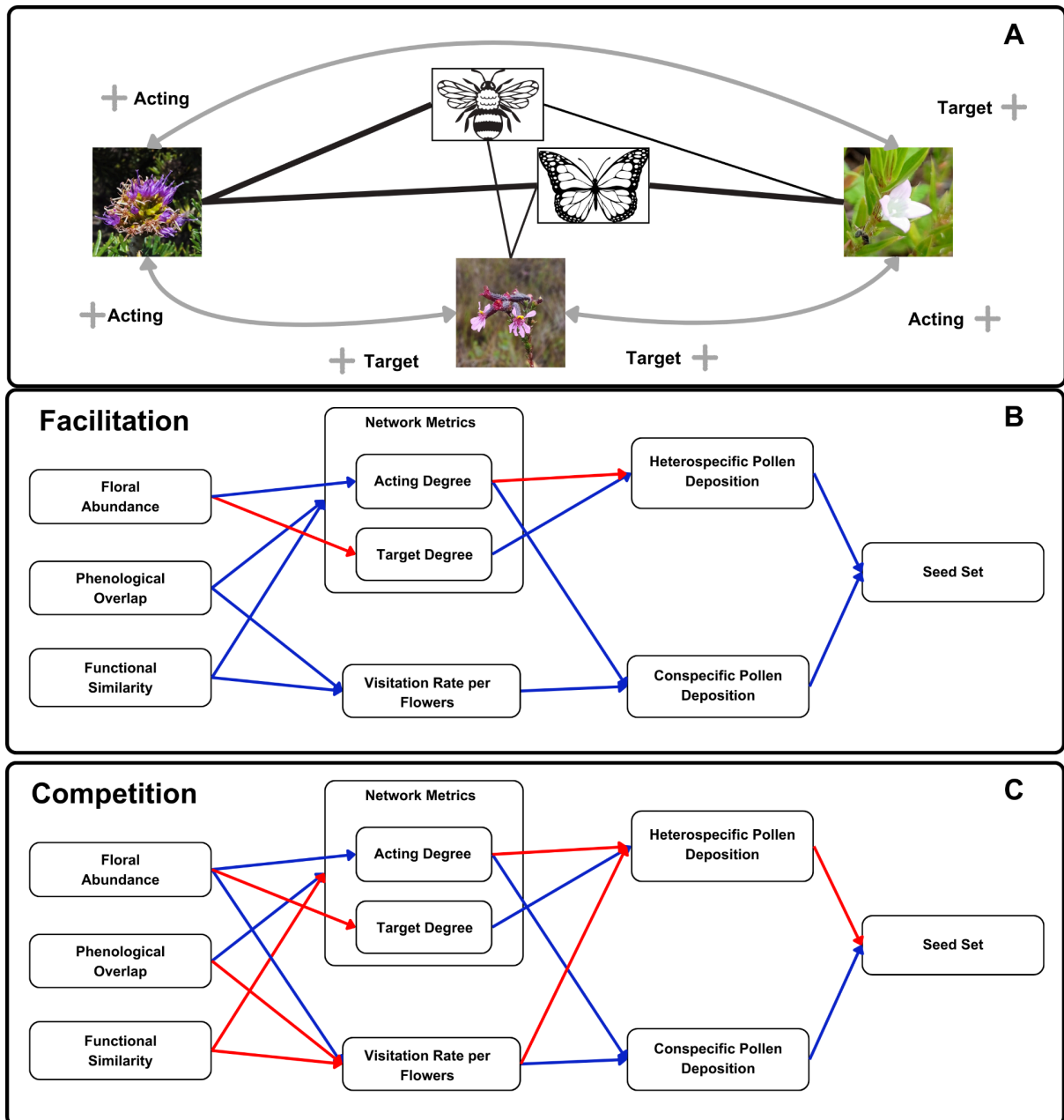


Figure 1. (A) Schematic representation of acting degree (+ Acting) and target degree (+ Target). Black lines and line thickness represent the frequency of interactions between plants and pollinators. Plant species with high acting degree (+ Acting) exhibit a higher frequency of interactions with a pollinator shared with other plant species, while plants with high target degree (+ Target) have a lower frequency of interactions with shared pollinators. (B and C) The analytical framework used in this study illustrates the division of variables into four parts and the flow of effects from left to right. The first part shows the community context (floral abundance, phenological overlap and functional similarity). The second part shows the acting and target degree and visitation rate that we used to understand the role of the plant species in the network. The third part displays conspecific pollen deposition and heterospecific pollen deposition, along with their effects on the fourth and final part, reproductive success (seed set). Blue and red arrows represent positive and negative relationships, respectively. (B) the scenarios in the facilitation context, (C) the scenarios in the competition context.

Material and method

Area of study and sampling design

Fieldwork was carried out in an area of campos rupestres within the campus of Universidade Federal dos Vales do Jequitinhonha e Mucuri, Brazil (18°11'48"S, 43°34'8"W), which has 240 ha of area and is contiguous to the protected area of Biribiri State Park, with 16998.66 ha. This region is situated at an altitude of 1300m above sea level. The climate is classified as a mesothermal, subtropical highland climate, characterized by humid temperate with dry and rainy seasons (Alvares et al, 2013). Campos rupestres (mountainous rocky grasslands), a vegetation within the Cerrado, occupies less than 1% of the Brazilian territory but encompasses more than 10% of the country's plant diversity (Silveira et al, 2016). Field sampling was conducted during the rainy season between October 2022 and April 2023 (INMET, 2020) as it is the period with the highest diversity of plant species in bloom (Monteiro et al., 2021; Luna et al., 2023).

We delimited 32 plots for the study, aiming to select areas with the greatest environmental heterogeneity (e.g., sandy soil, higher rock density, greater vegetation cover), each one with an area of 2.5m². In each plot, we identified plant individuals using numbered tags throughout the experiment. To identify plant species, we collected samples from outside the plots and cross-referenced them with the herbarium at the Universidade Federal dos Vales do Jequitinhonha e Mucuri and also consulted specialists when necessary. Examples of floral diversity are presented in Figure 2. During the study period we conducted sequential steps involving 15-days of active work in the plots followed by a one-week break, totalling nine work periods interspersed with eight breaks. During the 15-days work periods, we collected data on the number of flowers per individual, conducted observation of floral visitors, collected stigmas to quantify pollen deposition, and marked flowers to estimate seed set at the end of the study across all 32 plots. During the breaks, we collected data on the flower traits of the plant species, but for this we used individuals from outside of the plots to avoid disturbing plant-pollinator interactions in the plots.

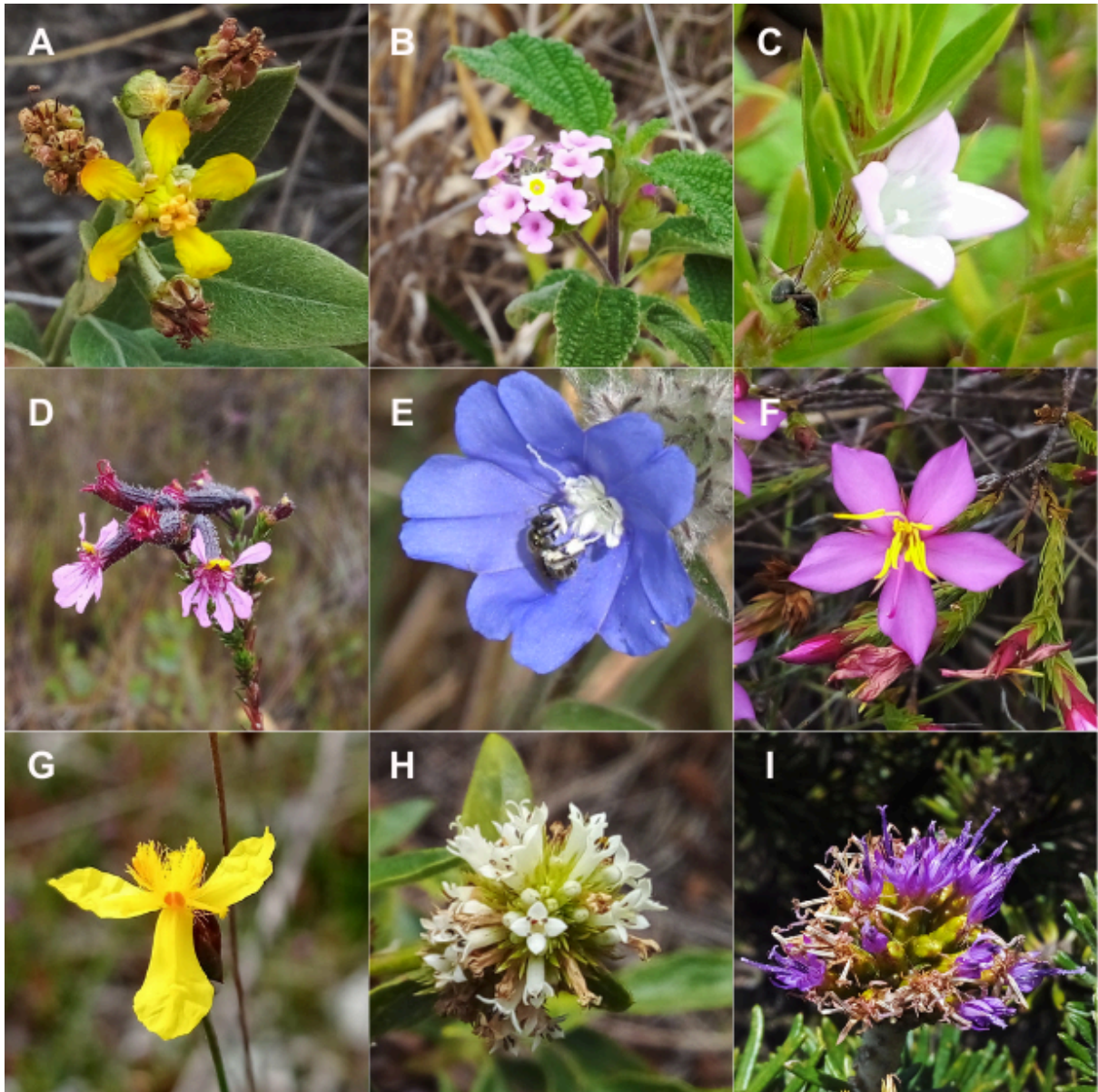


Figure 2. Examples of floral diversity found in the study. A) *Tetrapteryx microphylla* (Malpighiaceae); B) *Lantana hypoleuca* (Verbenaceae); C) *Richardia grandiflora* (Rubiaceae); D) *Cuphea disperma* (Lythraceae); E) *Evolvulus glomeratus* (Convolvulaceae); F) *Microlicia* sp. (Melastomataceae); G) *Xyris* sp. (Xyridaceae); H) *Borreria verticillata* (Rubiaceae); I) *Lychnophora pohlii* (Asteraceae).

Floral resources and visitors

To estimate the flower abundance to each species we used the total number of flowers per species counted during the floral visitor observations. For species with inflorescences, such as Asteraceae, we counted these as attractive units instead of the number of florets (Bergamo et al, 2020). We measured morphological flower traits known to impact interaction with pollinators, and thus pollinator sharing: corolla length, diameter of corolla opening, stigma and anther height for all species. Corolla length was considered as the distance from

the base of the corolla up to the apex of the corolla. Additionally, each species was categorized according to the floral resource offered: nectar, pollen and/or oil (for Malpighiaceae; Supplementary material S1: floral traits).

For the observation of floral visitors, we arrived at the plots and recorded the number of blooming plants before starting. We then filmed each blooming plant individually within the plot for 30 minutes using video cameras (SONY, HDR-CX405). These observations were conducted between 7 am and 3 pm throughout the study period, except on rainy days. By analyzing these recordings, we identified each visitor to the lowest taxonomic level possible, and counted the number of flowers visited. We determined whether the visitor made contact with the reproductive structures of the flowers, and when it did, we categorized these as potential pollinators. We recorded pollinators for 480 hours (mean = 15 hours and 30 minutes per species, according to flowering phenology; min = 30 minutes and max = 74 hours). We used the number of observations divided by the time of observation and the number of flowers observed to calculate a visitation rate per flower.

Characterization of floral neighborhood

To characterize how similar each of the plants are in the community regarding functional floral traits, we calculated the functional distinctiveness for each species with interaction with pollinators using the function *distinctiveness* of the package “funrar” (Grenié et al, 2017). To do so, we constructed a matrix of species x mean floral traits and resources, including corolla length, corolla opening diameter, stigma and anther height, all of which were log transformed, and floral resource type as categorical variables, and another matrix with species abundances to weight their contribution to functional distinctiveness in the ordinal space.

To estimate the flowering overlap between plant species we calculated pairwise phenological overlap between species by adapting the index described by Freitas and Bolmgren (2008). This index incorporates the flowering time and flower abundance to measure the synchrony between pairs of species. The total phenological overlap with neighbors for each plant species was estimated as the sum of the values obtained across all pairwise comparisons (Supplementary material S2: phenological matrix).

Pollen deposition and reproductive success

To quantify pollen deposition on flowers, we collected one stigma from each individual plant across all plots during the 15-day observation period. These stigmas were

collected from flowers nearing senescence and transported to the laboratory. The stigmas were then placed on a microscope slide with glycerinated gelatin with fuchsin for pollen staining. In each stigma, we counted the number of conspecific and heterospecific pollen types.

To estimate heterospecific pollen deposition per species we used the following equation (McLernon et al, 1996):

Heterospecific pollen deposition = $\Sigma(x)/\Sigma(n)$, where:

x = Heterospecific pollen deposited on stigmas to each plant species

n = Number of stigmas collected to each plant species

To achieve more standardized conspecific pollen deposition measures, since pollen production varies between species, we used the “min-max scaling” following equation:

Conspecific pollen deposition = $\text{mean}((x - \min(x))/(\max(x) - \min(x)))$, where:

x = Conspecific pollen deposited on stigmas to each plant species

$\min(x)$ = The minimum conspecific pollen found on the stigma to each plant species

$\max(x)$ = The maximum conspecific pollen found on the stigma to each plant species

For plant reproductive success, we marked open flowers in each individual plant across all plots during the 15-day observation period. These marked flowers were monitored until they developed into fruits. The fruits were then collected and placed in a fruit drying chamber. After drying, we counted the number of seeds per fruit. To compare seed production between species, we employed the same standardization used for conspecific pollen, considering the minimum and maximum seed production per species. Min-max standardization represents a relative reproductive success metric for the plants, useful in our case since we lack data on self-pollination or ovule number for the plant species. With this procedure, species with values closer to zero indicate that most individuals in that species had reproductive success closer to the individual with the fewest seeds, while higher values indicate that many individuals in that species had values closer to the maximum observed.

Network metrics

We first constructed a plant-pollinator interaction matrix with plant species in the columns and pollinators in the rows, with cells indicating the number of flowers visited by each pollinator. The interaction matrix was built pooling the sampling across all plots. Because it was not always possible to identify pollinators at the species level through recordings, we categorized the pollinators into morphotypes in most cases (Supplementary material S3). Since we were interested in pollinator sharing among plants more than in the importance of specific pollinator species, we assumed that our approach was able to represent

the extent to which plants shared similar pollinators. We calculated target degree and acting degree for each plant species (Bergamo et al, 2022), as well as the closeness centrality that measures how one plant species is connected with others throughout pollinators. To calculate the values of target degree and acting degree we used the “Müller’s index” (Müller et al. 1999), that represent the indirect relation for ecological networks:

$$d_{ij} = \sum_n \left[\frac{\alpha_{ik}}{\sum_l \alpha_{il}} \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \right]$$

Where,

d_{ij} = the effect of j plant species in the i plant species.

α_{ik} = the frequency of interactions between plant species i and pollinator k .

α_{jk} = the frequency of interactions between plant species j and pollinator k .

$\sum_l \alpha_{il}$ = the total of interaction of plant i .

$\sum_m \alpha_{mk}$ = the total of interaction of pollinator k .

Using Müller’s index, we obtained a plant-plant matrix, where rows represent the effect of other plants on the focal plant species and columns represent the effect a plant species had on all other plant species in the network. The target degree is calculated as the sum of the rows in the plant-plant matrix, excluding the focal species itself. It represents the effect of all other plant species on the focal plant species. The values range from 0 to 1, where 0 indicates no effect from the community, and 1 represents the maximum effect of the plant community on the focal plant species. The acting degree is calculated as the sum of the columns in the plant-plant matrix for each species, excluding itself. It represents the effect one plant species has on others. These values range from 0 (indicating no effect on other plants) to $n - 1$ (where n is the total number of plant species, minus the focal species itself), representing the maximum effect one plant species can have on others. However, the acting degree and closeness centrality were correlated (Estimate = 56.24, $p < 0.01$), therefore we chose to focus on acting degree for the analyses. All network indices were calculated with the bipartite R-package (Dormann et al. 2011).

Statistical analysis

To assess the effects of floral abundance, functional distinctiveness, phenological overlap, target and acting degrees, visitation rate, heterospecific and conspecific pollen deposition on reproductive success (seed set), we employed a piecewise structural equation model (SEM) with the function *psem* of *piecewiseSEM* R package (Lefcheck, 2016,

following Lázaro et al, 2020). We used SEM because it allows the simultaneous evaluation of direct and indirect relationships among variables, enabling an integrated understanding of the system. This method combines predictors across different levels to evaluate their cumulative effects and test the global coherence of the hypothesized model. Additionally, SEM applies the concept of directed separation, which tests whether excluded paths (hypotheses) between variables remain significant, ensuring that the model structure captures essential relationships. The significance of predictor variables in SEM was assessed by examining the p-values of the models. For clarity, the SEM analysis was divided into four parts (Figure 1). The first part of SEM included the effects of floral abundance, functional distinctiveness and phenological overlap on species level network metrics acting degree and target degree, as well as visitation rate per flower. For the second part, these variables were also included as predictors of heterospecific and conspecific pollen deposition. The third included all above mentioned variables plus heterospecific and conspecific pollen as predictors of reproductive success (seed set). We used the *simulateResiduals* function from the 'DHARMA' package (Hartig, 2022) to stabilize the residuals' variance for better model fit. Log transformations were applied as part of model adjustment, not to achieve normality in the predictors. Therefore, we used log-transformed values for floral abundance and heterospecific pollen deposition. For this analysis, we removed 12 species without complete data (i.e. missing information on visitation rate, pollen deposition and/or seed set, sample size = 19; see supplementary material S4). We also checked whether variables included as predictors were correlated, and proceeded with SEM after checking that they were not. For all models we used linear models with *lm* function and gaussian distribution.

All analyses were conducted using the R software (R Core Team, 2023). The data set used for the analyses is in Supplementary material S4.

Results

We recorded 404 interactions between 31 plant species and 35 pollinator morphospecies, with less than one visit per hour on average. The most frequent visitor was the honeybee *Apis mellifera* with 143 interactions, followed by stingless bee *Trigona* sp. with 42 interactions (Figure 3; Supplementary material S3). All plant species receive heterospecific pollen deposition, the per species mean varied between 0.3 to 45 pollen grains and the species abundance during the study varied between five to more than 100 individuals (Table 1).

Table 1. Average and standard deviation of heterospecific pollen deposition (HPD), conspecific pollen deposition (CPD) and seed set found by species during the study on the Campos Rupestres in Diamantina - Minas Gerais. N represents the number of samples (N1 - pollen deposition and N2 - seed set).

Code	N1	HPD		CPD		Seed set		
		Average	SD	Average	SD	N2	Average	SD
Ast_05	17	4.65	5.13	83.47	114.42	17	0.89	0.10
Ast_09	23	6.26	13.14	33.65	39.56	24	0.84	0.15
Ast_11	5	3.40	3.97	135.80	151.07	3	0.67	0.18
Cup_01	18	2.11	3.18	20.78	38.76	13	0.69	0.85
Cup_02	140	2.19	4.33	33.13	54.67	151	1.47	1.14
Flo_04	23	6.39	15.06	13.22	9.42	25	1.68	0.56
Flo_18	42	5.52	9.44	36.36	33.01	39	0.38	0.26
Flo_23	12	12.58	21.84	146.58	132.13	8	8.75	9.63
Flo_26	11	11.91	21.01	17.64	23.61	7	4.43	3.64
Gay_01	41	12.85	31.69	27.07	53.12	45	5.60	4.52
Lan_00	7	5.29	7.93	92.14	67.28	7	0.58	0.21
Mal_01	20	5.20	6.89	82.70	77.05	17	1.29	1.40
Mel_02	66	1.21	3.05	18.89	36.62	72	64.86	31.50
Mel_04	9	7.56	20.08	39.78	58.21	19	49.68	27.99
Mel_10	40	1.58	2.96	76.33	119.05	27	20.07	12.79
Mel_13	13	0.31	0.63	6.08	8.53	11	66.73	81.16
Pal_01	8	45.00	62.57	120.63	165.68	9	0.35	0.13
Pip_00	99	7.97	29.02	65.16	89.52	98	0.83	0.19
Vel_05	6	3.17	2.71	128.83	29.97	7	181.29	162.01

The SEM analysis showed good fit with the data (global goodness-of-fit: $C_{32} = 34.88$; $p = 0.33$; Figure 3). Visitation rate per flower decreased with floral abundance (Table 2; Figure 4A) and acting degree decreased with functional distinctiveness (Table 2; Figure 4B). Target degree did not show relationship with any of the variables (Table 2). Heterospecific pollen increased with acting degree (Table 2; Figure 5A) and had one indirect interaction: it decreased with functional distinctiveness (standardized estimate = -0.28; Table 2; Figure 5B). Conspecific pollen deposition increased with visitation rate (Table 2; Figure 5C) and with target degree (Table 2; Figure 5D). Conspecific pollen deposition also had one indirect interaction: it decreased with floral abundance (standardized estimate = -0.40; Figure 5E). Seed set did not show direct relation with conspecific and heterospecific pollen deposition (Table 2). However, seed set decreased with functional distinctiveness (estimate = -0.58; Table 2; Figure 6).

Table 2. Results of the SEM. log(HPD) represents heterospecific pollen deposition log-transformed. Both R-square and DF (degrees of freedom) represent parameters of the models. Bold and “*” mean significant values. Test: “Direct” refers to results from the models in the SEM while “Indirect” and “TD ” refers to results derived from recombination during SEM analysis, not directly tested in the models. Indirect represents the subsequent relationship between variables, for example: visitation rates are affected by phenological overlap and, in turn, affect conspecific pollen deposition. TD refers to Tests of Directed Separation.

Dependent	Independent	Test	R ²	DF	std estimate	Crit.Value	p-value
Visitation rate			0.55	15			
	Functional distinctiveness	direct			-0.10	-0.54	0.59
	log(Floral abundance)	direct			-0.59	-3.08	<0.01*
	Phenological overlap	direct			-0.32	-1.57	0.13
Acting degree			0.32	15			
	Functional distinctiveness	direct			-0.55	-2.26	0.03*
	log(Floral abundance)	direct			-0.08	-0.36	0.71
	Phenological overlap	direct			0.07	0.30	0.76
Target degree			0.08	15			
	Functional distinctiveness	direct			0.25	0.90	0.38
	log(Floral abundance)	direct			-0.07	-0.27	0.78
	Phenological overlap	direct			0.00	0.01	0.98
log(HPD)			0.29	15			
	Visitation rate	direct			0.33	1.52	0.14
	Acting degree	direct			0.51	2.23	0.04*
	Target degree	direct			0.17	0.78	0.44
	Functional distinctiveness	indirect			-0.28		
Conspecific pollen			0.56	15			
	Visitation rate	direct			0.68	3.87	<0.01*
	Acting degree	direct			0.11	0.62	0.54

Dependent	Independent	Test	R ²	DF	std estimate	Crit. Value	p-value
Seed set	Target degree	direct	0.16	16	0.39	2.21	0.04*
	log(Floral Abundance)	indirect			-0.40		
	Conspecific pollen deposition	direct			-0.06	-0.29	0.75
	log(HPD)	direct			0.39	1.71	0.09
	Functional distinctiveness	TD		15	-0.58	-2.25	0.03*

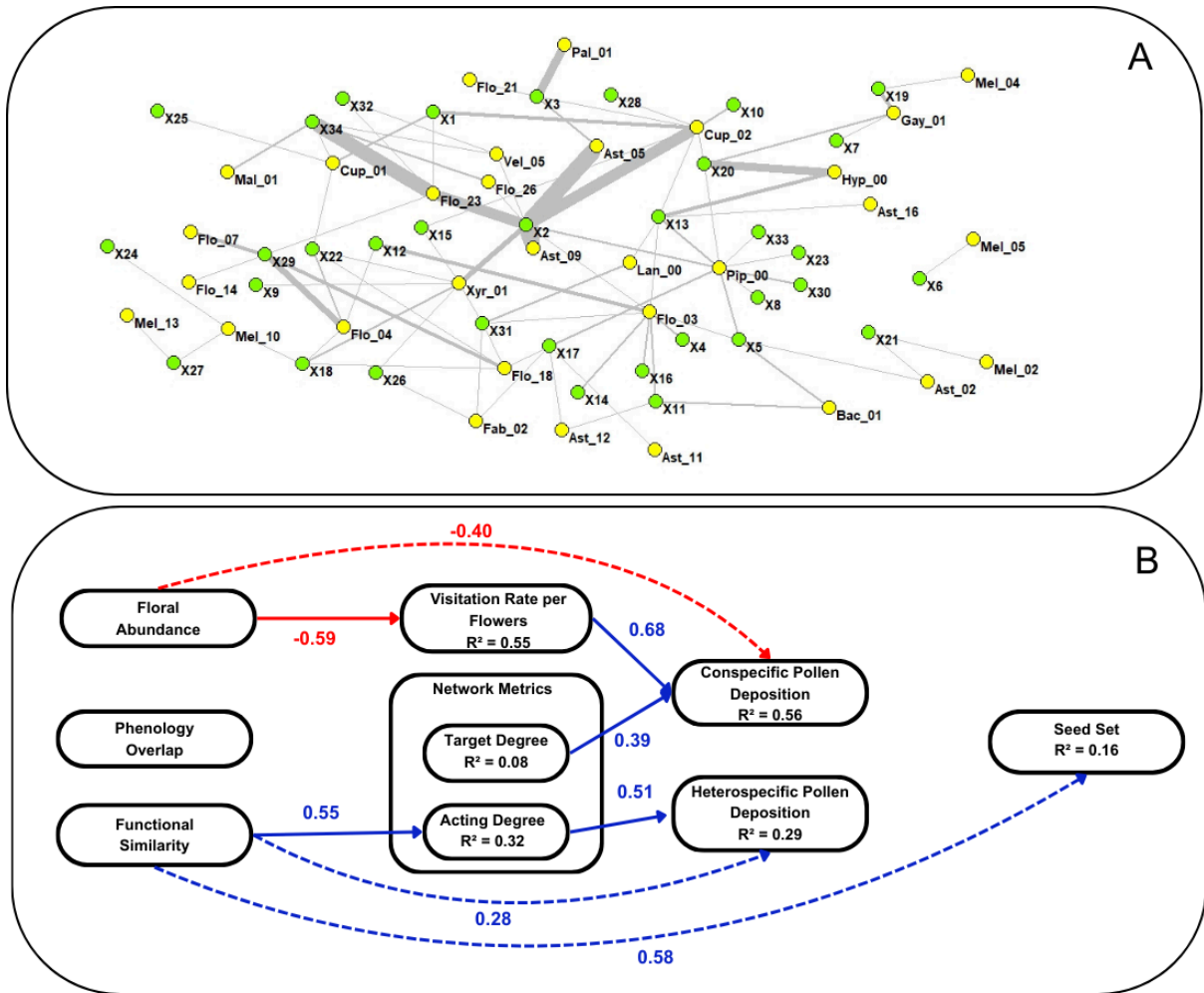


Figure 3. A) Network of plant-pollinator interactions. Pollinators are depicted in green circles and plants in yellow circles. Line thickness represents the interaction frequency. Species codes refer to species names in Table S1. B) Results of the SEM analysis. Solid lines represent direct effects ($p < 0.05$). Dashed lines represent “indirect” and “TD” effects, which refer to results derived from recombination during the SEM analysis (Table 2). Blue arrows represent a positive relationship. Red arrow represents a negative relationship.

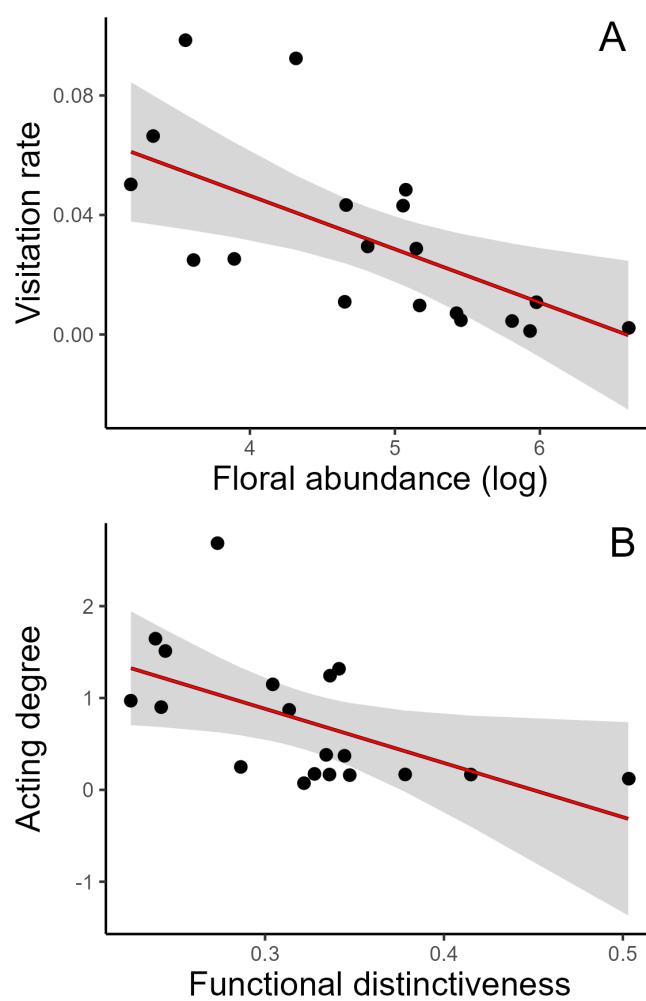


Figure 4. A) Negative relationships between visitation rate and floral abundance and B) negative relationships between acting degree and functional distinctiveness. Plants with a higher acting degree are those that receive more frequent visits from shared pollinators.

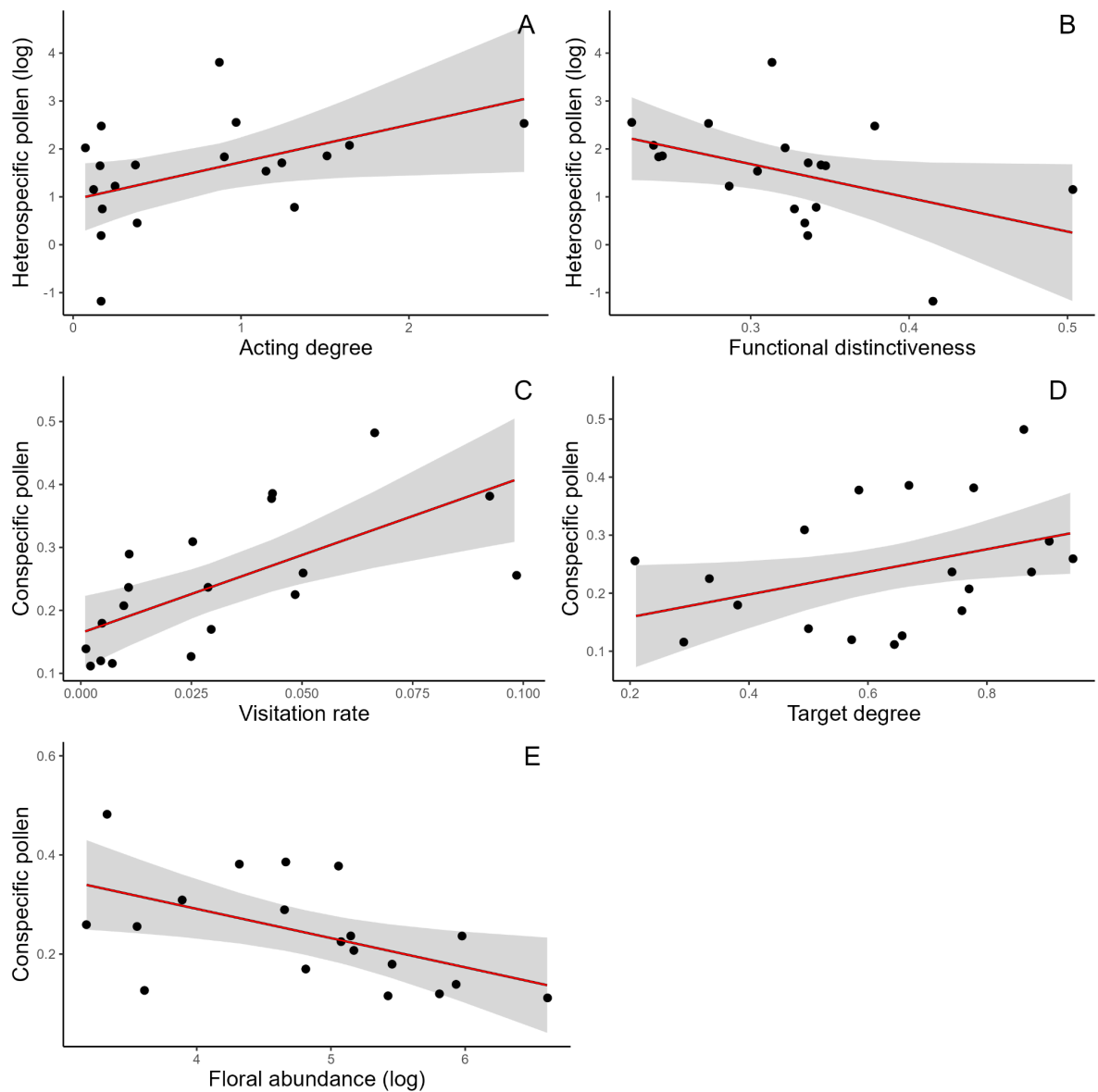


Figure 5. Relationship between heterospecific and conspecific pollen deposition and their predictors. A) Positive relationship between heterospecific pollen deposition and acting degree B) and indirect relationship between heterospecific pollen deposition and functional distinctiveness (standardized estimate -0.28). Relationship between conspecific pollen deposition and C) visitation rate and D) target degree. E) indirect relationship of conspecific pollen and floral abundance (standardized estimate -0.40).

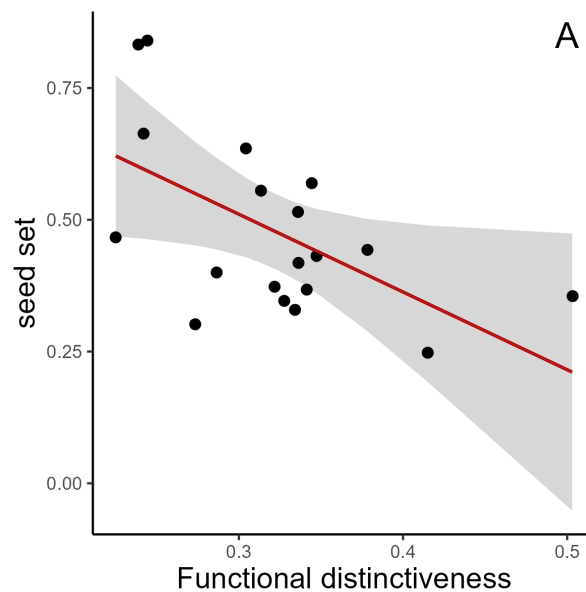


Figure 6. Indirect relationship between the seed set and functional distinctiveness (standardized estimate: -0.57) from tests of directed separation of SEM analysis.

Discussion

Here, we uncovered multiple direct and indirect relationships between species abundance, floral traits and phenology of neighbor plants, i.e, community context, on plant pollination and reproductive success. The positive effects of floral trait similarity on seed set support that pollination sharing has overall positive effects on plant reproductive success in the *Campos Rupestre*. This is because plant species exhibiting greater trait similarity tend to attract similar pollinators (Carvalho et al, 2014; Venjakob et al, 2016; Arroyo-Correa et al, 2024). Such positive impacts on seed set suggest facilitation as the main process driving pollination in the studied plant community (Ashman et al, 2020; Streher et al, 2020; Lopes et al, 2022; Arroyo-Correa et al, 2024).

The strong positive influence of visitation rate on conspecific pollen deposition was expected but, contrary to our hypotheses, abundant plants were associated with decreasing conspecific pollen and visitation rate per flower (Figure 1). These negative relationships could be related to intraspecific competition (Wei et al. 2021, Ye et al. 2023), where plant species with high numbers of flowers experience less visits per flower and less conspecific pollen as plant individuals compete for pollinator attraction (Pauw 2013; Monasterolo et al, 2022). However, the less abundant species, which received more conspecific pollen, did not produce more seeds (Figure 1). The lack of effect of conspecific pollen could be related to geitonogamy, where species that attract floral visitors end up depositing their own pollen or

that of close relatives (Mitchell et al., 2004; Karron et al., 2009). A negative relationship between seed production and geitonogamy makes sense, as *Campo Rupestre* plants generally are self-incompatible but have low dispersal ability, leading to isolated populations that are genetically similar to each other (Silveira et al., 2016; Monteiro et al., 2021). On the other hand, many plants we found during this study have few ovules, such as Asteraceae plants, *Lantana* (Verbenaceae), and *Palicourea* (Rubiaceae). Therefore, they would require only a few pollen grains to produce seeds, meaning there would not be a direct correlation between conspecific pollen deposition and seed production. This possibility is further supported by the fact that plants in the *Campo Rupestre* experience low pollen limitation levels (Lopes et al., 2023), reinforcing that a lack of pollen would not be the factor severely affecting their reproductive success.

We found that species with similar floral traits tended to share more pollinators with other plant species, occupying a more central role in the network and increasing heterospecific pollen deposition. This result supports our initial hypothesis based on the facilitation ecological process, which predicted that trait similarity would promote greater pollinator sharing among species, ultimately enhancing the transfer of heterospecific pollen (Figure 1; Arceo-Gómez et al. 2020, Bergamo et al. 2020; Lázaro et al. 2020). However, we found an opposite pattern than expected, as we hypothesized that species with a higher acting degree would receive less heterospecific pollen and more conspecific pollen while species with a higher target degree (relying on pollinators that also visit many plants) would receive more of both heterospecific and conspecific pollen (Bergamo et al., 2022). This surprising result could be related to the correlation between acting degree and closeness centrality (Supplementary material S5), as central species in the network, sharing more pollinators with all plant species, are expected to receive more heterospecific pollen.

Facilitation is an important strategy for plant survival in environments with low pollination, due to the low abundance of either pollinators or plant species (Ghazoul, 2006; Tur et al, 2016; Bergamo et al, 2020; Hederström et al, 2023; Arroyo-Correa et al, 2024). The campos rupestres are one of these habitats; besides the high plant endemism, the heterogeneity of soil features restricts the species to small, non connected areas (Silveira et al, 2016). Additionally, generalization in pollination systems is common in campos rupestres, where interactions between plant and pollinators appear to be characterized by some opportunism (co-occurrence and co-flowering) and floral abundance than to strict morphological specialization (Carstensen et al, 2014, Lopes et al., 2022; Monteiro et al, 2021, Amorim et al. 2022). Therefore, generalized plant species are expected to strongly share

pollinators in this ecosystem. In this context, facilitation through trait similarity may be an important mechanism ensuring reproductive success of co-flowering plant species.

In summary, our study revealed that plant species with high abundance had lower per flower visitation rates, which associated with reduced conspecific pollen deposition, suggest intraspecific competition. While, plant species with higher floral morphology similarity in relation to the neighborhood produced more seeds, indicating that facilitation predominated over competition at the seed set stage. Specifically under low pollination probability scenarios, these positive interactions between plant species show the potential to increase plant coexistence in the habitat. Therefore, plant diversity in the neighborhood and indirect interactions between plant species positively affected the reproduction of plants. To conclude, floral similarity and floral abundance shape the positive and negative indirect effects between plants in the whole pollination process.

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Author contributions

Marsal D. De Amorim, Elisa Thébault, Pedro J. Bergamo and Pietro K. M. Maruyama conceived the ideas; Marsal D. De Amorim, Pedro J. Bergamo, André R. Rech and Pietro K. M. Maruyama, designed methodology; Marsal D. De Amorim, Luís G. S. Perugini and Sabrina A. Lopes collected the data; All authors contributed critically to the writing of the manuscript.

Data Availability Statement

Data will be available from figshare.

Declaration of Competing Interest

The authors declare no conflict of interest

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EFEITO DA VIZINHANÇA PRÓXIMA

Contrasting effects of neighbouring plant diversity on pollinator-mediated indirect interactions

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Abstract

The attraction of pollinators to a plant depends on intrinsic factors, such as floral morphology and abundance, and extrinsic factors, such as the richness and morphology of neighboring plants, which can enhance or reduce reproductive success through facilitation or competition. We used the Brazilian Campos Rupestres from Brazil, an ecosystem with high species endemism, to investigate how spatial and temporal variations in plant communities affect reproductive performance at two scales: plot-level (2.5m²), covering all neighboring plant species, and species-level, focusing on two abundant species: *Piptolepis imbricata* (Asteraceae) and *Cuphea disperma* (Lythraceae). We collected data on floral abundance, species richness, floral visitors, deposition of conspecific and heterospecific pollen, and seed set per plot. Each plant species was characterized by corolla morphology (length and diameter), stigma, and anther height, which was used to calculate floral similarity in relation to neighbors. We tested the effect of the neighboring community on visitation, visitor richness, pollen deposition, and seed set. At the plot-level, conspecific pollen increased with floral similarity indicating a facilitation between plant species with similar morphology. However, no effect was found for seed set. At the species-level, plant abundance increased the probability of attracting visitors in both species, which can be explained by higher attractivity of resource-rich species. At the same time, while *C. disperma* showed a positive effect of neighbourhood floral similarity on reproductive success indicating facilitation, none of the evaluated variables affected *P. imbricata* reproduction. These species-level differences may explain why we found no effect on seed set as reproductive success measure at plot-level analyses. Therefore, we highlight the complex effect of pollinator-mediated indirect interactions between plants, which can be better understood by evaluating neighborhood processes.

Introduction

A plant's ability to attract pollinators is related to intrinsic factors such as floral morphology, resource availability (quantity and quality), and flower abundance, as well as to the community context, i.e. how these intrinsic characteristics interact with other plants in the community (Sritongchuay et al. 2020; Shibata & Kudo 2020, Peuker et al. 2020). The combination of plants' intrinsic factors and community context not only determines the presence of pollinators but also how these are shared among neighboring plants (Carvalho

et al. 2014; Bergamo et al. 2020). Pollinator sharing can lead to plant-plant indirect interactions that either enhance plant reproductive success through facilitation (Bergamo et al. 2020; Lopes et al. 2021) or reduce it via competition (Ha et al. 2020; Johnson et al. 2022). Thus, plant reproduction is context-dependent, influenced by the interplay between floral traits, richness and the abundance of co-flowering plant species in the community (Bergamo et al. 2018; Sritongchuay et al. 2020). Such dynamics of pollinator-mediated competition and facilitation can be crucial for community maintenance (Pauw 2013, Benadi 2018, Guimaraes et al. 2017, Duchenne et al. 2021; Arroyo-Correa et al. 2024).

In general, greater plant diversity is associated with higher pollinator attraction to the community (Ghazoul 2006; Lázaro et al. 2009; Fornoff et al. 2017). However, an increased attractiveness does not necessarily result in more pollinator visits and consequent higher reproductive success for individual plant species within the community (Fornoff et al. 2017; Arroyo-Correa et al. 2024). In more diverse communities, attracting more pollinators increases pollinator sharing among plants, which may lead to heterospecific pollen deposition and reduced reproductive success in a competition scenario (Arceo-Gómez & Ashman 2014; Ha et al. 2020). In contrast, in a facilitative context, it is expected that increased pollinator attraction will result in greater reproductive success for plant species (Bergamo et al. 2020; Lopes et al. 2022). This increase is usually associated with a lower negative effect of heterospecific pollen deposition on plant reproductive success (Streher et al. 2020; Lopes et al. 2022). Such negative (competition) or positive (facilitation) effects on pollen deposition and seed set are expected to be higher if plants share similar floral traits and share more pollinators (Arceo-Gómez & Ashman 2014; Carneiro et al. 2014; Lopes et al. 2022). Moreover, competition and facilitation often occur simultaneously within the community and are dependent on the community context as well as the ecological scale, whether at the species or community level (Lázaro et al. 2015; Ye et al. 2023).

Community context, represented by the diversity of neighboring species, can have a strong influence on pollination attraction (Albor et al. 2019; Arroyo-Correa et al. 2023), pollen deposition (Ashman & Wei 2023; Streher et al. 2024, pre-print) and seed set (Amorim et al. 2024). These effects are dependent on the spatial proximity of neighbors, as pollinator sharing between plants decreases with increasing spatial distance (Albor et al. 2019; Arroyo-Correa et al. 2024). Hence, the positive or negative effects of neighborhood plant diversity are particularly strong at shorter distances, and higher abundance of conspecific individuals can increase floral visits and seed set (Jiao et al. 2021). On the other hand, high conspecific abundance may have negative effects on pollination due to increased intraspecific

competition, such as higher selfing (Mitchell et al. 2004; Brys et al. 2008; Jiao et al. 2021). Such relationships are also constrained by floral morphology, such that larger flowers in low abundance can show higher pollen limitation (Lázaro et al. 2015, Fang & Huang 2013; Peucker et al. 2020), or that specialist species with more restrictive morphology may experience reduced heterospecific pollen deposition (Streher et al. 2024). Therefore, the reproductive success of plant species may strongly depend on conspecific and heterospecific floral abundance, floral diversity, and morphological traits of neighboring plants.

These factors then lead to interspecific differences in reproductive success within the community, where more abundant species attract more pollinators (Lázaro et al. 2020). However, less abundant species can benefit from attraction of shared pollinators by abundant neighboring plants, with increasing pollen deposition and seed set (Bergamo et al. 2020). Such sharing of pollinators can be especially important in ecosystems with low abundance of pollinators (Bergamo et al. 2020; Lopes et al. 2021), and at the same time characterized by high diversity of plants with low local abundance, including OCBILs - old, climatically buffered, infertile landscapes (Hopper 2009; Silveira et al. 2016). In these environments, plant-pollinator interactions are often opportunistic (Monteiro et al. 2021), and long-distance pollinators, such as large bees and hummingbirds, play a crucial role in maintaining gene flow between isolated populations (Hopper et al. 2021; Monteiro et al. 2021). Despite recent advances in understanding plant-plant indirect interactions via shared pollinators, there are still gaps in understanding the impact of neighborhood plant diversity on both the plant community and individual species, especially at close spatial proximity between plants and in tropical communities. Therefore, we investigated how spatial and temporal variations in plant species communities affect the reproductive performance of plants in Brazil's Campos Rupestres, a tropical OCBIL ecosystem with high species endemism (Silveira et al. 2016, Monteiro et al. 2021). For this, we analyzed our data at two scales: at the whole plot-level encompassing all neighbouring plant species and at the species-level, by selecting two focal species with distinct floral characteristics.

At the neighborhood (plot) level, our objective was to understand how the characteristics of nearby plant species affect the pollinator attractiveness and the reproductive success of the local community itself. We expect an increase in visitation and visitor species richness with increasing floral abundance and diversity (Amorim et al. [year]; Albor et al. 2019; Ye et al. 2023). For conspecific and heterospecific pollen deposition, we anticipate distinct responses to the surrounding community. Specifically, heterospecific pollen deposition is expected to increase with floral morphology similarity, while conspecific pollen

deposition should increase with plot-level floral abundance (Amorim et al. [year]). Previous studies conducted in the same area, at larger spatial scales *i.e.*, considering the whole sampled area as one community, have shown facilitative interactions between plant species (Lopes et al. 2021; Amorim et al. [year]), leading us to predict a positive effect of floral similarity on reproductive performance, with higher seed set observed when neighboring species exhibit similar morphology.

At the species-level, our objective was to understand how the features of nearby plant species affect the pollinator attractiveness and reproductive success of specific plant species within the community. We expected a positive effect of conspecific floral abundance on visitation. We also anticipate a positive effect of floral diversity and heterospecific floral abundance on heterospecific pollen deposition, while conspecific pollen deposition would be affected in a similar way by conspecific floral abundance. Finally, we predicted an increase in seed set when there is greater morphological similarity between neighboring plants, owing to higher diversity of shared pollinators and visits.

Material and methods

Study Area

The study was conducted in an area of Campos Rupestres covering 240 hectares, adjacent to Biribiri State Park, on the campus of Universidade Federal dos Vales do Jequitinhonha e Mucuri, Brazil (18°11'48"S, 43°34'8"W). Located at an elevation of 1,300 meters above sea level, the Campos Rupestres—mountainous rocky grasslands within the Cerrado biome—constitutes less than 1% of Brazil's territory but is home to over 10% of the country's plant diversity (Silveira et al., 2016). Field sampling occurred during the rainy season, from October 2022 to April 2023 (INMET, 2020).

Field Sampling

The dataset used here was previously reported by Amorim et al. ([Same data that Manuscript thesis]). Briefly, we delimited 32 plots of 2.5 m² each (Complete data can be found at: (Figshare)), where all plant individuals were marked and identified to the species-level. During the field sampling, the number of flowers, floral visitors, pollen deposition, and seed set were recorded for individuals each day for 15-days, then we took a free week before the next round of 15-days sampling. Each 15 days of sampling is henceforth referred to as “sampling period”. During the free week, data on floral morphology were

collected, including corolla length, diameter of corolla opening, stigma and anther height and resource type as a categorical value including nectar, pollen and oil (Table S1). In total, data were collected over nine sampling periods. Data on floral visitors, pollen deposition and seed were pooled across all species at the plot-level for the neighborhood-level analyses.

Additionally, we analyzed the data separately for two focal species, which were chosen based on their morphological differences and representativeness across different plots and time periods: *Piptolepis imbricata* (Gardner) Sch.Bip. (Asteraceae) and *Cuphea disperma* Koehne (Lythraceae) (Figure 1).



Figure 1. Focal species for the species-level analysis of this study, focusing on the effect of the neighborhood on the Campos Rupestres of Diamantina, Brazil: a) *Piptolepis imbricata* (Asteraceae) and b) *Cuphea disperma* (Lythraceae).

Piptolepis imbricata is an endangered bush belonging to the Asteraceae family, endemic to the Campos Rupestres of Brazil (Loeuille 2024). The flowers are tubular with purple corolla, offering nectar and pollen as resources. Its floral morphology is common for Asteraceae species, with exposed stigmas and short tube length suggesting a generalist pollination strategy (Ohashi et al. 2021). During our sampling, this species was visited by ants, bees, butterflies, and flies. Also, there are previous reports of hummingbird visitation in the study area (Queiroz 2018). *Cuphea disperma* is a subshrub in the Lythraceae family, also endemic to the Campos Rupestres (Cavalcanti et al. 2024). The flowers are tubular, with pink to purple corolla, and a more restricted morphology (Cavalcanti et al. 2024). The main floral resource is nectar. During our observations, this species was visited by bees and flies. Also,

there are previous reports of hummingbird visitation existing in the study area (Queiroz 2018).

Floral richness and abundance

We used the number of different species observed in each plot per sampling period as a measure of floral richness. To estimate floral abundance at plot-level, we used the sum of flowers per plant species in each plot per sampling period. For species with compact inflorescences, such as capitula in the Asteraceae family, we counted inflorescences as attractive units instead of counting individual florets (*sensu* Bergamo et al. 2020). To calculate floral abundance for species-level analysis, we used conspecific floral abundance, which was defined as the sum of flowers per species per plot and sampling period. Heterospecific floral abundance was calculated as the sum of flowers in the plot per sampling period, excluding conspecific flowers.

Floral traits

We measured the following morphological flower traits: corolla length, diameter of the corolla opening, and the heights of the stigma and anthers, using a digital caliper. Corolla length was defined as the distance from the base of the flower to the apex of the corolla. The corolla diameter was measured as the distance between the two sides of the corolla at its widest point. The heights of the anther and stigma were measured from the base of the structure to its tip. Additionally, each species was categorized according to the floral resources it offers: nectar, pollen, and/or oil (for Malpighiaceae; see Supplementary Material S2: Floral Traits).

Functional diversity

To estimate plot functional diversity, we used floral morphology traits such as stigma height, anther height, corolla length, and corolla diameter, along with resource type as floral traits. We calculated functional dispersion per plot per sampling period (including only the species flowering at that 15-day interval) using the *dbFD* function from the R package "FD" (Laliberté et al., 2014). Functional dispersion estimates were weighted by species floral abundance at that plot and sampling period. Higher functional dispersion values indicate greater species differences, while lower values signify increased similarity among species. The *dbFD* function also returns the community-weighted mean (CWM) for each trait. We used corolla diameter to represent the size of the flowers inside the plot.

At the species level, to characterize how similar *Cuphea disperma* and *Piptolepis imbricata* are to other plants in the neighborhood, we used the floral traits and abundance of each plant species in the plots to estimate their functional distinctiveness from other species in the plot, using the “distinctiveness” function from the “funrar” package (Grenié et al., 2017).

Floral visitors

Floral visitors were recorded for 30 minutes for each plant individual within the plot using video cameras (SONY, HDR-CX405). We observed between 7 am and 5 pm, except when it was raining. By analyzing these recordings, we identified each visitor to the lowest possible taxonomic level and determined whether the visitor made contact with the reproductive structures of the flowers. When they did, we categorized them as potential pollinators. We recorded floral visitors for a total of 480 hours, averaging 15 hours and 30 minutes per species. The minimum recording time was 30 minutes, while the maximum reached 74 hours, with total time per species varying according to flowering phenology. At plot-level we use the number of visits by time by number of flowers to estimate the visitation rate. However, for the analyses at species-level, several plots received no visits during the sampling period (33% of plots). Therefore, we used visits as a binary variable, as the presence (1) or absence (0) of visitors. We also calculated the number of visitor species per plot per sampling period (visitor richness).

Pollen deposition and reproductive success

During the sampling period, we collected one stigma from flowers nearing senescence and marked flowers from each plant individual in the plot. In the laboratory, we used glycerin gelatin with fuchsin dye for pollen staining and a microscope to count the number of conspecific and heterospecific pollen grains deposited on the stigma. To identify whether the pollen was conspecific or heterospecific, we made slides with pollen from the anthers of bud flowers to each species as a reference. To estimate the reproductive success of each plant individual, we collected fruits from the marked flowers and counted the number of seeds per fruit.

To estimate heterospecific pollen deposition per plot per sampling period, we used the number of heterospecific pollen grains deposited divided by the number of stigmas collected per plot in each observation. To achieve more standardized conspecific pollen deposition measurements, since pollen production varies between species, we scaled the data following the equation:

Conspecific pollen deposition = $(x - \min(x)) / (\max(x) - \min(x))$, where:

x = Conspecific pollen deposited on stigmas by species per plot per sampling period

Then we used the mean of conspecific pollen deposited on stigmas across species per plot per sampling period for our analyses. To compare seed sets between species at plot and species-level, we also employed this same standardization, considering the minimum and maximum seed set per plot and sampling period.

Statistical analysis

Plot-level

At plot-level, since we are interested in comparing plots and sampling periods, we removed plots with only one plant species, with missing data or samples where the min-max transformation for conspecific pollen deposition and seed set resulted in values of 1 or 0. This resulted in a total sample size of 111 plot-sampling period combinations (Table S2). We tested the effect of the nearby community on the visitation rate, visitor richness, heterospecific pollen, conspecific pollen and seed set. For each of these response variables, we created models considering all predictor variables (floral richness, floral abundance, functional dispersion, and CWM of diameter length) and included plot as a random effect. The model for visitation rate, conspecific pollen deposition and seed set, we used a beta distribution (zero-inflated for visitation). Heterospecific pollen was rounded and the models for visitor richness and heterospecific pollen followed a negative binomial distribution.

Species-level

At the species-level, we also removed plots as detailed before, resulting in a total sample size of 47 combinations of plots and sampling period, divided into 21 for *P. imbricata* and 26 for *C. disperma* (Table S2). *Piptolepis imbricata* occurred in seven plots and over nine sampling periods, while *C. disperma* occurred in ten plots and six sampling periods. We used as response variables the visitation likelihood, heterospecific and conspecific pollen and seed set (Table S3). Because only four samples had visitor richness higher than one, we did not use visitor richness as a response. We included as predictors: conspecific floral abundance, heterospecific floral abundance and functional distinctiveness, with species identity also included with an interaction term with each predictor. Neighboring plant richness increased the collinearity between the predictors variables, so it was removed as a predictor from the models. The visitation likelihood model used a binomial distribution to represent the presence (1) or absence (0) of pollinators. Heterospecific pollen was multiplied by ten and rounded to

use a negative binomial distribution, while we used a beta distribution for conspecific pollen and a Gaussian distribution for seed set. In all models, we included the plot identity as a random variable, but later removed it in models of visitation likelihood as response variables due to its very low variability (< 0.001). To estimate the differences between species, we used the function “`emtrends`” from the “`emmeans`” package (Lenth, 2024).

To check model assumptions, we used the “`check_collinearity`” and “`check_singularity`” function from the “`performance`” package (Lüdtke et al., 2021) and the “`simulateResiduals`” function from the “`DHARMA`” (Hartig, 2022). The models were fitted using the “`glmmTMB`” function from the “`glmmTMB`” package (Brooks et al. 2017). All analyses were conducted using the software R (R Core Team, 2024).

a) Results

At the plot level, visitation rate and pollinator richness did not show relation with any predictor (Table 1). Heterospecific pollen deposition increased with functional dispersion while conspecific pollen decreased (Table 1, Figure 2a and 2b, respectively). However, the seed set did not show relation with any predictor variables (Table 1).

Table 1. Results of the neighborhood level models testing the effect of the nearby community on visitation likelihood, visitor richness, heterospecific pollen, conspecific pollen and seed set on the Campos Rupestres of Diamantina, Brazil. RE represents random effect variance and between parentheses standardization deviance.

Response variable	Predictor Variable	Estimate	X^2	p-value
Visitation rate	Intercept	-3.70		
RE: No	Floral abundance	-0.00	0.13	0.71
	Floral richness	-0.06	0.32	0.56
	Functional dispersion	2.44	1.67	0.19
	CWM of corolla diameter	-0.22	1.09	0.29
Visitor richness	Intercept	-0.73		
RE: No	Floral abundance	0.00	0.52	0.46
	Floral richness	0.09	0.55	0.45
	Functional dispersion	0.28	0.02	0.87
	CWM of corolla diameter	0.04	0.04	0.84
Heterospecific pollen	Intercept	3.98		
RE: 0.18 (0.43)	Floral abundance	-0.00	0.72	0.39
	Floral richness	-0.06	0.17	0.67
	Functional dispersion	4.90	5.05	0.01*
	CWM of corolla diameter	-0.33	1.81	0.17
Conspecific pollen	Intercept	-0.59		
RE: 0.07(0.26)	Floral abundance	-0.01	2.99	0.08
	Floral richness	0.08	0.78	0.37
	Functional dispersion	-3.95	6.30	0.01*
	CWM of corolla diameter	-0.24	2.16	0.14
Seed set	Intercept	0.61		
RE: 0.14(0.37)	Floral abundance	-0.00	0.00	0.94
	Floral richness	-0.11	1.40	0.23
	Functional dispersion	0.00	0.00	0.99
	CWM of corolla diameter	-0.18	1.24	0.26

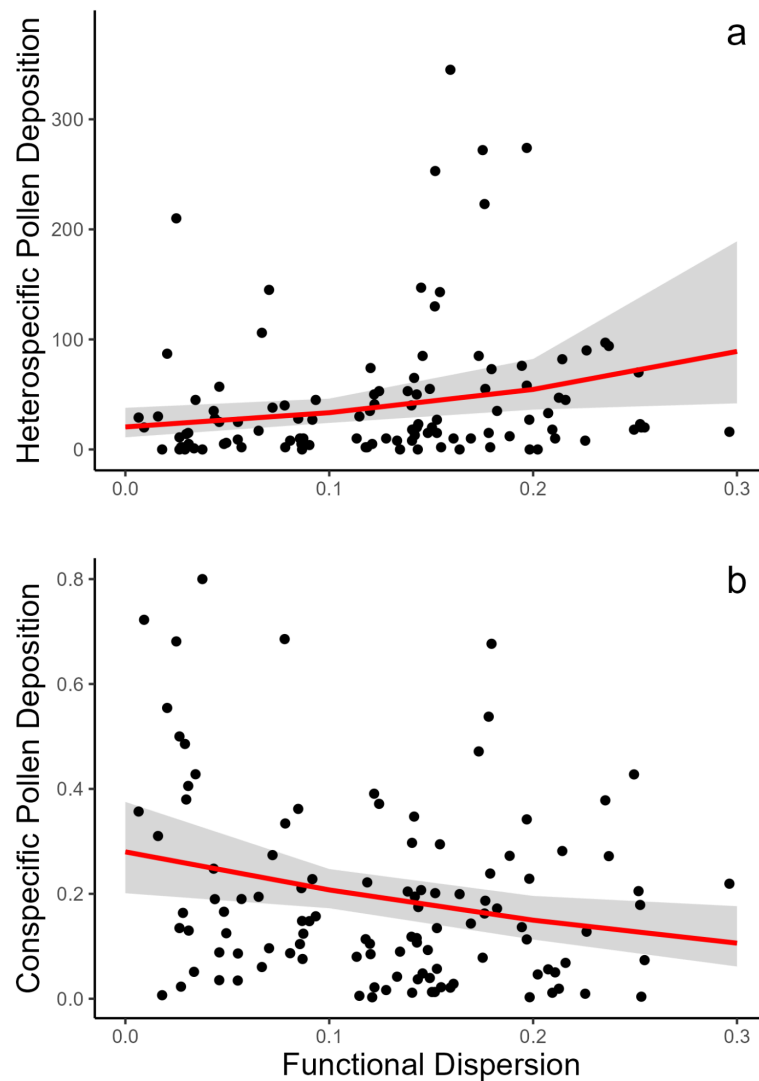


Figure 2. Results of the neighborhood level models testing the effect of the nearby community on pollinator heterospecific and conspecific pollen deposition on the Campos Rupestres of Diamantina, Brazil. Relationship at neighborhood level between a) heterospecific pollen deposition and b) conspecific pollen deposition with functional dispersion.

At the species level, the results highlight differences in visitation likelihood, pollen deposition, and seed set responses to neighborhood context for each plant species (Table 2). *Piptolepis imbricata* and *Cuphea disperma* had higher visitation likelihood with greater conspecific floral abundance (Table 2, Table 3, Figure 3a and 3b, respectively). Heterospecific pollen deposition decreased with conspecific floral abundance for *C. disperma* (Table 2, Table 3, Figure 4). However, for *Piptolepis imbricata*, heterospecific pollen was not influenced by any variable. For both species, conspecific pollen deposition was not affected by any of the predictors (Table 2). The seed set of *Cuphea disperma* decreased with functional distinctiveness (Table 2, Table 3, Figure 5), while the seed set to *P. imbricata* was not influenced by any variable.

Since the interaction between neighborhood variables and species had no effect on conspecific pollen deposition, we tested a model without species as a factor to assess whether the neighborhood alone influenced this variable. However, in this model, the neighborhood also had no significant effect (Conspecific floral abundance: $p = 0.81$; Functional distinctiveness: $p = 0.75$; Heterospecific floral abundance: $p = 0.45$).

Table 2. Results of the species-level models testing the effect of the nearby community on visitation likelihood, heterospecific pollen, conspecific pollen and seed set on the Campos Rupestres of Diamantina, Brazil. RE is random effect variance and between parenthesis standardization deviance.

Response variable	Predictor Variable	χ^2	p-value
Visitation likelihood RE: No	Conspecific floral abundance:Species	10.07	p < 0.01*
	Heterospecific floral abundance: Species	1.94	0.37
	Functional distinctiveness: Species	0.09	0.95
Heterospecific pollen RE: 0.01(0.13)	Conspecific floral abundance:Species	7.03	p = 0.02*
	Heterospecific floral abundance: Species	5.73	0.05
	Functional distinctiveness: Species	1.52	0.46
Conspecific pollen RE: 0.005(0.07)	Conspecific floral abundance:Species	3.14	0.20
	Heterospecific floral abundance: Species	0.25	0.88
	Functional distinctiveness: Species	0.50	0.77
Seed set RE: 0.01(0.11)	Conspecific floral abundance:Species	3.79	0.14
	Heterospecific floral abundance: Species	2.83	0.24
	Functional distinctiveness: Species	49.17	p < 0.01*

Table 3. Results of the species-level analysis for each plant species (Table 2). The effect of each variable on *Piptolepis imbricata* (Asteraceae) and *Cuphea disperma* (Lythraceae) in the models testing the effect of the nearby community on visitation likelihood, heterospecific and conspecific pollen, and seed set in the Campos Rupestres of Diamantina, Brazil. Bold represents significant results. Asterisk (*) represents significant results on table 2. “.trend” indicates the slope trend. SE represents the Standard Error. t.ratio indicates the t-test value for the slope.

Response	Predictor	.trend	SE	t.ratio	p-value
Visitation likelihood					
<i>Piptolepis imbricata</i>	Conspecific floral abundance	0.44	0.19	2.22	0.02*
	Heterospecific floral abundance	-0.01	0.83	-0.15	0.87
	Functional distinctiveness	1.84	5.87	0.31	0.75
<i>Cuphea disperma</i>	Conspecific floral abundance	0.05	0.02	2.40	0.01*
	Heterospecific floral abundance	0.00	0.00	1.35	0.17
	Functional distinctiveness	1.32	5.88	0.22	0.82
Heterospecific pollen					
<i>Piptolepis imbricata</i>	Conspecific floral abundance	-0.07	0.05	-1.33	0.18
	Heterospecific floral abundance	-0.08	0.04	-1.95	0.05
	Functional distinctiveness	1.25	2.24	0.55	0.57
<i>Cuphea disperma</i>	Conspecific floral abundance	-0.02	0.00	-2.41	0.01*
	Heterospecific floral abundance	0.00	0.00	-1.75	0.08
	Functional distinctiveness	-0.72	2.61	-0.27	0.78
Conspecific pollen					
<i>Piptolepis imbricata</i>	Conspecific floral abundance	0.00	0.00	-0.44	0.66
	Heterospecific floral abundance	0.00	0.00	-0.20	0.83
	Functional distinctiveness	-0.04	0.27	-0.15	0.87
<i>Cuphea disperma</i>	Conspecific floral abundance	0.00	0.00	1.71	0.09
	Heterospecific floral abundance	0.00	0.00	0.44	0.65
	Functional distinctiveness	0.07	0.23	0.30	0.76
Seed set					
<i>Piptolepis imbricata</i>	Conspecific floral abundance	0.00	0.00	-0.01	0.98
	Heterospecific floral abundance	0.00	0.00	1.44	0.15
	Functional distinctiveness	0.56	0.30	1.85	0.07
<i>Cuphea disperma</i>	Conspecific floral abundance	0.00	0.00	1.94	0.05
	Heterospecific floral abundance	0.00	0.00	0.96	0.34
	Functional distinctiveness	-0.70	0.30	-2.31	0.02*

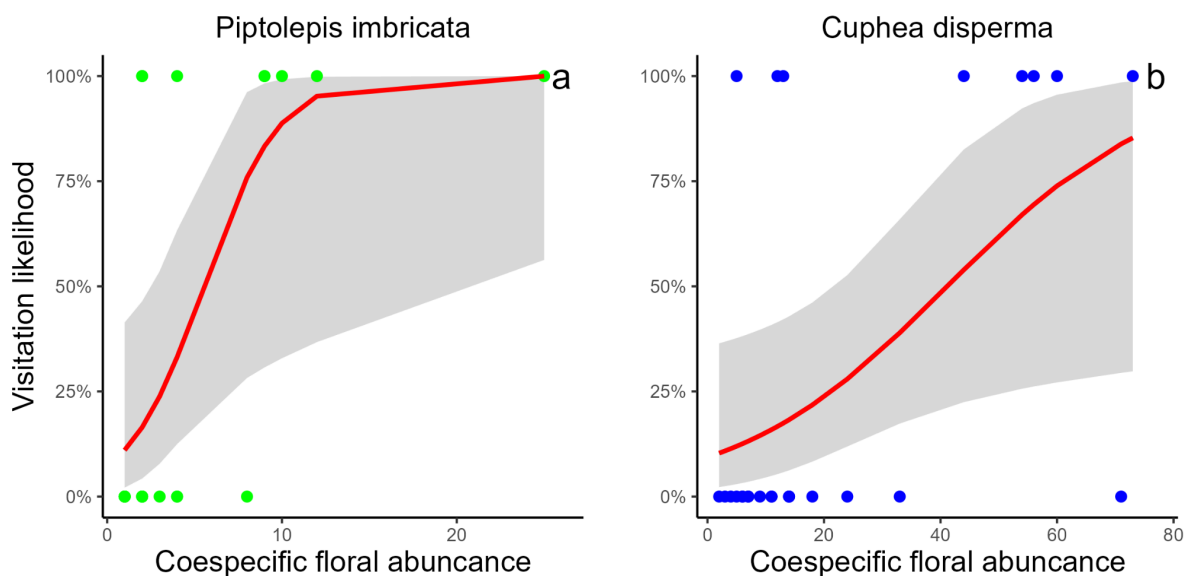


Figure 3. Results of the species-level to models testing the effect of the nearby community on visitation likelihood on the Campos Rupestres of Diamantina, Brazil. Relation between visitation likelihood of a) *Piptolepis imbricata* and b) *Cuphea disperma* with conspecific floral abundance. Color represents the plant species. Red line represents significant p-value to each species.

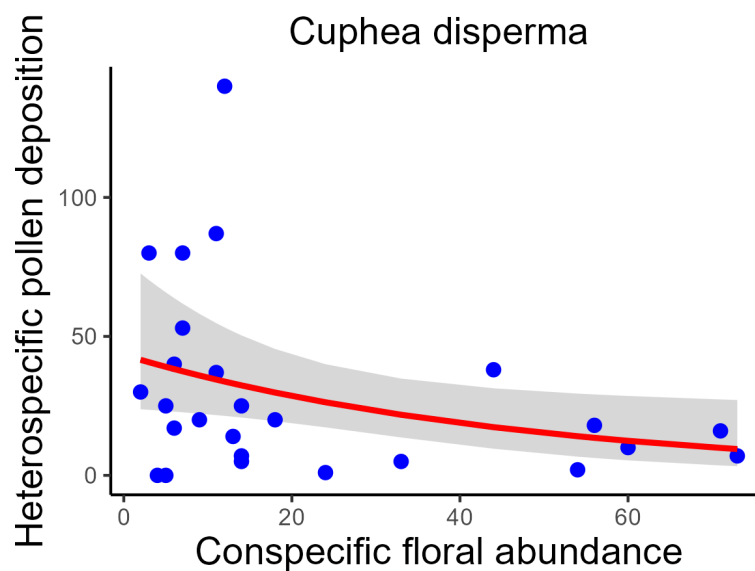


Figure 4. Results of the species-level to models testing the effect of the nearby community on heterospecific pollen deposition to *Cuphea disperma* on the Campos Rupestres of Diamantina, Brazil. Relation between heterospecific pollen deposition with conspecific floral abundance. Red line represents significant p-value to each species and the gray area represents confidence interval 0.95.

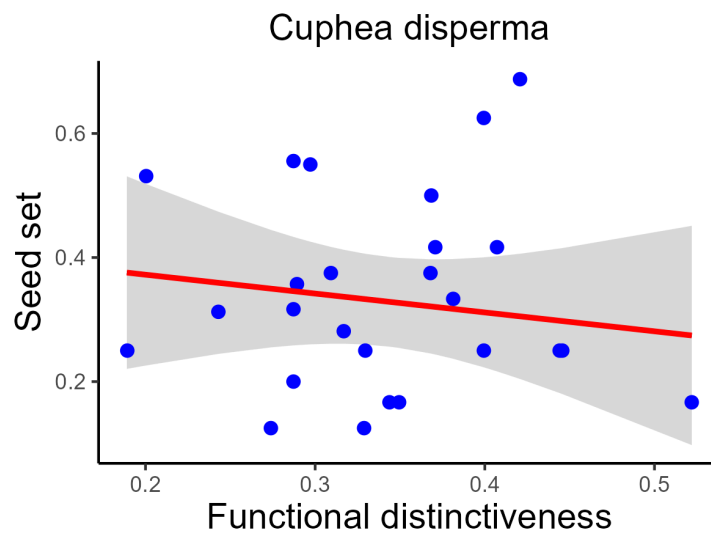


Figure 5. Results of the species-level to models testing the effect of the nearby community on seed set on the Campos Rupestres of Diamantina, Brazil. Relation between seed set of *Cuphea disperma* with functional distinctiveness. Red line represents significant p-value to each species and the gray area represents confidence interval 0.95.

Discussion

In this study, we showed that the neighborhood community influenced aspects of pollination and reproductive success, demonstrating that pollination depends on intrinsic plant traits and extrinsic factors. At the plot-level, heterospecific and conspecific pollen deposition were affected by floral morphology of the plant neighborhood, highlighting the importance of considering the neighborhood context. Besides, we did not detect an effect for the seed set, which represents the overall plant reproductive performance (at least the female function). In contrast, at the species-level, for both *Piptolepsis imbricata* and *Cuphea disperma* visitation likelihood was positively related to the conspecific floral abundance, reinforcing the importance of the flower abundance for interactions. The different effect of the neighbourhood functional dispersion on the reproductive success of *Piptolepsis imbricata* and *Cuphea disperma*, emphasizes context-dependent patterns that are only detected when we zoom in our analyses on focal species, underscoring the importance of considering different ecological scales to understand the effects of plant diversity on their reproduction within a community.

At the neighborhood level, we expected that similar morphology would increase heterospecific pollen deposition (Arceo-Gómez et al., 2019). Heterospecific pollen deposition is known to have a low reproductive cost for plants in campos rupestres (e.g., Lopes et al.,

2022). This suggests that the increased deposition of heterospecific pollen with greater dispersion of floral morphological traits across species may not be due to an effort to avoid heterospecific pollen but rather an adaptive strategy to increase attractiveness to a broader range of pollinators. This would be expected in cases in which there is an advantage of generalization and sharing pollinators (“adaptive generalization”, Waser et al., 1996; Chmel et al., 2021; Ohashi et al., 2021). Higher plant diversity with varying morphologies typically enhances pollinator diversity in the neighborhood (Lázaro et al., 2009; Junker et al., 2015). On the other hand, conspecific pollen deposition was higher when the neighborhood had greater floral similarity, indicating facilitation among plants with similar morphologies (e.g., Arceo-Gómez et al., 2020; Bergamo et al., 2020). The increase in the average conspecific pollen deposition in plots with more similar flowers occurs because visitation rates may be more similar between these similar neighboring plants. Another possible explanation for the increase in heterospecific pollen deposition with higher neighborhood dissimilarity—while conspecific pollen deposition shows the opposite pattern—could be the presence of a highly attractive plant in a less attractive but functionally diverse neighborhood. In such cases, heterospecific pollen deposition would be high in less attractive plants, potentially leading to competition (Ashman et al., 2020; Tur et al., 2016). A more detailed study of these interactions at the local neighborhood scale is needed to tear apart these processes.

At the species level, both species showed increased visitation likelihood with conspecific floral abundance, as we predicted. In general, conspecific floral abundance is an important factor in attracting pollinators (Peuker et al., 2020; Ye et al., 2023), potentially leading to greater reproductive success (Lázaro et al., 2020; Resasco et al., 2021). Despite the positive effect of conspecific floral abundance in attracting visitors to *P. imbricata*, the reproductive success was not influenced by the neighborhood community. This lack of effect on seed production may be because each flower has only one ovule, requiring little pollen and few visits to produce seeds.

Cuphea disperma received less heterospecific pollen in abundant conspecific neighborhoods. This was expected, as if fewer closeby heterospecific plant species would be sharing pollinators with this focal plant (Ashman and Wei, 2023; Streher et al., 2024). At the same time, when *C. disperma* had a more similar morphology to its neighboring plants, reproductive success increased, suggesting facilitation by other species (Bergamo et al., 2020; Amorim et al. [year]). Considering our two scales of analyses, the lack of neighborhood effects at the neighborhood level on seed set—despite increased pollinator attraction to more diverse neighborhoods (Carvalho et al., 2014; Bergamo et al., 2020; Lopes et al., 2021; Bi

et al., 2024)—may result from a balance of positive, neutral, and negative effects at the species-level, as we found contrasting results for the two focal species. Therefore, understanding these complex interactions requires considering indirect plant-plant interactions across different spatial scales.

We show that facilitation among plants is directly related to how species interact with the floral similarity of nearby plants. Further studies are needed, considering more plant species, to understand how spatial and temporal variation at small scales affects indirect interactions between plant species and how these relationships are influenced by community context, particularly floral morphology. In summary, we highlight that the effects of close plant neighborhoods on pollination and reproductive success vary with the scale of analysis. At the species-level, these effects are stronger, while at the neighborhood level, positive, neutral, and negative effects tend to dilute the effects on plant reproductive success. Therefore, we reinforce the importance of considering multiple scales to fully understand the indirect interactions between plant species mediated by pollinators.

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EFEITO DA VIZINHANÇA NA REPRODUÇÃO DA LANTANA HYPOLEUCA

Neighborhood flower diversity increases the reproductive success of *Lantana hypoleuca* Briq (Verbenaceae)

Running head: **Neighborhood flowers increase reproductive success**

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Summary sentence

Neighborhood plant richness positively increases reproductive success.

Abstract

The attraction of floral visitors depends on intrinsic plant traits and the surrounding floral abundance and diversity. Therefore, it is important to consider the conspecific and heterospecific co-flowering context to understand plant-pollinator interactions, and consequently, plant reproductive success. We investigated the influence of the floral neighborhood on the pollination of *Lantana hypoleuca* (Verbenaceae) in the Brazilian *Campos Rupestres*. We have evaluated how flower richness, conspecific and heterospecific abundance, and similarity in corolla length influence the reproductive success (conspecific pollen deposition, heterospecific pollen deposition, and likelihood of fruit production) of *L. hypoleuca* plant individuals. For this, we evaluated the surrounding neighborhood of 20 *L. hypoleuca* individuals. We recorded 73 visits of bees, butterflies, and wasps. Conspecific pollen did not show a relationship with any of the studied variables, while heterospecific pollen increased with plant richness. Finally, the likelihood of fruit production increased with plant species richness and decreased with conspecific floral abundance. The positive effect of plant species richness on plant reproduction suggests facilitative interactions, in which higher community diversity may attract a more diverse set of pollinators to *L. hypoleuca*. Our results stress the importance of assessing multiple community features and plant reproductive steps to better understand the complex co-flowering effects on pollination and reproduction.

Introduction

About ~90% of the Angiosperms depend on animal pollination (Ollerton *et al.* 2011; Tong *et al.* 2023), and many floral traits, such as color and shape, are essential in attracting pollinators (Dudash *et al.* 2011). In addition to flower traits, the attraction of floral visitors also depends on individual floral display and the abundance and diversity of other plants in the neighborhood (Sritongchuay *et al.* 2020; Shibata & Kudo 2020). This is because plants often share generalist pollinators with other plant species (Waser *et al.*, 1996; Resasco *et al.*, 2021). For instance, plant communities composed by species with high floral trait similarity are often interpreted as the result of pollination facilitation (Sargent & Ackerly 2008). Therefore, it is important to consider the conspecific and heterospecific co-flowering context to understand pollination patterns even for a single plant species (Bergamo *et al.* 2018; Sritongchuay *et al.* 2020).

Heterospecific neighbors can influence multiple aspects of plant reproduction, including the abundance and diversity of pollinators visiting an individual plant (Lázaro *et al.* 2009), pollen deposition (Bergamo *et al.* 2020) and seed production (Nottebrock *et al.* 2017). Co-flowering plant neighbors may attract a greater pollinator diversity than monospecific plant neighborhoods (Lázaro *et al.* 2009), especially if plant species exhibit distinct floral traits (Ghazoul 2006; Fornoff *et al.* 2017). This increased trait similarity between plant species may attract a variety of pollinators without necessarily resulting in more visits to each plant (Fornoff *et al.* 2017). Plants with similar traits, such as corolla length and opening, flower size, and floral reflectance, may also engage in facilitative interactions because trait similarity facilitates pollinator sharing (Bergamo *et al.* 2020; Lopes *et al.* 2021). In this context, a community rich in species with similar morphologies may attract more visits (Carvalho *et al.* 2014; Bergamo *et al.* 2020), but receive more heterospecific pollen (Arceo-Gómez & Ashman 2014). Nevertheless, much remains unclear regarding how conspecific and heterospecific flowers in the neighborhood mediate distinct consequences of plant-pollinator interactions, such as pollen deposition and fecundity in plants.

Facilitative interactions lead to enhanced pollinator visitation between plant species sharing pollinators, ultimately increasing plant reproductive success (Ghazoul 2006; Tur *et al.* 2016; Bergamo *et al.* 2024). On the other hand, competition occurs when sharing pollinators causes heterospecific pollen deposition (Arceo-Gómez & Ashman 2014) and per-plant reduction of floral visitation rates, leading to reduced reproductive success (Mitchell *et al.* 2009; Ha *et al.* 2020; Johnson *et al.* 2022). In the competition context, reduced levels of

pollination niche overlap are important to avoid the negative consequences of pollinator sharing (Wei *et al.* 2021). Nevertheless, heterospecific pollen deposition does not always relate to strong negative effects (Streher *et al.*, 2020; Lopes *et al.* 2021). Facilitation and competition often occur simultaneously in plant communities, and the interaction sign depends on the plant species, community context (i.e. plant neighborhood), and scale (Lázaro *et al.* 2015; Bergamo *et al.* 2020; Ye *et al.* 2023). Given this complexity, evaluating multiple aspects of the plant neighborhood, such as abundance, richness, and flower morphology, is important to untangle facilitative vs. competitive interactions for pollination.

We investigated the reproductive biology of *Lantana hypoleuca* Briq. in the Brazilian *Campos Rupestres*. We explored the effects of similarity in corolla length, plant richness, and heterospecific and conspecific neighbor abundance on pollen deposition and fruit set. In facilitative interactions, we hypothesize that individuals of *L. hypoleuca* in plots with more similar corolla length compared to other plant species will share more pollinators, resulting in more heterospecific and conspecific pollen deposition, and this could result in higher reproductive success. Moreover, we expected a positive effect of richness and floral abundance of heterospecific plants on conspecific and heterospecific pollen deposition, and reproductive success. Therefore, we expected a low negative effect of heterospecific pollen deposition (Streher *et al.*, 2020; Lopes *et al.*, 2021). On the other hand, if the plants in the neighborhood are competing for pollinators, we expect that the floral similarity between the plants will lead to greater deposition of heterospecific pollen and a greater reduction in reproductive success. In contrast, in plots where *Lantana* is dominant, it will receive more conspecific pollen and less heterospecific pollen, leading to higher reproductive success.

Material and methods

Study area

This study was carried out in an area of 240 ha of *Campos Rupestres* at the *campus* Juscelino Kubitschek of the Universidade Federal dos Vales do Jequitinhonha e Mucuri, Diamantina, Minas Gerais, Brazil (18°11'48.23"S, 43°34'8.74"W). *Campos Rupestres* is a kind of mountainous grassland vegetation, and it exhibits remarkable plant diversity and endemism. Despite covering less than 1% of Brazil's territory, it accounts for over 10% of its plant diversity (Silveira *et al.* 2016). The study site is situated at an elevation of approximately 1,300m a.s.l.. It is characterized by rocky outcrops and shallow soils, located

in the central region of the Serra do Espinhaço Mountain range. The climate is mesothermal temperate (Cwb type). Sampling was conducted between October and December 2021, coinciding with the onset of the rainy season in the region, where more plant species are blooming.

Study species

Lantana hypoleuca is a shrub, typically between 0.5 to 2 m high, it bears lilac flowers with a yellow nectar guide and vinaceous ripe fruits (Figure 1; Silva *et al.* 2020). The species is native to Brazil and occurs in the Caatinga, Cerrado, and Atlantic Forest biomes (Silva *et al.* 2020). Additionally, *L. hypoleuca* is visited by generalist pollinators such as bees, butterflies, and hummingbirds and is also capable of self-pollination (Queiroz 2018; Lopes *et al.* 2021; Amorim *et al.* 2022).



Figure 1. From a to d are *Lantana hypoleuca* (Verbenaceae): a) inflorescence, b) detail of a flower showing the yellow guide at its center. From c to f represent the floral diversity found during the study on the *Campos Rupestres* in Diamantina, MG, Brazil. c) *Tetrapteryx microphylla* (Malpighiaceae); d) *Cuphea diosmifolia* (Lythraceae); e) *Ludwigia myrtifolia* (Onagraceae); f) *Lavoisiera sampaioana* (Melastomataceae).

Sampling design

We marked 20 individuals of *L. hypoleuca* and delimited a circular plot of 1.5m radius around each individual. These individuals were selected based on the criteria of being in bloom, located at a minimum distance of 10 meters between each other, and considering the heterogeneity of rupestrian grassland landscapes, such as rocky outcrops and open field areas. In hyperdiverse plant communities such as *Campos rupestres*, plant species form small populations restricted to small areas (Silveira et al., 2016). Therefore, we sampled in an area with a higher abundance of individuals relatively close to each other to establish the plots. In each plot, we recorded the floral visitors of *L. hypoleuca* through focal observations for one hour per individual (except P01, P02, P10 and P16 individuals that stopped flowering before all observations; see Supplementary Material S1). The observations were divided into 20-minute observation sessions on three different days for a total of 19 hours of observation. During the observations, we counted the number of flower visitors in the focal plant (Supplementary Material S1). Before starting the observations, we counted plant species richness within the plots and the number of flowers for each focal *L. hypoleuca* (floral display). During the observations, we also recorded the number of flowers of all *L. hypoleuca* individuals within the plot (conspecific floral abundance) and the sum of the number of flowers of all other species within the plot (heterospecific floral abundance). We considered the conspecific and heterospecific floral abundance as the average of the sum of flowers across all the days of field observation (Supplementary Material S2). Similarly, we considered plant species richness as the average number of species flowering across all the days of field observation.

Similar morphology

To evaluate the similarity in floral morphology at the community scale, we measured the corolla length of one flower from the minimum of five individuals of each plant species found within the plot, including *L. hypoleuca*. To measure corolla length, we used any individual of the species we found outside the plot. Corolla length was measured as the distance from the base to the tip of the corolla. Out of the 29 plant species in the plots, we measured the corolla length of 24 species (Table 1). We chose corolla length to represent flower size, which is an important factor for attracting floral visitors. However in a tube flower such as *L. hypoleuca*, corolla length also should be related to restrictiveness (distance

to nectaries). We used these morphological data to calculate the distance between the corolla length of heterospecific flowers and *L. hypoleuca*. Specifically, we subtracted the corolla length of each flower species in the plot from that of *L. hypoleuca*. The similarity in morphology was defined as the mean distance from *L. hypoleuca* to each other species within the plot.

Table 1. Plant species found during the study. Code represents the species in the supplementary material S3. Corolla length was measured in mm and size is the number of mensured flowers.

	Code	Corolla length		Size
		sd	average	
<i>Lantana hypoleuca</i>	Lan_hy	0.27	1.19	20
Asteraceae sp01	Ast_01	0.07	0.30	6
<i>Lepidaploa</i> sp	Ast_03	0.66	4.85	10
Asteraceae sp02	Ast_04	NA	NA	0
<i>Jacaranda oxyphylla</i>	Big_01	0.75	4.46	10
<i>Chamaecrista choriophylla</i>	Cha_01	0.21	1.88	4
<i>Chamaecrista</i> sp01	Cha_02	0.17	1.35	10
<i>Cuphea diosmifolia</i>	Cup_01	0.11	0.38	10
<i>Cuphea disperma</i>	Cup_02	0.10	0.23	7
<i>Evolvulus glomeratus</i>	Esp_01	0.15	0.69	10
N.I 03	Esp_04	0.04	0.10	10
N.I 04	Esp_07	NA	NA	0
N.I 01	Esp_13	0.07	0.19	10
<i>Pfaffia aphylla</i>	Esp_16	0.15	0.52	10
N.I 02	Esp_19	0.22	0.70	10
<i>Borreria verticillata</i>	Esp_21	1.22	3.70	5
<i>Marsypianthes chamaedrys</i>	Esp_25	0.08	1.03	10
<i>Ludwigia myrtifolia</i>	Esp_26	0.20	1.25	10
N.I 05	Esp_28	NA	NA	0
N.I 06	Esp_29	NA	NA	0
N.I 07	Esp_30	NA	NA	0
Fabaceae sp01	Fab_01	0.19	0.70	10
<i>Tetrapteryx microphylla</i>	Mal_01	0.05	0.35	10
Malpighiaceae sp01	Mal_02	0.15	0.58	10
<i>Pleroma candolleanum</i>	Mel_01	0.61	2.87	10
Melastomataceae sp	Mel_02	0.11	0.53	10
<i>Lavoisiera sampaoana</i>	Mel_05	0.23	2.18	10
<i>Piptolepis imbricata</i>	Pip_im	0.12	0.81	10
Velloziaceae sp01	Vel_01	NA	NA	0

Pollen deposition and reproductive success

We estimated pollen deposition and fruit set of each focal *L. hypoleuca* plant. For pollen deposition, we selected two near-senescent flowers from each focal *L. hypoleuca* plant (n = 40). The stigmas of these selected flowers were removed and taken to the

laboratory, where they were placed on glass slides with carmine glycerin gelatin to stain the pollen and were observed under a light microscope. We counted the number of conspecific and heterospecific pollen grains. To distinguish between conspecific and heterospecific pollen, we used pollen from the anthers of *L. hypoleuca* as a reference. For this, we collected some anthers of *L. hypoleuca* and prepared slides using glycerinated gelatin with fuchsin for pollen identification. We then determined conspecific and heterospecific pollen by comparing the pollen found in the anthers with the pollen observed on the stigma slides. We estimated the average heterospecific and conspecific pollen across the stigmas of each focal individual (Supplementary Material S3). To assess the fruit set, we marked an inflorescence with a minimum of eight buds and a maximum of 51 buds in each focal *L. hypoleuca* individual (Supplementary Material S3). The reproductive success was the rate between the number of fruits and the total number of marked flowers.

Pollinator dependence

To estimate pollinator dependence in *L. hypoleuca*, we marked flowers at the bud stage for spontaneous self-pollination and natural pollination treatments ($n = 20$ and 23 , respectively). In the spontaneous self-pollination treatment, we bagged buds to prevent visits by pollinators, while the flowers in the natural pollination treatment were left exposed to visitors.

Statistical analyses

We made three global models to investigate the relationship between *L. hypoleuca* heterospecific and conspecific pollen deposition and likelihood of fruit production and the plant neighborhood:

- (1) The effect of plant neighborhood (similarity in corolla length, plant species richness, conspecific and heterospecific floral abundance) on heterospecific pollen; Since heterospecific floral abundance and floral richness are correlated, we only used floral richness in the models ($\text{cor} = 0.57$; $t = 2.99$; $\text{df} = 18$; $p\text{-value} < 0.01$).
- (2) The effect of plant neighborhood (similarity in corolla length, plant species richness and conspecific floral abundance) on conspecific pollen;
- (3) The effect of plant neighborhood and conspecific and heterospecific pollen on the likelihood of fruit production. As heterospecific pollen deposition and conspecific pollen deposition are correlated we only used conspecific pollen deposition on the models ($\text{cor} = 0.68$; $t = 3.93$; $\text{df} = 18$; $p\text{-value} < 0.01$).

Heterospecific pollen deposition was log-transformed in all models to improve model fit, and Gaussian distribution was used for models (1) and (2) while binomial distribution was used for model (3). We fitted generalized linear mixed models (GLMM) with the *glmmTMB* function in the “glmmTMB” package (Brooks et al. 2017), and the *simulateResiduals* function from the “DHARMA” package (Hartig, 2022) and *check_collinearity* function from the “performance” package (Lüdtke et al., 2021) to check model assumptions.

As we had many predictors, we performed model selection to avoid overfitting the models. For this, we used the “MuMIn” package (Barton, 2023) to identify the most parsimonious models based on Akaike’s Information Criterion to small samples (AICc). All data used for analysis are available in Supplementary Materials S4.

Finally, to estimate pollinator dependence of *L. hypoleuca*, we used a chi-square test with the presence or absence of seed in the marked buds as the response variable and treatments (natural and self-pollination) as predictors.

All analyses were conducted using the R software (R Core Team 2023).

Results

During the observations, we recorded a total of 73 visits (56 by bees, 15 by butterflies, 207 and 2 by wasps; Table S1). The bees visited only flowers of *L. hypoleuca* with the yellow guide, despite some initially approaching the flowers without the visible guide.

Although correlated ($r=0.68$), conspecific and heterospecific pollen deposition did not exhibit the same relationships with the predictor variables. The best model for heterospecific pollen deposition included only plant species richness (Estimate = 0.54; $X^2 = 3.97$; p-value = 0.04; Table 2; Figure 2a), while only the intercept (null model) was the best to explain conspecific pollen deposition (Table 2). The likelihood of fruit production increased with plant species richness (Estimate = 0.27; $X^2 = 4.47$; p-value < 0.01; Table 2; Figure 2b) and decreased with conspecific floral abundance (Estimate = -0.004; $X^2 = 6.92$; p-value = 0.03; Table 2; Figure 2c).

Table 2. Results of the model selection for the variables heterospecific pollen deposition, conspecific pollen deposition, and fruit set. The table shows the best models according to $AICc$ until the first $\Delta AICc$ bigger than two, and finally, the full model including all variables. Richness refers to the plant species richness. CFA is conspecific floral abundance. Corolla length similarity is the average similarity in corolla length of *L. hypoleuca* in relation to heterospecific plant species. Bold represents the best model.

Response variable	Models	AIC	ΔAIC
Heterospecific pollen	~Richness	62	0.00
	~CFA + Richness	62.8	0.81
	~1	62.8	0.83
	~ CFA	64.1	2.06
Conspecific pollen	~1	204.3	0.00
	~CFA	205.8	1.53
	~Richness	206.2	1.87
	~Corolla length similarity	207.7	2.73
Fruit/Buds	~CFA + Richness	112.7	0.00
	~CFA + Richness + Conspecific pollen	114.2	1.43
	~CFA	114.5	1.78
	~Conspecific pollen	114.7	1.95
	~Richness + Conspecific pollen	114.8	2.12

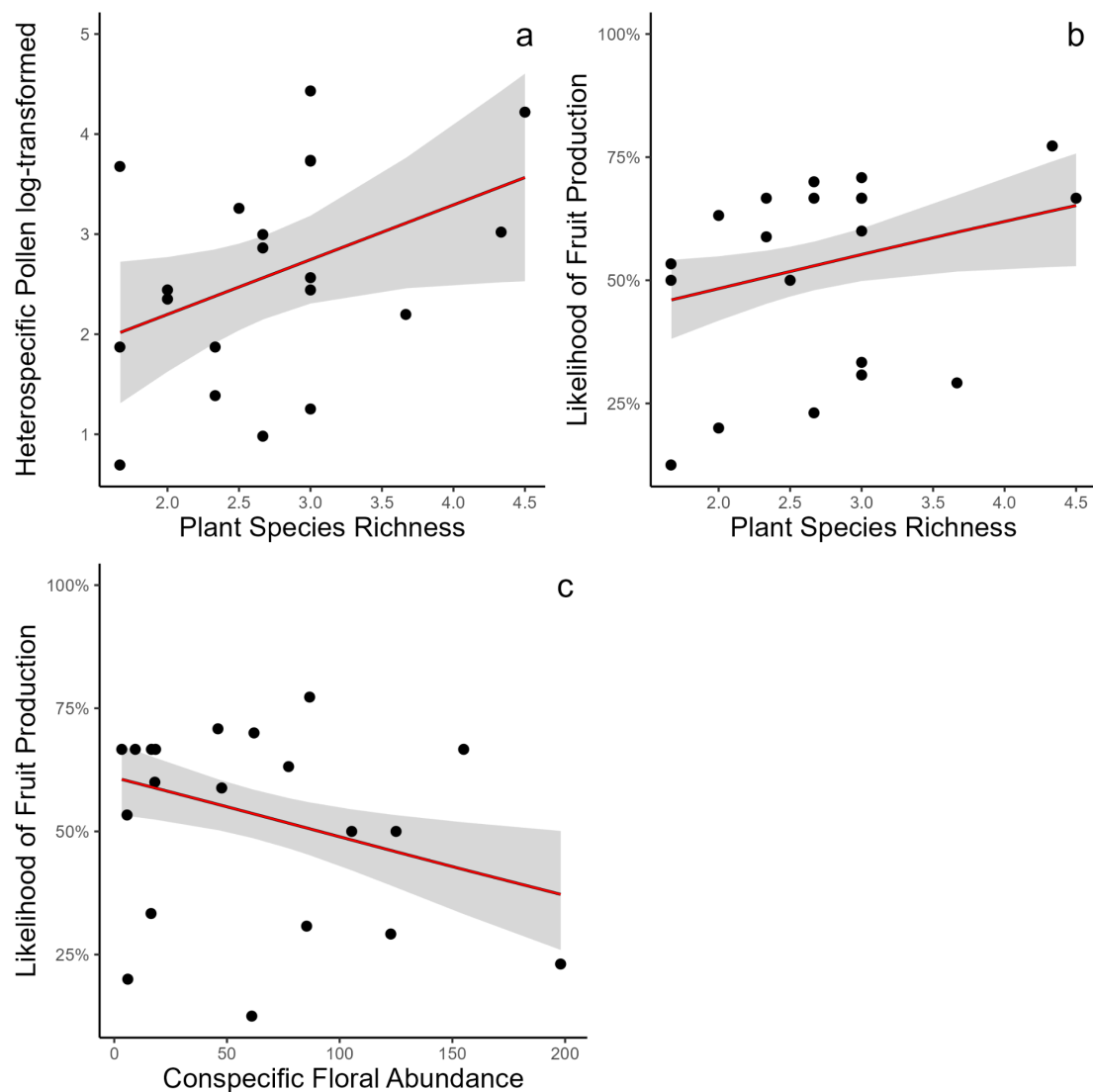


Figure 2. a) Relationship between heterospecific pollen deposition and plant species richness. Relationships between likelihood of fruit production and b) plant species richness and c) conspecific floral abundance. Each dot represents a distinct *L. hypoleuca* individual and the red line indicates a significant relationship at $p < 0.05$ and the gray area represents the 95% confidence interval.

Lantana hypoleuca did not exclusively require pollinators to set fruit, with a fruit set of spontaneous self-pollination of 0.30 ± 0.47 fruit/flowers. However, natural pollination had a fruit set of 0.73 ± 0.44 fruits/flowers. Therefore, pollinators enhanced the fruit set ($\chi^2 = 6.62$; $p = 0.01$).

Discussion

The plant neighborhood influenced each step of the reproductive process, from pollen deposition to fruit production. The increase in heterospecific pollen deposition with surrounding plant species richness indicates that pollinator sharing mediates patterns of pollen

deposition. Individuals of *Lantana hypoleuca* increased their reproductive success when surrounded by plants from different species, indicating a facilitative relationship between heterospecific neighborhood plants and *L. hypoleuca*. Despite not requiring pollinators for reproduction, flowers exposed to visitors showed higher reproductive success, reinforcing the importance of heterospecific neighborhood plants for *L. hypoleuca* reproductive success.

The increase in heterospecific pollen deposition with plant richness indicates that *L. hypoleuca* is receiving visitors from subsequent visits from other plant species. As we hypothesized, the plant species that received more heterospecific pollen also received more conspecific pollen deposition. However, despite the correlation, conspecific deposition did not respond to the neighborhood in the same way as heterospecific pollen deposition did. Additionally, reproductive success also increased with plant species richness, suggesting that flowering in diverse plant neighborhoods is advantageous for *L. hypoleuca*. Past studies have shown a negative association between heterospecific pollen deposition and plant reproduction (Ashman et al., 2020; Morales & Traveset 2008). For *L. hypoleuca*, self-pollination and the low number of ovules may mitigate the negative effect of heterospecific pollen, as it does not require large amounts of conspecific pollen for reproduction. Even in the presence of heterospecific pollen, a few conspecific grains would be enough for a fruit set. Especially considering that higher plant species diversity surrounding the focal species can enhance pollinator attraction, increasing heterospecific pollen deposition and fruit set through a facilitation process (Arroyo-Correa et al., 2024; Bergamo *et al.* 2024). The facilitation effect is further strengthened by the negative relationship between the abundance of conspecific flowers (and, therefore, plants with high floral display being more likely to self-pollinate) and lower fruit set. *Campos rupestres* are characterized by harsh environmental conditions and varying pollination rates, where plant-pollinator interactions are more likely to be opportunistic (Monteiro et al., 2021). In such environments, pollinators would exhibit generalist behaviour, leading to more pollinator sharing. In this context, pressures that foster the benefits of pollinator sharing through facilitation are expected (Eisen et al. 2020). Further studies using other species and more floral traits, such as resources offered by the flowers and color, will be important to better understand the niche overlap between the plant species and the neighborhood.

Lantana hypoleuca reproduction (likelihood of fruit production) peaked in plots with high heterospecific floral abundance, suggesting the benefits of sharing pollinators. Therefore, our study demonstrates the importance of considering the neighborhood of plant reproduction. Moreover, the effect of the multiple variables describing the surrounding neighborhood on *L.*

hypoleuca depended on the pollination stage considered: pollen deposition and reproductive success. This stresses the complexity of indirect interactions between plant species sharing pollinators and the necessity of evaluating multiple reproductive stages of plant reproduction. Furthermore, as these context-dependent relationships-such as plant richness and the abundance of flowering plants-can vary over the years, we emphasize the importance of long-term studies to better understand the variation in neighborhood composition and abundance. In summary, the process influencing the reproduction of *Lantana hypoleuca* seems to be the facilitation provided by the shared pollinators with the neighboring plant species.

Declaration of Competing Interest

The authors declare no conflict of interest

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CONCLUSÃO GERAL

Nesta tese objetivou-se entender o efeito de diferentes contexto de vizinhanças florais no sucesso reprodutivo das plantas. No contexto de comunidade, o aumento na abundância de flores florindo ao mesmo tempo gerou uma redução nas visitas (Figura 2a) e menos pólen chegou ao pistilo das plantas (Figura 2b e 2c), indicando que as espécies de plantas estão competindo umas com as outras. No entanto, as flores com morfologias similares receberam maiores cargas de pólen vindo de outras plantas (Figura 2d) e também produziram mais sementes (Figura 2e) mostrando que as plantas que têm flores mais parecidas têm um benefício reprodutivo. Sugerindo que as plantas estão se facilitando entre si – e esta facilitação resulta em sucesso reprodutivo. Por outro, quando consideramos a vizinhança próxima, as parcelas com plantas morfologicamente similares receberam maiores cargas de pólen coespecífico (Figura 3). Nesse caso, apesar das plantas estarem competindo pelo pólen coespecífico no contexto da comunidade, esse efeito parece não ocorrer entre as plantas que estão na vizinhança mais próximas.

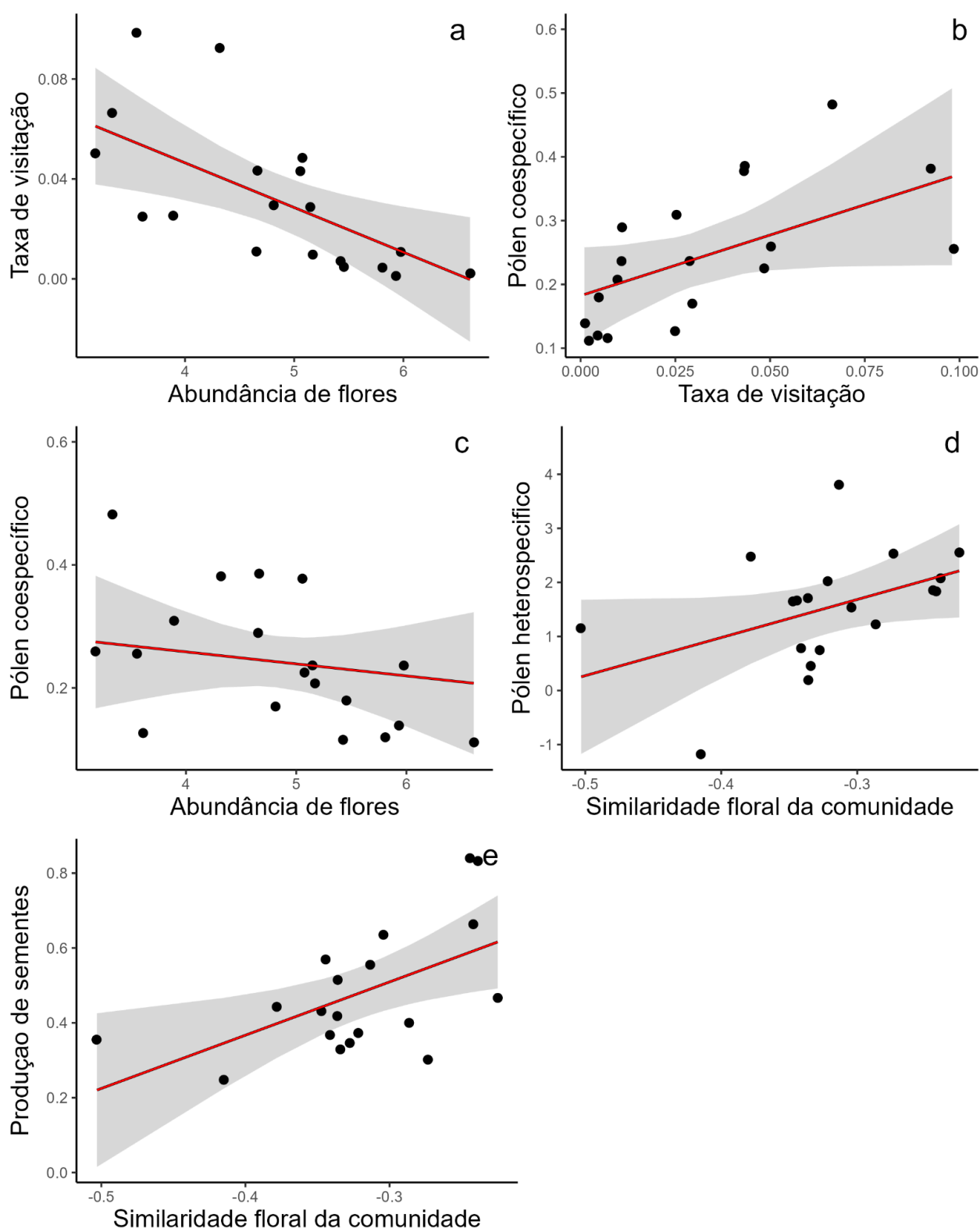


Figura 2. A relação entre o contexto da comunidade e a taxa de visitação, deposição de pólen e sucesso reprodutivo das plantas no Campo Rupestre de Diamantina, MG, Brasil. (a) A taxa de visitação diminuiu com o aumento da abundância de flores. (b) A deposição de pólen coespecífico aumentou com a taxa de visitas. (c) A deposição de pólen coespecífico diminuiu com a abundância de flores. (d) A deposição de pólen heteroespecífico aumentou para plantas com flores mais similares. (e) A produção de sementes foi maior em plantas com flores mais similares.

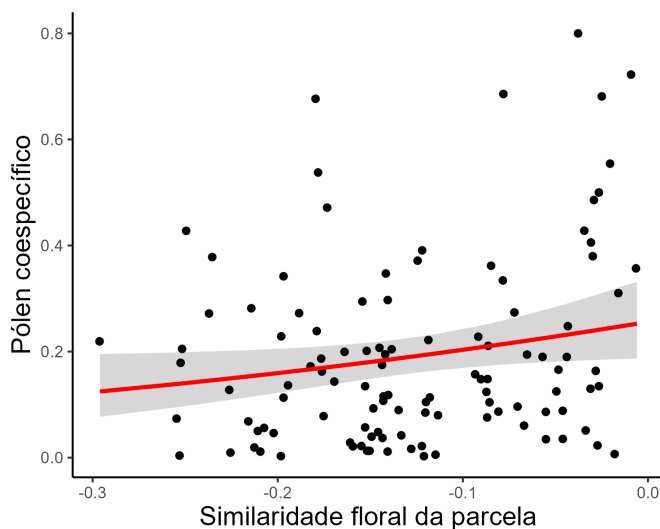


Figura 3. A deposição de pólen coespecífico aumenta com o aumento da similaridade floral da parcela no Campo Rupestre de Diamantina, MG, Brasil.

No contexto das espécies, para *Piptolepsis imbricata* e *Cuphea disperma* a abundância de flores de uma mesma espécie aumentou a visitação (Figura 4a e 4b), mas não apresentou efeito para o sucesso reprodutivo, mostrando que apesar da produção de sementes ser consequência da visitação, ambos os processos podem ser influenciados por fatores diferentes. Ao mesmo tempo, para a *Cuphea dispermia*, a produção de sementes foi maior quando as plantas no entorno eram mais similares (Figura 4c). Já para a *Lantana hypoleuca* a riqueza de espécies floridas que aumentou a produção de frutos (Figura 4d). Ambos os resultados indicam um efeito positivo da floração conjunta de mais espécies de plantas e facilitação entre elas. Por fim, a abundância de flores da mesma espécie teve um efeito negativo para a reprodução da *Lantana hypoleuca* (Figura 4e), indicando que em alguns casos pode ocorrer competição dos indivíduos de plantas dentro da mesma espécie.

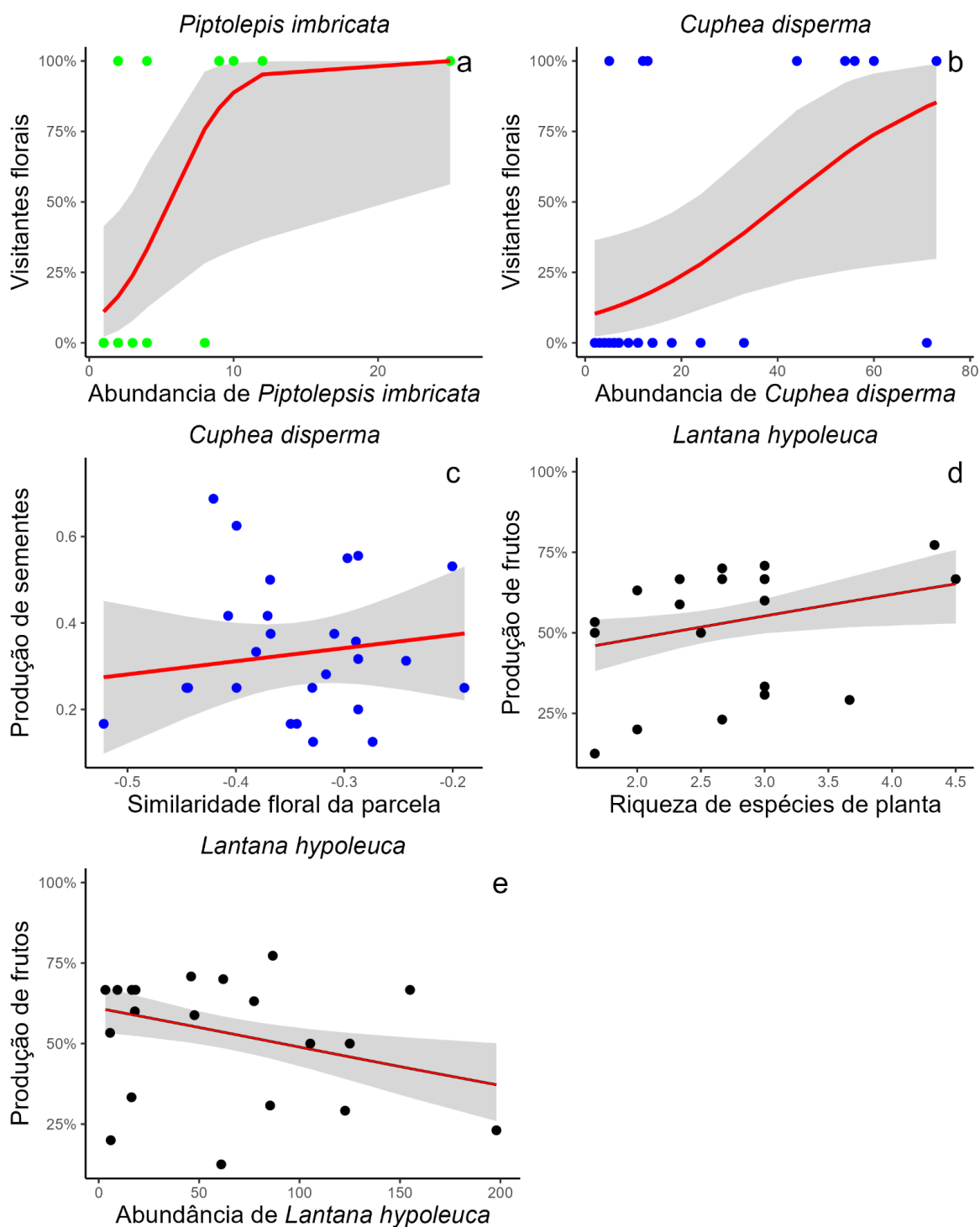


Figura 4. Relação entre abundância floral, taxa de visitação e sucesso reprodutivo para *Piptolepis imbricata*, *Cuphea disperma* e *Lantana hypoleuca* no Campo Rupestre de Diamantina, MG, Brasil. (a, b) Para *Piptolepis imbricata* e *Cuphea disperma* a taxa de visitação foi maior quando essas espécies eram mais abundantes. (c) Para *Cuphea disperma*, a produção de sementes aumentou quando as plantas ao seu redor eram mais similares. Para *Lantana hypoleuca* a produção de frutos aumentou quando havia (d) maior riqueza de plantas florindo ao seu redor e (e) diminuiu quando mais indivíduos de *Lantana hypoleuca* estavam florindo no mesmo local.

No Campo Rupestre, nossos resultados mostraram que as plantas se beneficiam de ocorrerem em ambientes rodeados de plantas de outras espécies, principalmente quando a morfologia floral entre elas é similar, indicando que a facilitação é um mecanismo preponderante na estruturação da comunidade. A deposição de pólen de outras plantas apresenta um efeito negativo pequeno ou nulo no sucesso reprodutivo das plantas (Lopes et al. 2021), o que também indica facilitação na comunidade. Nesse contexto, a floração conjunta de várias espécies é necessária para a manutenção dos polinizadores, principalmente em um ambiente onde eles são escassos. No entanto, ainda é um ambiente complexo, onde a competição também exerce um papel importante na comunidade, principalmente para a deposição de pólen da mesma espécie.

Neste estudo, também foi explorado as relações dentro da comunidade, diferenciando o efeito da comunidade como um todo, para pequenas distâncias e por espécies. Independente do foco, a abundância de flores foi um *proxy* importante para a visitação, na qual a maior abundância de flores gerou maior frequência de visitação. No entanto, o sucesso reprodutivo e a deposição de pólen das espécies estão mais relacionados à presença de plantas vizinhas e a similaridade na morfologia floral dessas plantas em todos os contextos. No contexto da comunidade, ter uma morfologia similar têm um efeito positivo na reprodução. Esse efeito positivo é em algum grau reforçado pela maior taxa de deposição de pólen da mesma espécie entre plantas similares e vizinhas próximas. Esse resultado indica que florir próximo de uma espécie morfológicamente similar é vantajoso. Isso poderia ser explicado pois o mesmo visitante floral visitaria todas as plantas no entorno, mantendo-o mais próximo e por mais tempo no mesmo local, por exemplo. Ainda, a vantagem de ter mais flores de outras espécies próximas ocorreu para duas das três espécies analisadas, *Lantana hypoleuca* e *Cuphea dispermia*. Nos três contextos observados, a facilitação entre as plantas foi um fator preponderante, o que reforça que, assim como competição, a facilitação também tem um papel fundamental na estrutura das comunidades de polinizadores.

Independente do contexto da comunidade, o pólen heteroespecífico e o sucesso reprodutivo das plantas esteve intimamente relacionado à morfologia floral das plantas vizinhas. A discussão sobre a relação entre morfologia floral, visitantes e sucesso reprodutivo, seja por síndromes ou sistemas de polinização, ou usando o contexto da comunidade é uma discussão longa e central na biologia da polinização (Faegri e Pijl, 1979; Waser et al. 1996; Castellanos et al. 2004; Camargo et al. 2019; Amorim et al. 2021; Camargo et al. 2023). Nosso estudo contribui para essa discussão demonstrando o efeito da morfologia em vários contextos, esse efeito é preponderantemente positivo quando as flores são similares, portanto

se parecer com as plantas no entorno leva a um efeito positivo no sucesso reprodutivo das flores, mesmo que acarrete em maior deposição de pólen heteroespecífico. A distribuição das espécies em pequenas populações distantes entre si que corre nos Campo Rupestre pode favorecer a facilitação por meio da similaridade morfológica. Isso poderia ocorrer porque o solo pobre em nutrientes do Campo Rupestre (Silveira et al. 2016), pode gerar uma vantagem nas plantas que oferecem menos recursos, sejam flores ou néctar, mas ocorrem em manchas com espécies de diferentes florindo ao mesmo tempo. Neste estudo, por exemplo, a maioria das plantas que encontramos possuem flores pequenas, com pouco volume de néctar (Supplementary material S1 em Efeito da comunidade nas plantas). Nesse caso, as manchas de flores geram recursos suficientes para manutenção dos polinizadores. Ao mesmo tempo, que a floração contínua de várias espécies similares (veja Camargo et al. 2023) também favorece a manutenção dos polinizadores por ofertar recursos continuamente. No entanto, seriam necessários mais estudos para validar essa possibilidade. Portanto, nesse estudo, a morfologia similar das plantas na comunidade favorece o compartilhamento dos polinizadores através da facilitação levando a um maior sucesso reprodutivo das plantas.

Uma limitação deste estudo foi a baixa taxa de visitação das plantas, que impediu uma caracterização melhor do compartilhamento dos visitantes florais entre as plantas. Porém, a deposição de pólen heteroespecífico e a similaridade floral de plantas que florescem ao mesmo tempo indicam que há compartilhamento de polinizadores entre as plantas. Caracterizar melhor o compartilhamento de visitantes entre as plantas é um passo fundamental para compreender melhor as relações indiretas entre as plantas, principalmente quando as interações entre planta e polinizador estão mais relacionadas ao oportunismo que a uma especialização ecológica (Monteiro et al. 2021). Portanto, o contexto da comunidade, riqueza, abundância, similaridade da morfologia floral das plantas no entorno florindo ao mesmo tempo terão uma grande influência no sucesso reprodutivo das plantas.

Por fim, os achados deste estudo mostraram que é importante conhecer as relações dentro de uma comunidade de plantas em seus vários contextos de vizinhança, desde as espécies até a comunidade. As relações entre as plantas são complexas, dependem de vários fatores, que vão além do indivíduo. O conhecimento dessas interações é necessário para formular estratégias de conservação eficientes para os Campos Rupestres. Principalmente, pela alta diversidade de plantas, muitas restritas a esses locais e as ameaças geradas pelas ações antrópicas como mineração a céu aberto, queimadas e urbanização que vem levando muitas espécies a serem classificadas como ameaçadas de extinção. Portanto, conservar é

importante, pois para restabelecer essas relações em seus vários níveis, sendo muitas delas ainda desconhecidas, pode ser um desafio muito mais complexo.

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MATERIAL SUPLEMENTAR

Efeito da comunidade nas plantas

Supplementary material S1. Table with the species names and floral traits. Code means the name of the species and figures and tables. The floral traits are millimeters (mm). Resources are a categorical variable where P indicate pollen, N indicate nectar and O indicated oil.

Species name	Code	Stigma length		Anther length		Corolla length		Corolla diameter		Resource
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	
<i>Emilia fosbergii</i> Nicolson	Ast_02	11.36	1.64	11.36	1.64	9.99	1.34	2.74	0.55	P/N
<i>Lychnophora pohlii</i> Sch.Bip.	Ast_05	17.66	1.76	10.25	1.42	12.36	1.73	8.95	0.91	P/N
<i>Lepidaploa lilacina</i> (Mart. ex DC.) H.Rob.	Ast_09	8.51	1.67	8.51	1.67	6.74	1.06	3.24	0.99	P/N
<i>Lepidaploa rufogrisea</i> (A.St.-Hil.) H.Rob.	Ast_11	12.17	1.20	12.17	1.20	10.33	1.11	4.46	1.24	P/N
<i>Chromolaena cylindrocephala</i> (Sch.Bip. ex Baker) R.M.King & H.Rob.	Ast_12	9.00	1.21	9.00	1.21	5.09	0.74	1.25	0.24	P/N
<i>Chromolaena</i> sp.	Ast_16	9.11	1.22	9.11	1.22	4.97	0.68	1.38	0.30	P/N
<i>Baccharis dracunculifolia</i> DC.	Bac_01	3.43	0.50	3.59	0.37	2.45	0.48	0.58	0.24	P/N
<i>Cuphea diosmifolia</i> A.St.-Hil.	Cup_01	2.86	0.57	2.14	0.61	4.42	0.48	11.50	1.09	N
<i>Cuphea disperma</i> Koehne	Cup_02	3.87	0.92	2.66	0.67	3.95	0.57	9.22	0.98	N
<i>Stylosanthes gracilis</i> Kunth	Fab_02	4.12	0.84	4.12	0.84	5.66	1.18	3.30	1.09	N
<i>Borreria verticillata</i> (L.) G.Mey.	Flo_03	2.64	1.47	3.21	1.05	3.86	1.38	2.61	0.90	P/N
<i>Richardia grandiflora</i> (Cham. & Schltdl.) Steud.	Flo_04	8.07	1.02	6.88	1.07	9.29	1.37	5.82	1.44	P/N
<i>Pfaffia denudata</i> (Moq.) Kuntze	Flo_07	0.82	0.16	2.94	0.29	3.78	0.57	3.29	0.39	P/N
<i>Pfaffia aphylla</i> Suess.	Flo_14	0.57	0.07	1.93	0.36	3.37	0.38	1.33	0.51	P/N
<i>Evolvulus glomeratus</i> Nees & Mart.	Flo_18	8.62	1.98	8.63	1.99	12.05	3.45	16.07	3.37	P
<i>Encholirium scrutor</i> (L.B.Sm.) Rauh	Flo_21	10.65	0.65	10.17	0.89	23.60	3.54	7.68	0.44	P/N
<i>Portulaca hirsutissima</i> Cambess.	Flo_23	8.62	1.80	6.72	1.25	11.91	1.63	19.77	4.06	P
<i>Diplusodon helianthemifolius</i> DC.	Flo_26	14.36	1.81	6.33	2.06	15.60	2.92	30.55	4.48	P
<i>Gaylussacia virgata</i> Mart. ex Meisn.	Gay_01	5.61	0.70	4.08	0.62	7.02	0.74	3.61	0.60	P/N
<i>Hyptis passerina</i> Mart. ex Benth.	Hyp_00	7.33	0.68	7.33	0.68	5.64	0.82	3.66	0.73	P/N

Species name	Code	Stigma length		Anther length		Corolla length		Corolla diameter		Resource
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	
<i>Lantana hypoleuca</i> Briq.	Lan_00	1.26	0.43	2.71	0.74	6.70	1.15	4.10	0.72	N
<i>Tetrapteryx microphylla</i> (A.Juss.) Nied.	Mal_01	1.92	0.37	3.28	0.65	4.94	0.49	12.19	0.93	O
Melastomataceae A . Juss.	Mel_02	10.62	1.67	10.67	1.13	6.26	1.09	12.75	2.65	P
<i>Marcetia canescens</i> Naudin	Mel_04	9.60	1.58	8.99	1.52	5.89	1.39	12.68	2.43	P
<i>Pleroma candolleanum</i> (Mart. ex DC.) Triana	Mel_05	18.89	3.14	17.27	1.64	26.60	4.42	53.03	8.60	P
<i>Microlicia</i> D.Don	Mel_10	6.92	1.25	9.13	1.70	9.69	1.64	18.39	2.45	P
<i>Lavoisiera caryophyllea</i> A.St.-Hil. ex Naudin	Mel_13	10.40	3.95	13.80	2.82	17.40	4.67	34.40	5.08	P
<i>Palicourea rigida</i> Kunth	Pal_01	13.48	3.23	13.32	2.79	15.25	1.92	7.69	1.54	P/N
<i>Piptolepis imbricata</i> (Gardner) Sch.Bip.	Pip_00	7.21	0.97	7.21	0.97	6.91	0.83	4.32	0.74	P/N
<i>Vellozia variabilis</i> Mart. ex Schult. & Schult.f.	Vel_05	28.33	2.89	19.07	2.18	40.79	6.63	76.46	8.85	P/N
<i>Xyris</i> Gronov. ex L.	Xyr_01	3.05	0.31	2.71	0.51	5.07	0.49	8.75	1.42	P

Supplementary material S2. Phenology matrix with flower counts per species. Code represents the species name in Table S1; T1 to T9 represent the nine periods of data collection between October 2022 and April 2023.

Code	T1	T2	T3	T4	T5	T6	T7	T8	T9
Ast_02	2	0	3	4	0	0	0	0	0
Ast_05	0	0	1	0	19	96	7	0	0
Ast_09	0	0	0	0	0	0	10	43	119
Ast_11	0	0	0	0	0	0	0	45	30
Ast_12	0	0	0	0	0	0	0	1	1
Ast_16	0	0	0	0	0	0	0	0	10
Bac_01	0	0	0	0	0	0	110	228	55
Cup_01	3	12	13	6	0	2	1	0	0
Cup_02	0	0	4	72	276	298	61	23	11
Fab_02	0	0	0	0	3	6	13	3	1
Flo_03	1	1	11	155	528	577	359	160	4
Flo_04	8	12	28	22	10	19	15	28	15
Flo_07	8	7	7	0	0	0	0	0	0
Flo_14	1	1	1	1	0	0	0	0	0
Flo_18	0	0	4	13	41	95	15	8	0
Flo_21	0	0	3	0	0	0	0	1	0
Flo_23	0	0	10	0	10	16	6	7	0
Flo_26	0	0	0	0	1	6	13	4	0
Gay_01	32	34	7	34	20	3	22	61	14
Hyp_00	0	0	0	0	0	0	0	0	30
Lan_00	92	13	0	0	0	0	0	0	1
Mal_01	38	18	10	7	1	2	12	10	7
Mel_02	10	4	80	1	5	23	93	92	69
Mel_04	1	0	0	0	0	0	0	194	199
Mel_05	13	0	0	0	0	0	0	0	0
Mel_10	0	0	0	0	220	13	1	0	0
Mel_13	0	0	0	0	0	0	1	0	159
Pal_01	9	7	10	9	0	0	0	0	0
Pip_00	61	37	31	19	15	6	12	55	97
Vel_05	0	0	0	0	0	0	2	0	26
Xyr_01	14	9	2	9	19	28	91	42	38

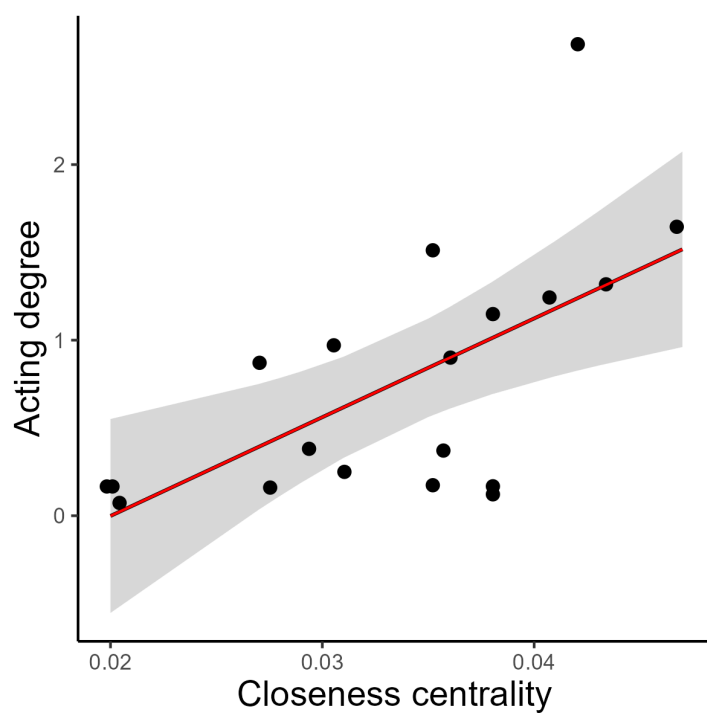
Supplementary material S3. Interaction frequency matrix. Code represents the plant species on rows (following names in Table S1) and the columns represent animal groups. X1: Anthidiini; X2: *Apis mellifera*; X3: *Augastes scutatus*; X4: Halictidae morpho 1; X5: *Camponotus* sp; X6: *Centris* sp; X7: *Chlorostilbon lucidus*; X8: *Cogia* sp; X9: Colletidae sp; X10: *Eufriesea* sp; X11: fly sp01; X12: fly sp02; X13: fly sp03; X14: fly sp04; X15: fly sp07; X16: fly sp09; X17: fly sp10; X18: Halictidae morpho 2; X19: Halictidae morpho 3; X20: Halictidae morpho 4; X21: Halictidae morpho 5; X22: Halictidae morpho 6; X23: HesperIIDae sp; X24: Large bees; X25: Megachilidae sp01; X26: Megachilidae sp02; X27: *Melipona* sp; X28: Meliponini sp; X29: Small bees; X30: Bees sp; X31: Small insects; X32: *Paratrigona* sp; X33: Riodinidae sp; X34: *Tetragonisca* sp; X35: *Trigona* sp.

Code	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14	X15	X16	X17	X18	X19	X20	X21	X22	X23	X24	X25	X26	X27	X28	X29	X30	X31	X32	X33	X34	X35	
Ast_02	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ast_05	0	36	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ast_09	0	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ast_11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ast_12	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ast_16	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Bac_01	0	0	0	0	5	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cup_01	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	
Cup_02	8	26	1	0	0	0	0	0	0	4	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Fab_02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	
Flo_03	0	1	0	3	2	0	0	0	0	0	3	7	1	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
Flo_04	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0	0	14	0	0	0	0	0	
Flo_07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	
Flo_14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Flo_18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	8	0	1	0	0	0	0
Flo_21	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Flo_23	1	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	33	
Flo_26	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
Gay_01	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hyp_00	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Lan_00	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	
Mal_01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	

Code	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14	X15	X16	X17	X18	X19	X20	X21	X22	X23	X24	X25	X26	X27	X28	X29	X30	X31	X32	X33	X34	X35
Mel_02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mel_04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Mel_05	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mel_10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0
Mel_13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Pal_01	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pip_00	0	4	0	0	5	0	0	1	0	0	0	0	4	0	0	0	3	0	0	1	0	0	1	0	0	0	0	0	0	3	0	0	1	0	0
Vel_05	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	
Xyr_01	0	11	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	3	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0

Supplementary material S4. Data set of the SEM analysis. **Code** represents the name of the plant species (following species names in Table S1). **CPD** is conspecific pollen deposition. **HPD** is Heterospecific pollen deposition average and log transformed. **Rate** is visitation rate. **Target** is target degree. **Acting** is acting degree. **Closeness** is closeness centrality. **Abundance** represents floral abundance sum and log transformed. **FunD** is Functional distinctiveness. **Overlap** is floral overlap.

Code	Seed set	CPD	HPD		Rate	Target	Acting	Closeness	Abundance		FunD	Overlap
			Average	log					sum	log		
Ast_05	0.64	0.17	4.65	1.54	0.03	0.76	1.15	0.04	123.00	4.81	0.30	1.69
Ast_09	0.66	0.24	6.26	1.83	0.03	0.74	0.90	0.04	172.00	5.15	0.24	1.60
Ast_11	0.40	0.38	3.40	1.22	0.09	0.78	0.25	0.03	75.00	4.32	0.29	0.91
Cup_01	0.35	0.13	2.11	0.75	0.02	0.66	0.17	0.04	37.00	3.61	0.33	3.44
Cup_02	0.37	0.11	2.19	0.78	0.00	0.64	1.32	0.04	745.00	6.61	0.34	4.55
Flo_04	0.84	0.38	6.39	1.85	0.04	0.58	1.51	0.04	157.00	5.06	0.24	8.09
Flo_18	0.42	0.21	5.52	1.71	0.01	0.77	1.24	0.04	176.00	5.17	0.34	3.58
Flo_23	0.30	0.31	12.58	2.53	0.03	0.49	2.69	0.04	49.00	3.89	0.27	3.03
Flo_26	0.44	0.26	11.91	2.48	0.05	0.94	0.17	0.04	24.00	3.18	0.38	2.06
Gay_01	0.47	0.12	12.85	2.55	0.01	0.29	0.97	0.03	227.00	5.42	0.22	7.78
Lan_00	0.57	0.39	5.29	1.67	0.04	0.67	0.37	0.04	106.00	4.66	0.34	1.04
Mal_01	0.43	0.29	5.20	1.65	0.01	0.90	0.16	0.03	105.00	4.65	0.35	7.61
Mel_02	0.51	0.14	1.21	0.19	0.00	0.50	0.17	0.02	377.00	5.93	0.34	7.90
Mel_04	0.37	0.24	7.56	2.02	0.01	0.88	0.07	0.02	394.00	5.98	0.32	1.52
Mel_10	0.33	0.18	1.58	0.45	0.00	0.38	0.38	0.03	234.00	5.46	0.33	0.90
Mel_13	0.25	0.23	0.31	-1.18	0.05	0.33	0.17	0.02	160.00	5.08	0.42	0.76
Pal_01	0.56	0.26	45.00	3.81	0.10	0.21	0.87	0.03	35.00	3.56	0.31	1.83
Pip_00	0.83	0.12	7.97	2.08	0.00	0.57	1.65	0.05	333.00	5.81	0.24	8.10
Vel_05	0.36	0.48	3.17	1.15	0.07	0.86	0.12	0.04	28.00	3.33	0.50	0.82



Supplementary material S5. Correlation between the network metrics acting degree and closeness centrality (Estimate = 56.24, $p < 0.01$).

Efeito da vizinhança próxima

Table S1. Floral morphology of all species found during the study on the Campos Rupestres of Diamantina, Brazil. The values are the mean of the morphology in millimeters. In resources, P represents pollen, N represents nectar and O represents Oil. NA are plant species with missing information

Family	Species name	Height		Corolla		Resource
		Stigma	Anther	Length	Diameter	
Asteraceae	<i>Richterago elegans</i> Roque	8.40	8.40	6.73	2.48	PN
Asteraceae	<i>Emilia fosbergii</i> Nicolson	11.36	11.36	9.99	2.74	PN
Asteraceae	<i>Pseudobrickellia</i> sp R.M. King & H. Rob.	5.33	5.33	3.25	0.68	NA
Asteraceae	<i>Symphopappus angustifolius</i> Cabrera	4.89	4.89	3.22	1.28	PN
Asteraceae	<i>Lychnophora pohlii</i> Sch.Bip.	17.66	10.25	12.36	8.95	PN
Asteraceae	<i>Ageratum conyzoides</i> L.	5.81	5.81	3.48	1.28	PN
Asteraceae	<i>Ageratum fastigiatum</i> (Gardner) R.M.King & H.Rob.	4.32	4.32	1.86	1.22	PN
Asteraceae	<i>Lepidaploa lilacina</i> (Mart. ex DC.) H.Rob.	8.51	8.51	6.74	3.24	PN
Asteraceae	<i>Lepidaploa rufogrisea</i> (A.St.-Hil.) H.Rob.	12.17	12.17	10.33	4.46	PN
Asteraceae	<i>Chromolaena cylindrocephala</i> (Sch.Bip. ex Baker) R.M.King & H.Rob.	9.00	9.00	9.91	1.25	PN
Asteraceae	<i>Chromolaena</i> sp DC.	9.11	9.11	4.97	1.38	PN
Asteraceae	<i>Baccharis dracunculifolia</i> DC.	3.43	3.59	2.45	0.58	PN
Bignoniaceae	<i>Jacaranda oxyphylla</i> Cham.	25.04	21.41	55.63	27.52	N
Fabaceae	<i>Chamaecrista</i> sp1 Moench	10.67	7.26	16.89	17.08	P
Fabaceae	<i>Chamaecrista</i> sp2 Moench	4.84	4.12	5.97	5.63	P
Lythraceae	<i>Cuphea diosmifolia</i> A.St.-Hil.	2.86	2.14	4.42	11.50	N
Lythraceae	<i>Cuphea disperma</i> Koehne	3.87	2.66	3.95	9.22	N
Fabaceae	<i>Crotalaria unifoliolata</i> Benth.	11.40	10.38	12.03	10.61	N
Fabaceae	<i>Stylosanthes gracilis</i> Kunth	4.12	4.12	5.66	3.30	N
Portulacaceae	<i>Portulaca hirsutissima</i> Cambess.	7.15	5.87	16.55	33.48	P
Rubiaceae	<i>Borreria verticillata</i> (L.) G.Mey.	2.64	3.21	3.86	2.61	PN
Rubiaceae	<i>Richardia grandiflora</i> (Cham. & Schltdl.) Steud.	8.07	6.88	9.29	5.82	PN
Amaranthaceae	<i>Pfaffia denudata</i> (Moq.) Kuntze	0.82	2.94	3.78	3.29	PN
Myrtaceae	<i>Campomanesia adamantium</i> (Cambess.) O.Berg	5.23	5.54	8.09	20.51	PN
Primulaceae	<i>Myrsine monticola</i> Mart.	1.04	0.93	1.47	3.09	NA
Amaranthaceae	<i>Pfaffia aphylla</i> Suess.	0.57	1.93	3.37	1.33	PN
Euphorbiaceae	<i>Croton antisiphiliticus</i> Mart.	3.74	3.71	1.78	3.23	NA
Convolvulaceae	<i>Evolvulus glomeratus</i> Nees & Mart.	8.62	8.63	12.05	16.07	P
Onagraceae	<i>Ludwigia myrtifolia</i> (Cambess.) H.Hara	5.33	6.63	14.59	18.79	O
Bromeliaceae	<i>Encholirium scrutator</i> (L.B.Sm.) Rauh	10.65	10.17	15.36	7.68	PN

Family	Species name	Height		Corolla		Resource
		Stigma	Anther	Length	Diameter	
Malvaceae	<i>Waltheria indica</i> L.	2.52	2.13	2.62	1.91	PN
Portulacaceae	<i>Portulaca hirsutissima</i> Cambess.	8.62	6.72	11.91	19.77	PN
Lamiaceae	<i>Marsypianthes chamaedrys</i> (Vahl) Kuntze	5.60	6.25	7.92	4.11	N
Lythraceae	<i>Diplusodon helianthemifolius</i> DC.	14.36	6.33	15.60	30.55	P
Apocynaceae	<i>Minaria cordata</i> (Turcz.) T.U.P.Konno & Rapini	1.47	1.47	3.17	3.00	NA
Ericaceae	<i>Gaylussacia virgata</i> Mart. ex Meisn.	5.61	4.08	7.02	3.61	PN
Lamiaceae	<i>Hyptis passerina</i> Mart. ex Benth.	7.33	7.33	5.64	3.66	PN
Verbenaceae	<i>Lantana hypoleuca</i> Briq.	1.26	2.71	6.70	4.10	N
Malpighiaceae	<i>Tetrapteryx microphylla</i> (A.Juss.) Nied.	1.92	3.28	4.94	12.19	PO
Melastomataceae	<i>Fritzschia sertularia</i> (Schränk & Mart. ex DC.) M.J.R.Rocha & P.J.F.Guim.	9.07	8.68	8.11	16.31	P
Melastomataceae	Melastomataceae sp. A . Juss.	10.62	10.67	6.26	12.75	P
Melastomataceae	<i>Lavoisiera sampaioana</i> Barreto	7.84	10.19	19.00	37.43	P
Melastomataceae	<i>Marcetia canescens</i> Naudin	9.60	8.99	5.89	12.68	P
Melastomataceae	<i>Pleroma candolleanum</i> (Mart. ex DC.) Triana	18.89	17.27	26.60	53.03	P
Melastomataceae	<i>Pleroma heteromallum</i> (D. Don) D.Don	6.10	11.00	15.14	29.83	P
Melastomataceae	<i>Microlicia</i> sp D.Don	6.92	9.13	9.69	18.39	P
Melastomataceae	<i>Microlicia pilosissima</i> Cogn.	4.62	6.66	8.40	17.25	P
Melastomataceae	<i>Lavoisiera caryophyllea</i> A.St.-Hil. ex Naudin	10.40	13.80	17.40	34.40	P
Rubiaceae	<i>Palicourea rigida</i> Kunth	13.48	13.32	15.25	7.69	PN
Asteraceae	<i>Piptolepis imbricata</i> (Gardner) Sch.Bip.	7.21	7.21	6.91	4.32	PN
Rubiaceae	<i>Psyllocarpus laricoides</i> Mart. ex Mart. & Zucc.	0.95	2.03	7.16	5.14	N
Velloziaceae	<i>Vellozia ornithophila</i> Mello-Silva	12.33	8.55	14.81	28.83	PN
Velloziaceae	<i>Vellozia aloifolia</i> Mart.	41.19	29.29	60.82	77.72	PN
Velloziaceae	<i>Vellozia variabilis</i> Mart. ex Schult. & Schult.f.	28.33	19.07	40.79	76.46	PN
Verbenaceae	<i>Lippia stachyoides</i> Cham.	0.89	1.96	4.57	2.72	NA
Xyridaceae	<i>Xyris</i> sp. Gronov. ex L.	3.05	2.71	5.07	8.75	P

Table S2. Data set of the neighborhood levell models testing the effect of the nearby community on heterospecific pollen, conspecific pollen and seed set on the Campos Rupestres of Diamantina, Brazil. Obs is the time of observation (1 to 9). RPlant is plant richness in the plot per time. Abund is abundance of plant in the plot per time. FDis is functional dispersion per plot per time. CWM is average of corolla length (Comp) and corolla diameter (Diam). HP is heterospecific pollen deposition. CP is conspecific pollen deposition.

Plot	Obs	RPlant	Abund	FDis	CWM		Visits		HP		CP	Seed Set
					Comp	Diam	Rate	Richness	Average	Round *10		
AM2413	9	2	46	0.07	2.22	2.95	0.000	0	10.58	106	0.06	0.26
AM2414	6	2	8	0.23	2.06	2.82	0.000	0	9.00	90	0.13	0.70
LA7613	6	5	12	0.18	2.18	2.39	0.001	1	5.50	55	0.19	0.19
LA7613	7	3	17	0.09	1.08	0.86	0.000	0	0.50	5	0.21	0.18
LA7613	8	3	13	0.25	1.90	1.88	0.000	0	7.00	70	0.21	0.33
LA7614	1	4	23	0.14	1.94	1.75	0.001	1	1.33	13	0.19	0.58
LA7614	2	2	11	0.09	2.06	2.55	0.004	1	1.00	10	0.10	0.68
LA7614	3	3	12	0.14	2.23	2.38	0.000	0	1.75	18	0.01	0.54
LA7614	4	2	2	0.15	1.88	2.00	0.000	0	1.50	15	0.09	0.55
LA7614	5	3	8	0.12	2.43	3.05	0.000	0	0.25	2	0.22	0.17
LA7614	9	2	7	0.07	2.07	2.60	0.000	0	14.50	145	0.10	0.27
LA7615	3	2	6	0.16	1.83	1.70	0.010	1	34.50	345	0.02	0.54
LA7615	4	3	13	0.11	1.68	2.03	0.042	1	3.00	30	0.01	0.46
LA7615	5	4	72	0.20	1.71	1.47	0.008	1	5.85	58	0.11	0.60
LA7615	6	4	8	0.19	1.85	1.78	0.000	0	7.56	76	0.14	0.45
LA7616	3	3	17	0.03	2.52	2.83	0.086	3	4.50	45	0.43	0.75
LA7616	6	2	21	0.15	2.21	2.80	0.059	1	14.67	147	0.21	0.32
LA7616	7	2	8	0.18	2.35	2.65	0.008	1	1.50	15	0.54	0.32
LA7617	1	2	17	0.05	1.89	1.48	0.000	0	0.50	5	0.17	0.66
LA7617	3	2	5	0.15	2.38	1.71	0.000	0	13.00	130	0.01	0.68
LA7617	4	2	13	0.13	2.43	2.23	0.000	0	0.00	0	0.09	0.68
LA7617	5	3	73	0.20	1.80	2.41	0.001	1	27.38	274	0.34	0.68

Plot	Obs	RPlant	Abund	FDis	CWM		Visits		HP		CP	Seed Set
					Comp	Diam	Rate	Richness	Average	Round *10		
LA7617	6	3	70	0.12	1.49	2.12	0.005	1	7.38	74	0.08	0.65
LA7617	7	3	37	0.18	1.33	1.06	0.055	1	0.25	2	0.24	0.42
LA7617	8	2	32	0.12	1.27	0.68	0.000	0	5.33	53	0.37	0.50
LA7618	5	2	16	0.15	1.49	2.30	0.003	1	8.50	85	0.05	0.13
LA7618	6	2	16	0.09	1.49	2.31	0.000	0	0.33	3	0.08	0.21
LA7618	7	3	16	0.14	1.65	2.35	0.000	0	0.00	0	0.04	0.53
LA7618	8	4	10	0.15	2.10	2.83	0.000	0	0.17	2	0.02	0.40
LA7619	5	3	4	0.21	1.83	2.60	0.000	0	4.67	47	0.02	0.20
LA7619	7	2	48	0.03	1.82	2.53	0.000	0	0.50	5	0.13	0.11
LA7619	8	2	40	0.03	1.84	2.48	0.000	0	0.17	2	0.02	0.69
LA7619	9	3	57	0.08	2.04	2.54	0.000	0	0.17	2	0.33	0.73
LA7620	5	3	18	0.06	1.50	2.10	0.000	0	2.50	25	0.09	0.25
LA7620	6	4	79	0.03	1.42	2.20	0.000	1	0.22	2	0.16	0.16
LA7620	7	3	22	0.14	1.49	2.35	0.000	0	5.33	53	0.20	0.06
LA7623	1	2	13	0.15	1.84	1.68	0.001	1	1.50	15	0.13	0.92
LA7623	2	2	13	0.15	1.84	1.68	0.004	1	2.67	27	0.06	0.80
LA7623	4	4	7	0.19	2.31	2.38	0.000	0	1.25	12	0.27	0.51
LA7623	5	3	5	0.12	2.31	2.51	0.000	0	0.50	5	0.00	0.90
LA7623	8	2	10	0.12	2.10	1.85	0.000	0	0.25	2	0.11	0.90
LA7623	9	2	26	0.03	1.92	1.49	0.001	2	1.14	11	0.13	0.86
LA7624	5	4	49	0.24	1.97	2.33	0.000	0	9.67	97	0.38	0.75
LA7624	6	3	24	0.08	2.51	3.04	0.000	0	4.00	40	0.69	0.34
LA7624	9	3	88	0.20	2.40	2.59	0.014	2	0.00	0	0.05	0.24
LA7625	5	3	9	0.17	1.73	1.58	0.024	2	8.50	85	0.47	0.69
LA7625	9	3	41	0.02	1.82	2.57	0.018	2	3.00	30	0.31	0.27
LA7626	1	2	9	0.04	2.13	1.67	0.000	0	0.00	0	0.80	0.75

Plot	Obs	RPlant	Abund	FDis	CWM		Visits		HP		CP	Seed Set
					Comp	Diam	Rate	Richness	Average	Round *10		
LA7626	2	2	12	0.03	2.16	1.69	0.042	1	0.00	0	0.49	0.83
LA7626	4	3	123	0.08	1.43	1.22	0.012	3	2.75	28	0.36	0.78
LA7626	5	3	310	0.06	1.37	1.11	0.000	0	0.25	2	0.19	0.68
LA7626	6	2	234	0.03	1.35	1.03	0.001	1	1.40	14	0.38	0.20
LA7626	8	2	59	0.09	1.72	1.30	0.000	0	4.50	45	0.16	0.75
LA7627	5	3	610	0.09	1.35	1.20	0.003	2	1.00	10	0.12	0.32
LA7627	6	3	649	0.03	1.35	1.04	0.000	0	0.11	1	0.05	0.56
LA7627	7	6	706	0.05	1.24	0.60	0.031	1	2.50	25	0.04	0.38
LA7627	9	6	66	0.16	1.12	0.58	0.031	2	1.00	10	0.03	0.21
LA7628	5	5	29	0.18	2.00	2.45	0.005	1	3.54	35	0.17	0.40
LA7628	6	3	6	0.20	1.75	2.54	0.004	1	0.00	0	0.00	0.15
LA7628	7	3	22	0.14	1.77	1.59	0.000	0	4.00	40	0.12	0.26
LA7628	9	3	29	0.20	2.54	2.79	0.000	0	2.67	27	0.23	0.48
LA7630	5	2	10	0.14	2.14	2.33	0.000	0	5.00	50	0.12	0.49
LA7631	2	4	11	0.25	2.12	2.23	0.000	0	2.00	20	0.00	0.47
LA7631	4	2	3	0.13	2.04	2.35	0.000	0	1.00	10	0.02	0.54
LA7631	6	3	9	0.23	1.84	2.58	0.022	1	0.83	8	0.01	0.26
LA7631	9	3	17	0.14	2.33	2.18	0.023	4	0.75	8	0.30	0.38
LA7632	7	2	11	0.02	1.96	1.27	0.000	0	8.67	87	0.55	0.66
LA7632	8	2	41	0.12	1.85	1.37	0.008	1	4.14	41	0.02	0.90
LA7632	9	2	88	0.01	1.89	1.13	0.005	1	2.88	29	0.36	0.48
LA7633	1	3	7	0.16	1.43	1.74	0.033	1	0.00	0	0.20	0.67
LA7633	3	2	10	0.14	1.44	2.07	0.000	0	2.33	23	0.17	0.50
LA7634	5	2	3	0.09	2.06	2.66	0.000	0	0.00	0	0.15	0.52
LA7634	6	2	9	0.03	2.22	2.93	0.000	0	0.00	0	0.50	0.22
LA7635	6	2	22	0.03	1.82	2.51	0.000	0	1.50	15	0.41	0.39

Plot	Obs	RPlant	Abund	FDis	CWM		Visits		HP		CP	Seed Set
					Comp	Diam	Rate	Richness	Average	Round *10		
LA7635	7	4	52	0.09	1.74	2.36	0.000	0	0.44	4	0.15	0.59
LA7635	8	3	46	0.08	1.78	2.44	0.000	0	0.80	8	0.09	0.52
LA7636	5	2	141	0.06	2.24	2.77	0.000	0	0.92	9	0.03	0.41
LA7636	6	3	7	0.18	1.95	2.06	0.005	2	22.33	223	0.16	0.08
LA7636	7	3	11	0.12	1.84	2.28	0.000	0	3.50	35	0.10	0.41
LA7636	8	3	56	0.18	1.88	1.81	0.004	1	27.25	272	0.08	0.40
LA7638	4	6	25	0.30	2.20	2.09	0.000	0	1.63	16	0.22	0.53
LA7638	5	4	74	0.07	1.52	2.06	0.005	3	1.72	17	0.19	0.55
LA7638	6	4	84	0.07	1.46	2.17	0.000	0	3.77	38	0.27	0.51
LA7638	7	3	32	0.24	2.08	2.56	0.001	1	9.39	94	0.27	0.27
LA7638	8	6	215	0.04	1.78	2.47	0.000	1	3.50	35	0.25	0.62
LA7638	9	5	160	0.05	1.80	2.48	0.027	2	0.63	6	0.12	0.69
LA7640	3	2	11	0.11	1.66	2.31	0.000	0	1.00	10	0.08	0.50
LA7640	4	2	8	0.14	1.68	2.24	0.000	0	2.00	20	0.11	0.59
LA7640	5	2	32	0.02	2.26	2.87	0.003	2	0.00	0	0.01	0.49
LA7640	7	2	3	0.17	1.71	2.15	0.000	0	1.00	10	0.14	0.77
LA7640	8	2	10	0.12	1.66	2.29	0.000	0	5.00	50	0.39	0.31
LA7640	9	2	15	0.25	3.15	3.85	0.016	3	2.00	20	0.07	0.74
LA7643	3	3	13	0.15	2.28	1.79	0.006	3	25.33	253	0.20	0.61
LA7643	5	2	18	0.22	2.07	2.18	0.071	1	4.50	45	0.07	0.83
LA7643	6	2	26	0.21	2.00	2.18	0.050	1	1.00	10	0.05	0.22
LA7643	8	2	15	0.15	1.75	1.82	0.000	0	2.00	20	0.01	0.08
LA7644	1	3	47	0.15	1.72	2.06	0.000	0	14.33	143	0.29	0.53
LA7644	2	3	32	0.18	1.81	1.76	0.002	1	7.33	73	0.68	0.79
LA7644	9	2	11	0.13	1.85	1.62	0.021	1	0.75	8	0.04	0.78
LA7645	5	2	13	0.15	2.33	1.96	0.000	0	5.50	55	0.04	0.33

Plot	Obs	RPlant	Abund	FDis	CWM		Visits		HP		CP	Seed Set
					Comp	Diam	Rate	Richness	Average	Round *10		
LA7645	6	2	86	0.05	2.47	2.13	0.041	2	5.67	57	0.09	0.44
LA7645	7	2	14	0.14	1.90	1.41	0.042	3	6.50	65	0.35	0.87
LA7645	9	3	27	0.02	1.97	1.22	0.011	1	21.00	210	0.68	0.58
LA7646	6	2	70	0.04	2.49	2.74	0.001	2	2.85	28	0.19	0.51
LA7646	7	3	90	0.09	2.39	2.57	0.001	1	2.71	27	0.23	0.32
LA7646	9	3	39	0.01	2.31	1.45	0.000	0	2.00	20	0.72	0.20
LA7648	4	3	7	0.21	2.57	2.58	0.010	1	8.17	82	0.28	0.30
LA7648	6	4	11	0.21	1.91	2.55	0.000	0	1.75	18	0.01	0.55
LA7648	7	4	10	0.25	2.11	2.53	0.031	1	1.75	18	0.43	0.01
LA7648	8	3	5	0.21	1.87	2.57	0.030	1	3.33	33	0.06	0.43
LA7648	9	2	9	0.25	3.50	3.88	0.007	2	2.33	23	0.18	0.49

Table S3. Data set of the species level models testing the effect of the nearby community on heterospecific pollen, conspecific pollen and seed set on the Campos Rupestres of Diamantina, Brazil. Obs is the time of observation (1 to 9). Code represents the plant species used in the study. Pip represent *Piptolepis imbricata* and Cup represent *Cuphea disperma*. RPlant is plant richness in the plot per sampling period. Abundance is the number of flowers per plot per sampling period. Cons is Conspecific floral abundance and Hete is heterospecific floral abundance. CwmD is corolla diameter average. Dist is functional distinctiveness. HP is heterospecific pollen deposition. CP is conspecific pollen deposition.

Code	Obs	Plot	RPlant	Abundance		CwmD	Dist	Visits		HP		CP	Seed Set
				Consp	Hete			Presence	Mean	Round*10			
<i>Cuphea disperma</i>	4	LA7626	3	18	105	1.22	0.29	0	2.00	20	0.30	0.55	
<i>Cuphea disperma</i>	5	LA7617	3	44	29	2.41	0.42	1	3.75	38	0.02	0.69	
<i>Cuphea disperma</i>	5	LA7618	2	12	4	2.30	0.39	1	14.00	140	0.07	0.25	
<i>Cuphea disperma</i>	5	LA7620	3	14	4	2.10	0.18	0	2.50	25	0.10	0.25	
<i>Cuphea disperma</i>	5	LA7626	3	33	277	1.11	0.28	0	0.50	5	0.18	0.36	
<i>Cuphea disperma</i>	5	LA7627	3	60	550	1.20	0.28	1	1.00	10	0.12	0.32	
<i>Cuphea disperma</i>	5	LA7628	5	6	23	2.45	0.38	0	4.00	40	0.14	0.33	
<i>Cuphea disperma</i>	5	LA7638	4	54	20	2.06	0.20	1	0.17	2	0.02	0.53	
<i>Cuphea disperma</i>	6	LA7617	3	56	14	2.12	0.29	1	1.75	18	0.07	0.63	
<i>Cuphea disperma</i>	6	LA7618	2	14	2	2.31	0.40	0	0.67	7	0.15	0.42	
<i>Cuphea disperma</i>	6	LA7620	4	73	6	2.20	0.24	1	0.67	7	0.11	0.31	
<i>Cuphea disperma</i>	6	LA7624	3	2	22	3.04	0.44	0	3.00	30	0.47	0.25	
<i>Cuphea disperma</i>	6	LA7626	2	13	221	1.03	0.28	1	1.40	14	0.38	0.20	
<i>Cuphea disperma</i>	6	LA7627	3	24	625	1.04	0.28	0	0.11	1	0.05	0.56	
<i>Cuphea disperma</i>	6	LA7631	3	6	3	2.58	0.52	0	1.67	17	0.02	0.17	
<i>Cuphea disperma</i>	6	LA7638	4	71	13	2.17	0.31	0	1.57	16	0.10	0.28	
<i>Cuphea disperma</i>	6	LA7648	4	5	6	2.55	0.36	0	0.00	0	0.02	0.38	
<i>Cuphea disperma</i>	7	LA7617	3	14	23	1.06	0.37	0	0.50	5	0.23	0.42	
<i>Cuphea disperma</i>	7	LA7618	3	4	12	2.35	0.32	0	0.00	0	0.07	0.25	
<i>Cuphea disperma</i>	7	LA7620	3	11	11	2.35	0.27	0	3.67	37	0.17	0.13	
<i>Cuphea disperma</i>	7	LA7627	6	5	701	0.60	0.30	1	2.50	25	0.04	0.38	
<i>Cuphea disperma</i>	7	LA7628	3	7	14	1.59	0.32	0	8.00	80	0.10	0.13	
<i>Cuphea disperma</i>	7	LA7638	3	11	21	2.56	0.34	0	8.67	87	0.23	0.17	
<i>Cuphea disperma</i>	8	LA7617	2	7	25	0.68	0.36	0	5.33	53	0.37	0.50	
<i>Cuphea disperma</i>	8	LA7648	3	3	2	2.57	0.44	0	8.00	80	0.05	0.25	
<i>Cuphea disperma</i>	9	LA7627	6	9	57	0.58	0.34	0	2.00	20	0.00	0.17	
<i>Piptolepis imbricata</i>	1	LA7614	4	10	13	1.75	0.22	1	4.00	40	0.08	0.93	
<i>Piptolepis imbricata</i>	1	LA7623	2	9	4	1.68	0.40	1	1.50	15	0.13	0.92	
<i>Piptolepis imbricata</i>	2	LA7614	2	2	9	2.55	0.30	1	2.00	20	0.01	0.95	
<i>Piptolepis imbricata</i>	2	LA7623	2	9	4	1.68	0.40	1	2.67	27	0.06	0.80	

Code	Obs	Plot	RPlant	Abundance		CwmD	Dist	Visits	HP		CP	Seed Set
				Consp	Hete			Presence	Mean	Round*10		
<i>Piptolepis imbricata</i>	2	LA7631	4	3	8	2.23	0.47	0	6.00	60	0.01	0.92
<i>Piptolepis imbricata</i>	3	LA7614	3	2	10	2.38	0.25	0	3.50	35	0.02	0.83
<i>Piptolepis imbricata</i>	3	LA7615	2	4	2	1.70	0.40	1	34.50	345	0.02	0.54
<i>Piptolepis imbricata</i>	4	LA7614	2	1	1	2.00	0.32	0	3.00	30	0.19	0.92
<i>Piptolepis imbricata</i>	4	LA7615	3	2	11	2.03	0.40	1	3.00	30	0.01	0.46
<i>Piptolepis imbricata</i>	4	LA7640	2	2	6	2.24	0.44	0	4.00	40	0.03	0.85
<i>Piptolepis imbricata</i>	5	LA7623	3	2	3	2.51	0.24	0	1.00	10	0.01	0.90
<i>Piptolepis imbricata</i>	5	LA7630	2	4	6	2.33	0.31	0	8.00	80	0.01	0.70
<i>Piptolepis imbricata</i>	5	LA7640	2	1	31	2.87	0.31	0	0.00	0	0.01	0.78
<i>Piptolepis imbricata</i>	6	LA7615	4	1	7	1.78	0.26	0	15.00	150	0.12	0.45
<i>Piptolepis imbricata</i>	7	LA7628	3	1	14	1.59	0.18	0	4.00	40	0.25	0.67
<i>Piptolepis imbricata</i>	7	LA7640	2	1	2	2.15	0.44	0	1.00	10	0.14	0.77
<i>Piptolepis imbricata</i>	8	LA7623	2	8	2	1.85	0.41	0	0.50	5	0.21	0.80
<i>Piptolepis imbricata</i>	8	LA7640	2	2	8	2.29	0.44	0	6.00	60	0.12	0.62
<i>Piptolepis imbricata</i>	9	LA7623	2	25	1	1.49	0.40	1	1.14	11	0.13	0.86
<i>Piptolepis imbricata</i>	9	LA7628	3	4	25	2.79	0.36	0	1.00	10	0.28	0.88
<i>Piptolepis imbricata</i>	9	LA7631	3	12	5	2.18	0.44	1	1.50	15	0.05	0.75

Efeito da vizinhança na *Lantana hypoleuca*

Supplementary Material S1. Visitation to *Lantana hypoleuca* flowers during the observation sessions. Plot is the focal *L. hypoleuca*. Date is the month/day of observation. Flower number is the number of flowers in the focal *L. hypoleuca*. Visitor is the identity of the visitor. NA represents the absence of visitors.

Plot	Date	Flower Number	Visitor
P01	11/10	3	NA
	11/17	2	NA
P02	10/27	2	NA
P03	10/27	37	<i>Apis mellifera</i>
	11/05	14	NA
	11/10	4	NA
P04	10/27	13	NA
	11/05	2	Butterfly
			Butterfly
	11/18	2	NA
P05	10/27	48	Bees
			Bees
			Bees
			Bees
			Bees
			Bees
			Bees
	11/17	47	Bees
			Butterfly
			Bees
	11/18	43	Bees
P07	10/25	4	<i>Apis mellifera</i>
	11/18	3	Bees
	11/19	3	NA
P08	10/25	285	<i>Apis mellifera</i>
			Butterfly
	11/18	6	NA
	11/19	5	NA
P09	10/25	4	NA
	11/18	4	NA
	11/19	2	NA
P10	10/27	95	<i>Apis mellifera</i>
			<i>Xylocopa</i> sp
			<i>Apis mellifera</i>
	11/19	5	NA
P11	10/25	200	Bees
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
	11/18	22	Butterfly
	11/19	14	NA
P12	10/25	4	NA
	11/03	2	NA
	11/11	2	NA
P13	10/25	18	Butterfly
			<i>Apis mellifera</i>
	11/03	15	<i>Apis mellifera</i>
	11/03	1	<i>Apis mellifera</i>
	11/18	4	NA
P15	10/27	63	<i>Apis mellifera</i>
	11/05	32	Bees
			Bees

Plot	Date	Flower Number	Visitor
	11/17	16	Butterfly
			Bees
P16	10/27	4	NA
	11/05	9	NA
P17	10/27	152	<i>Trigona</i> sp
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			Butterfly
	11/03	94	<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			Butterfly
	11/17	8	NA
P18	10/27	12	Bees
	10/27	12	Bees
			Bees
			Bees
			Bees
	11/18	3	<i>Bombus</i> sp
	11/19	2	Butterfly
P19	10/27	420	<i>Xylocopa</i> sp
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
	11/18	13	NA
	11/19	15	Bees
P20	10/27	31	NA
	11/18	12	Butterfly
			Bees
	11/19	11	Wasp
P21	10/26	86	NA
			Bees
	11/10	101	Butterfly
			Butterfly
			Bees
	11/17	41	<i>Apis mellifera</i>
			Bees
P22	10/27	126	<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			<i>Apis mellifera</i>
			Bees
			Wasp
			<i>Apis mellifera</i>
	11/18	11	NA
	11/19	6	NA

Supplementary Material S2: Matrix with the abundance of plant species (Code) on each plot. Code is the same code of Table 1.

[illegible]

Supplementary Material S3. Conspecific and heterospecific pollen found in each stigma of *L. hypoleuca*. Plot represent the focal *L. hypoleuca* and n represent each of the stigmas collected.

Plots	Pollen		Fruit	Buds
	Conspecific	Heterospecific		
P01	139	94	12	18
	153	42		
P02	23	0	3	15
	129	21		
P03	92	35	6	8
	27	32	8	13
	30	58		
P04	106	74	15	17
	137	5	9	28
P05	76	44	5	11
	199	40	12	13
P07	63	9	1	8
	29	4		
P08	24	9	4	14
			3	10
P09	67	0	8	12
	105	8		
P10	109	52	6	12
	19	0		
P11	28	4	11	22
	59	0		
P12	24	0	5	15
	92	26		
P13	37	9	12	19
	54	14		
P15	54	22	4	13
	185	146		
P16	58	7	9	15
	11	0		
P17	123	23	12	18
	76	0		
P18	31	24	8	12
	76	11		
P19	8	0	4	18
	82	8	2	8
	33	0		
P20	98	13	7	10
	123	27		
P21	59	35	17	22
	68	6		
P22	26	0	3	14
	80	13	8	9
			19	28

Supplementary Material S5. Data set of the model to investigate the effect of community context on pollen deposition and on fruit set. Plot is the focal *L. hypoleuca*. CPD is conspecific pollen deposition. HPD and log(HPD) is heterospecific pollen deposition and its respective log transformation. CFA is conspecific floral abundance and HFA is heterospecific floral abundance. Richness is the plant species richness. Morphology is the similarity in corolla length of *L. hypoleuca* in relation to other plant species.

Plot	Fruit	Buds	CPD	HPD	log(HPD)	CFA	HFA	Richness	Morphology
P01	12	18	146.00	68.00	4.22	16.50	35.00	4.50	0.34
P02	3	15	76.00	10.50	2.35	6.00	3.00	2.00	0.00
P03	14	21	49.67	41.67	3.73	18.33	12.33	3.00	0.61
P04	24	45	121.50	39.50	3.68	5.67	6.00	1.67	-1.33
P05	17	24	137.50	42.00	3.74	46.00	16.33	3.00	0.50
P07	1	8	46.00	6.50	1.87	61.00	7.67	1.67	0.73
P08	7	24	24.00	9.00	2.20	122.67	61.67	3.67	0.66
P09	8	12	86.00	4.00	1.39	3.33	15.67	2.33	0.47
P10	6	12	64.00	26.00	3.26	125.00	15.00	2.50	0.86
P11	11	22	43.50	2.00	0.69	105.33	6.67	1.67	0.59
P12	5	15	58.00	13.00	2.56	16.33	5.00	3.00	-0.33
P13	12	19	45.50	11.50	2.44	77.33	6.33	2.00	0.66
P15	4	13	119.50	84.00	4.43	85.33	2.67	3.00	0.58
P16	9	15	34.50	3.50	1.25	18.00	11.50	3.00	-1.05
P17	12	18	99.50	11.50	2.44	155.00	6.00	3.00	0.61
P18	8	12	53.50	17.50	2.86	9.33	6.00	2.67	-0.29
P19	6	26	41.00	2.67	0.98	198.00	9.00	2.67	-0.17
P20	7	10	110.50	20.00	3.00	62.00	7.00	2.67	0.09
P21	17	22	63.50	20.50	3.02	86.67	16.00	4.33	0.18
P22	30	51	53.00	6.50	1.87	47.67	1.33	2.33	0.50