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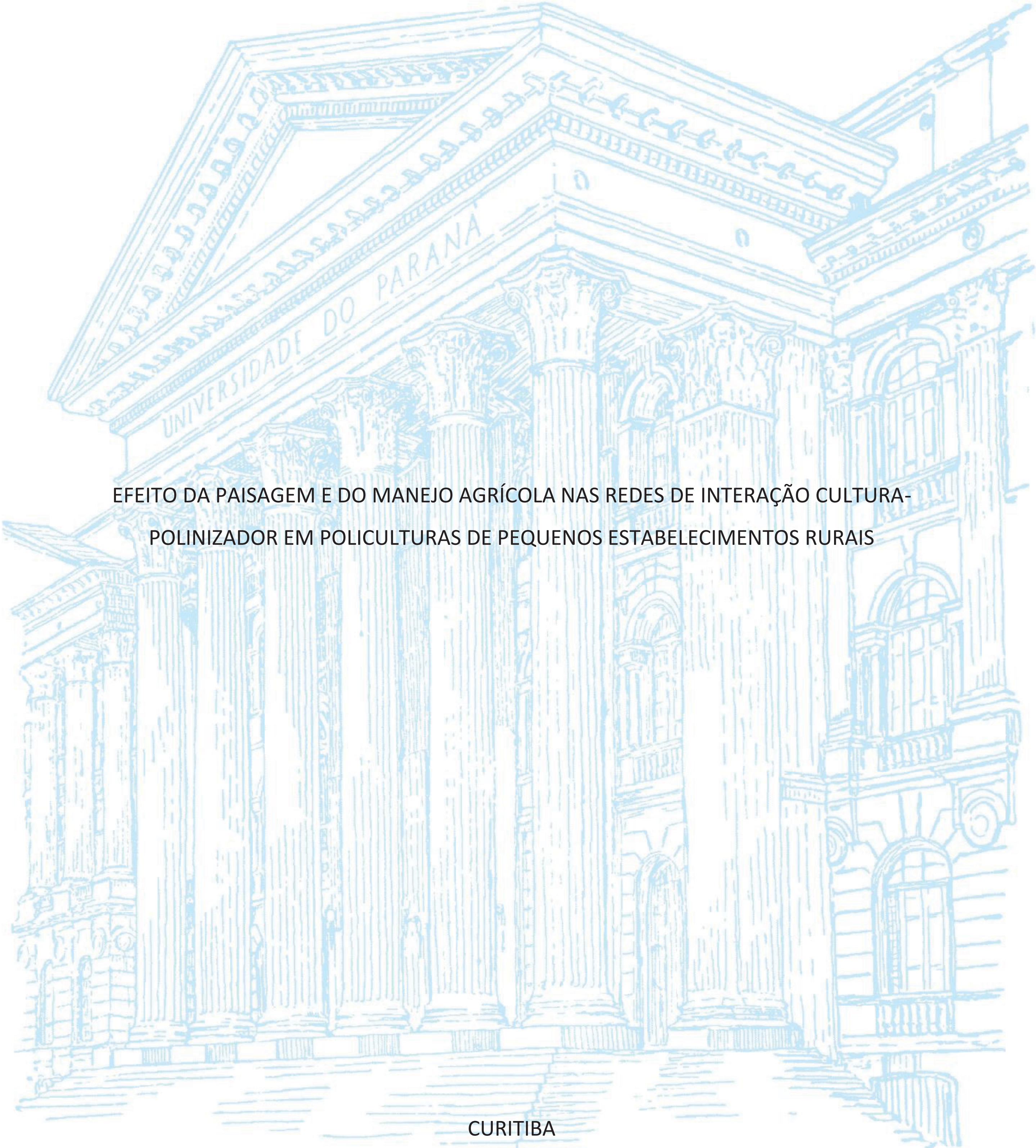
FERNANDO FORTUNATO JERONIMO



EFEITO DA PAISAGEM E DO MANEJO AGRÍCOLA NAS REDES DE INTERAÇÃO CULTURA-POLINIZADOR EM POLICULTURAS DE PEQUENOS ESTABELECIMENTOS RURAIS

CURITIBA

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Tese apresentada ao Programa de Pós-graduação em Botânica, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Botânica.

Orientadora: Isabela Galarda Varassin

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação BOTÂNICA da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **FERNANDO FORTUNATO JERONIMO**, intitulada: **Efeito da paisagem e do manejo agrícola nas redes de interação cultura-polinizador em policulturas de pequenos estabelecimentos rurais**, sob orientação da Profa. Dra. ISABELA GALARDA VARASSIN, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 25 de Abril de 2025.

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ISABELA GALARDA VARASSIN
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Café (1935)

Cândido Portinari

Dedico este trabalho a todos os homens e mulheres da agricultura familiar.

A verdadeira força de trabalho que alimenta o Brasil.

Fazer ciência é um desafio colossal que exige muita dedicação e muita renúncia. Fazer um doutorado é um desafio particularmente difícil dentro da carreira científica. Para ousar transpor algum paradigma científico, por um milímetro que seja, é necessário trabalho árduo e incessante. É uma jornada que nos impõe dor e introspecção, e, às vezes, também sofrimento e solidão. Apesar disso, tenho a sorte de poder dizer que, em poucas vezes nessa minha jornada, essa dor se transformou em sofrimento. Quando isso aconteceu, eu não estava sozinho. Nos momentos em que me afundei nas minhas próprias ideias, fui confrontado e resgatado por novas e brilhantes ideias vindas de pessoas brilhantes. É por isso que, nesta seção, agradeço às pessoas que me ajudaram nessa jornada; afinal de contas, fazer ciência é um ato coletivo. Este trabalho é fruto de muita orientação, mentoria, colaboração, parceria, amizade, cuidado e amor. Ele se manifestou pelas minhas mãos e tem minha autoria, mas foi feito com ideias, trabalho e apoio de muitas pessoas. Pessoas que foram o veículo da realização de um sonho e que representam o maior ganho pessoal que tive com este trabalho.

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***

Diante da vastidão do tempo e da imensidão do universo, é um imenso prazer para mim dividir um planeta e uma época com vocês.

Adaptado de Cosmos (1980)

Carl Sagan

Debulhar o trigo
Recolher cada bago do trigo
Forjar no trigo o milagre do pão
E se fartar de pão

Decepar a cana
Recolher a garapa da cana
Roubar da cana a doçura do mel
Se lambuzar de mel

Afagar a terra
Conhecer os desejos da terra
Cio da terra, a propícia estação
E fecundar o chão

O cio da terra (1977)
Chico Buarque & Milton Nascimento

RESUMO

A polinização biótica é um dos serviços ecossistêmicos mais valiosos para a agricultura, aumentando a qualidade e a quantidade da produção. No entanto, esse serviço está ameaçado por mudanças ambientais intensas, especialmente pela conversão da cobertura e uso do solo decorrentes da intensificação agrícola. O uso intensivo do solo impacta os ecossistemas em diferentes escalas, promovendo a simplificação ecológica que desencadeia a perda da biodiversidade e da funcionalidade ecossistêmica. Polinizadores essenciais, como as abelhas, têm acesso reduzido a recursos e habitats, comprometendo sua riqueza e interações. A perda dessas interações ameaça o serviço de polinização, colocando em risco a produção agrícola e a segurança alimentar. Nesta tese, investigamos como a agricultura, em diferentes escalas, afeta as redes de interação cultura-polinizador. Analisamos variáveis emergentes no entorno dos estabelecimentos agrícolas (estrutura da paisagem e configuração florestal) e na área interna dos estabelecimentos (complexidade do uso da terra e heterogeneidade do cultivo). Avaliamos seus efeitos sobre a composição (índices de β-diversidade de interações: β_{WS}, β_{ST}, β'_{OS} e $\beta_{ST.h}$; Capítulo I), estrutura (métricas de topologia: assimetria, conectância, modularidade, aninhamento e especialização; Capítulo II) e robustez (computada em diferentes cenários de extinção; Capítulo III) das redes formadas por culturas e abelhas polinizadoras. Nós coletamos os dados de interação em 15 estabelecimentos agrícolas familiares com plantio de policulturas manejadas de forma convencional ou orgânica (São José dos Pinhais, Paraná, Brasil). Ao todo analisamos 6571 interações entre 26 espécies de culturas e 103 espécies de abelhas. Nossos resultados indicam que as redes cultura-polinizador são afetadas tanto em escala regional quanto local, mas os efeitos mais evidentes emergem na escala local. Isso reforça o papel central do produtor na conservação das interações de polinização, pois suas decisões de manejo afetam diretamente essas interações. Todas as variáveis analisadas influenciaram pelo menos um aspecto das redes, evidenciando a natureza multicausal e complexa dos efeitos da agricultura sobre a biodiversidade e as interações ecológicas. A eficácia das medidas locais depende de um contexto paisagístico favorável, demandando mobilização comunitária e políticas públicas para preservar os serviços ecossistêmicos. Assim, ações para a conservação da polinização, essencial para a segurança alimentar, deve considerar múltiplas escalas e envolver diversos atores sociais, desde produtores rurais até formuladores de políticas ambientais.

Palavras-chave: agricultura sustentável, cobertura e uso do solo, polinização agrícola, segurança alimentar, serviços ecossistêmicos.

ABSTRACT

Biotic pollination is one of the most valuable ecosystem services for agriculture, increasing both the quality and quantity of production. However, this service is threatened by intense environmental changes, particularly by land cover and land use conversion resulting from agricultural intensification. Intensive land use impacts ecosystems at different scales, promoting ecological simplification that triggers biodiversity loss and ecosystem functionality decline. Essential pollinators, such as bees, have reduced access to resources and habitats, compromising their richness and interactions. The loss of these interactions threatens pollination services, endangering agricultural production and food security. In this thesis, we investigate how agriculture, at different scales, affects aspects of crop-pollinator interaction networks. We analysed emerging variables in the surroundings of farms (landscape structure and forest configuration) and within farms (farm complexity and crop heterogeneity). We assessed their effects on the composition (interaction β-diversity indices: β_{WS}, β_{ST}, β'_{OS} and $\beta_{ST.h}$; Chapter I), structure (network topology metrics: asymmetry, connectance, modularity, nestedness and specialisation; Chapter II), and robustness (under different extinction scenarios; Chapter III) of networks formed between crops and pollinating bees. We collected interaction data in 15 smallholder farms with polyculture systems managed conventionally or organically (São José dos Pinhais, Paraná, Brazil). In total, we analysed 6571 interactions among 26 crop species and 103 bee species. Our results indicate that crop-pollinator networks are affected both at regional and local scales, but the strongest effects emerge at the local scale. This reinforces the central role of farmers in pollination interaction conservation, as their management decisions directly affect these interactions. All analysed variables influenced at least one aspect of the networks, highlighting the multicausal and complex nature of agricultural impacts on biodiversity and ecological interactions. The effectiveness of local measures depends on a favourable landscape context, requiring community engagement and public policies to preserve ecosystem services. Thus, actions to conserve pollination, essential for food security, must consider multiple scales and involve a range of social actors, from farmers to environmental policymakers.

Keywords: agricultural pollination, ecosystem services, food security, land cover and land use, sustainable agriculture.

RESUMEN

La polinización biótica es uno de los servicios ecosistémicos más valiosos para la agricultura, aumentando la calidad y la cantidad de la producción. Sin embargo, este servicio está amenazado por cambios ambientales intensos, especialmente por la conversión de la cobertura y el uso del suelo resultantes de la intensificación agrícola. El uso intensivo del suelo impacta los ecosistemas a diferentes escalas, promoviendo la simplificación ecológica que desencadena la pérdida de biodiversidad y funcionalidad ecosistémica. Polinizadores esenciales, como las abejas, tienen acceso reducido a recursos y hábitats, comprometiendo su riqueza e interacciones. La pérdida de estas interacciones amenaza el servicio de polinización, poniendo en riesgo la producción agrícola y la seguridad alimentaria. En esta tesis, investigamos cómo la agricultura, en diferentes escalas, afecta las redes de interacción cultivo-polinizador. Analizamos variables emergentes en el entorno de las granjas (estructura del paisaje y configuración forestal) y en el área interna de las granjas (complejidad del uso del suelo y heterogeneidad de los cultivos). Evaluamos sus efectos sobre la composición (índices de β-diversidad de interacciones: β_{WS}, β_{ST}, β'_{OS} y $\beta_{ST.h}$; Capítulo I), estructura (métricas de topología de red: asimetría, conectancia, modularidad, anidamiento y especialización; Capítulo II), y robustez (bajo diferentes escenarios de extinciones; Capítulo III) de las redes formadas entre cultivos y abejas polinizadoras. Recopilamos los datos de interacción en 15 granjas familiares con cultivo de policultivos manejados de forma convencional u orgánica (São José dos Pinhais, Paraná, Brasil). En total, analizamos 6571 interacciones entre 26 especies de cultivos y 103 especies de abejas. Nuestros resultados indican que las redes cultivo-polinizador son afectadas tanto a escala regional como local, pero los efectos más evidentes emergen a escala local. Esto refuerza el papel central del productor en la conservación de las interacciones de polinización, ya que sus decisiones de manejo afectan directamente estas interacciones. Todas las variables analizadas influyeron en al menos un aspecto de las redes, evidenciando la naturaleza multicausal y compleja de los efectos de la agricultura sobre la biodiversidad y las interacciones ecológicas. La eficacia de las medidas locales depende de un contexto paisajístico favorable, lo que exige una movilización comunitaria y políticas públicas para preservar los servicios ecosistémicos. Así, las acciones para conservar la polinización, esencial para la seguridad alimentaria, deben considerar múltiples escalas e involucrar a diversos actores sociales, desde agricultores hasta responsables de políticas ambientales.

Palabras clave: agricultura sostenible, cobertura y uso del suelo, polinización agrícola, seguridad alimentaria, servicios ecosistémicos.

SUMÁRIO

1. INTRODUÇÃO GERAL

A polinização representa um dos serviços ecossistêmicos mais importantes para a agricultura, atividade essencial para a sociedade humana. Considerado um serviço de provisão, a polinização incrementa a produtividade de cerca de 75 % das culturas destinadas ao consumo humano (Klein et al., 2007). Esse incremento é proveniente da melhora da produção, tanto em termos quantitativos (e.g., taxa de produção de frutos, taxa de produção de sementes – Garibaldi et al., 2013), quanto qualitativos (e.g., melhora a aparência, aumento a vida de prateleira – Classen et al., 2014; Klatt et al., 2014). Além disso, estima-se que cerca de 90 % das angiospermas dependam da polinização biótica para a reprodução (Ollerton et al., 2011; Tong et al., 2023). Portanto, também contribui indiretamente com a agricultura ao desempenhar papel fundamental na manutenção da estrutura vegetal natural, que regula, direta ou indiretamente, outros serviços ecossistêmicos para a agricultura como controle de pragas, regulação de microclima e formação de solo (Kremen and Merenlender, 2018; Potts et al., 2016; Tscharntke et al., 2012a).

O Brasil é um dos maiores produtores e exportadores de produtos agropecuários do planeta, e estima-se que o país produza alimento para 800 milhões de pessoas, equivalente a 10% da população global (Guaraldo, 2021; OECD e FAO, 2015). Portanto, no contexto brasileiro, o serviço de polinização tem um papel central tanto para a economia interna quanto para a segurança alimentar nacional e global. Das culturas produzidas no Brasil para as quais é possível inferir a dependência da polinização, 77 % apresentam algum tipo de dependência da polinização. 32 % são consideradas essencialmente dependentes, ou seja, não produzem sem esse serviço. Com isso, estima-se que o valor de contribuição da polinização para a agricultura seja de 43 bilhões de reais/ano. Deste número impressionante, 72 % da sua composição vem da produção de soja e café, culturas consideradas apenas moderadamente dependentes da polinização (BPBES e REBIPP, 2019).

Dentre os agentes de polinização biótica, destacam-se as abelhas. Estudos revelam que elas são responsáveis pela polinização de 73 % das culturas globais (Klein et al., 2007). A importância das abelhas na polinização emerge de sua história evolutiva, intimamente ligada à diversificação das angiospermas (Cardinal e Danforth, 2013). Essa importância não emerge de uma relação coevolutiva estrita, par a par, mas justamente da flexibilidade dessa interação mutualística (Ollerton, 2017). Existem fortes evidências de que a polinização é mais eficiente quando realizada por uma maior riqueza de espécies de abelhas (Garibaldi et al., 2013). Além disso, o aumento da diversidade funcional (Martins et al., 2015) e filogenética (Grab et al., 2019) das abelhas também amplifica os efeitos positivos da polinização para a produção agrícola. Esse contexto da polinização também é particularmente interessante para o Brasil, que abriga aproximadamente 1700 espécies de abelhas, a maior diversidade do grupo no planeta (Moure et al., 2007), apresentando, portanto, o maior potencial desse serviço .

Apesar da sua evidente importância para a humanidade, as abelhas e o serviço que elas provêm estão ameaçados pelas intensas mudanças ambientais do Antropoceno (Potts et al., 2016). Dentre as causas da perda da biodiversidade de polinizadores, destaca-se a conversão da cobertura e do uso do solo (Sánchez-Bayo and Wyckhuys, 2019; Tscharntke et al., 2012b). Essa conversão é caracterizada pela intensa e abrupta transformação de áreas de vegetação natural em áreas urbanas e agropecuárias, que geralmente acarreta na homogeneização da paisagem em ampla escala (Tscharntke et al., 2012b). Por sua vez, a homogeneização da paisagem é vinculada à simplificação ecológica das paisagens, desencadeando a redução ou perda da funcionalidade ecossistêmica (Foley et al., 2005). A perda de funcionalidade está diretamente atrelada à redução e perda de habitats e recursos para as espécies e comunidades provedoras dos serviços ecossistêmicos, como as abelhas (Kennedy et al., 2013).

A intensificação da agricultura, iniciada durante a chamada Revolução Verde (ou terceira revolução agrícola), é tida como a principal causa da simplificação das paisagens e da consequente perda da diversidade de polinizadores (Sánchez-Bayo e Wyckhuys, 2019). Em escala local, o plantio de monoculturas proporciona uma drástica redução na diversidade de recursos florais para os polinizadores (Kennedy et al., 2013). Adicionalmente, o uso de pesticidas inseticidas neurotóxicos não específicos não atinge apenas as pragas agrícolas, mas também as abelhas (Goulson et al., 2015; Sponsler et al., 2023). Além disso, pesticidas herbicidas, além de reduzirem a diversidade de recursos florais ao dizimarem plantas daninhas e plantas ruderais, podem ser incorporados nos produtos coloniais das abelhas (Goulson et al., 2015; Krupke et al., 2012; Sponsler et al., 2023). Ainda, práticas como a apicultura e a meliponicultura promovem a inserção de espécies exóticas que acirram a competição por recursos e podem transmitir parasitas e patógenos (Mallinger et al., 2017).

Apesar de um panorama geral de agricultura intensiva, sistemas mais sustentáveis voltados à intensificação ecológica dos sistemas agrícolas (e.g., sistemas agroflorestais, de integração lavoura-pecuária-floresta, orgânicos) se apresentam como alternativa para se alcançar segurança alimentar, agregando aspectos econômicos e socioambientais (Bommarco et al., 2013). Como alteram menos a paisagem e conservam mais diversidade nativa, estabelecimentos com manejo sustentável são notadamente mais benéficos para as abelhas e outras espécies provedoras de serviços ecossistêmicos (Kleijn et al., 2019). Portanto, em regra, são as que recebem maior aporte de serviços ecossistêmicos como a polinização (Bommarco et al., 2013; Dainese et al., 2019; Kleijn et al., 2019). Isso põe este tipo de manejo como central para a conservação da diversidade de polinizadores e da polinização e para a segurança alimentar humana a longo prazo (Bommarco et al., 2013).

Dado esse contexto, em que a agricultura é praticada em um gradiente de intensidade de manejo que afeta a biodiversidade de diferentes formas, as policulturas de pequeno porte representam um ambiente com enorme potencial para aliar produção e conservação (Bloom et al., 2023; Happe et al., 2018; Touch et al., 2024). Estabelecimentos com esse perfil podem atuar como fontes de polinizadores para sistemas mais simplificados, especialmente quando é aplicado o manejo orgânico, promovendo o serviço de polinização tanto interna quanto externamente (Happe et al., 2018). Na mesma medida em que esses estabelecimentos podem ser usados como ferramentas de manejo para a promoção dos serviços ecossistêmicos, são também os que, proporcionalmente, mais tendem a se beneficiar dos bens e valores promovidos por esses serviços (Bloom et al., 2023; Touch et al., 2024).

No contexto brasileiro, as unidades familiares de produção agrária adotam majoritariamente sistemas de policultura em pequenos estabelecimentos. Elas correspondem a 78% dos estabelecimentos agropecuários e geram 23% do valor bruto da produção nacional, mesmo ocupando apenas 23% da área produtiva do país (IBGE, 2017). Esses estabelecimentos respondem por parte significativa da produção de importantes commodities, além de leguminosas, hortaliças e frutos consumidos diariamente, os quais dependem da polinização (BPBES and REBIPP, 2019; IBGE, 2017). Apesar da relevância desse sistema, especialmente em países de economia emergente, não identificamos, ao longo deste trabalho, estudos que abordem interações em sistemas de policultura compostos apenas por plantas cultiváveis. Assim, pouco se sabe sobre os riscos e oportunidades que esses sistemas representam para a conservação do serviço de polinização e seus impactos na segurança alimentar e socioeconômica dos produtores. Tradicionalmente, os estudos sobre polinização focam nas monoculturas de commodities (e.g., Classen et al., 2014) ou analisam redes de interação que misturam plantas cultiváveis e espécies ruderais (e.g., Morrison et al., 2020), mas não exclusivamente nas policulturas.

Os efeitos da agricultura sobre a diversidade de abelhas não se restringem apenas à dimensão taxonômica. Além da redução na riqueza de espécies de abelhas, há evidências de alterações nas diversidades funcional (Coutinho et al., 2021) e filogenética das abelhas (Grab et al., 2019). A redução da diversidade das abelhas em suas diferentes dimensões afeta, em última instância, suas interações com as plantas (Bascompte e Jordano, 2007; Olesen et al., 2007). Inclusive, essas interações tendem a ser extintas de forma insidiosa, antes mesmo de as espécies envolvidas desaparecerem do ambiente (Janzen, 1974). Por isso, é fundamental compreender como as redes de interação se comportam dentro dos sistemas agrícolas em seus diferentes níveis de intensidade (Tylianakis et al., 2010). A extinção dessas interações, mesmo diante da persistência residual das espécies de polinizadores no ambiente, representa a redução ou perda do serviço de polinização, comprometendo, portanto, a produção agrícola (Valiente-Banuet et al., 2015).

As interações mutualísticas são um objeto de estudo complexo, pois além de dependerem de dinâmicas ecológicas das espécies interagentes, as interações *per se* apresentam as suas próprias dinâmicas (Bascompte e Jordano, 2007). Não basta apenas a obrigatória coexistência espacial e temporal das espécies interagentes para que ela ocorra. Para ocorrer, as interações também demandam uma série de outros ajustes ecológicos entre as espécies: fenologia, morfologia, demografia, comportamento, disponibilidade de habitat, disputa de recursos e outras interações paralelas (Ollerton, 2017). Portanto as interações são sensíveis a gradientes ambientais em diferentes intensidades e dependentes da matriz da paisagem (Tylianakis e Morris, 2017). Compreender em completude como as interações, especialmente a polinização, se comportam nos sistemas agrícolas é, portanto, fundamental. Primeiro porque a produção agrícola depende deste serviço (Klein et al., 2007); segundo porque a conservação deste serviço é imperativa para a saúde da economia e da segurança alimentar do Brasil (BPBES and REBIPP, 2019; Giannini et al., 2015).

1.1. OBJETIVOS

1.1.1. Gerais

O objetivo geral desta tese é compreender como o manejo agrícola, em suas diferentes escalas: paisagem e manejo local, afeta as interações entre as culturas e seus polinizadores. Para se ter uma observação deste sistema, nós analisamos redes de polinização compostas exclusivamente por plantas agriculturáveis e abelhas, que são os principais agentes polinizadores nos sistemas agrícolas. Para obter um gradiente de agricultura mais evidente, optamos por trabalhar com estabelecimentos de pequeno porte, classificados como unidades familiares de produção agrária (IBGE, 2017), inseridos numa matriz também dominada por este tipo de estabelecimentos. Neste porte, a agricultura tende a ser mais diversa em termos de produção, com estabelecimentos voltados para a produção comercial e de subsistência. Portanto, geralmente mesclam a produção de commodities ou frutos preferenciais com a produção de hortaliças e outros grupos de culturas. Também é evidente um gradiente de manejo, que vão desde estabelecimentos convencionais e mais mecanizadas até aquelas com manejos menos intensivo e ecologicamente intensivas (IBGE, 2017).

Para compreender as diferentes escalas do efeito da agricultura sobre a polinização nós trabalhamos com variáveis sintéticas construídas em dois níveis: no entorno dos estabelecimentos, que denominamos escala de paisagem; dentro do limite imediato dos estabelecimentos, que denominamos com escala do estabelecimento ou manejo local. Na escala de paisagem, trabalhamos com as variáveis: estrutura da paisagem (*landscape structure*) e configuração florestal (*forest configuration*), com as quais buscamos acessar mecanismos regionais, promovidos ou afetados pelo contexto agrícola da região, que afetam a diversidade de interações. Na escala do estabelecimento, trabalhamos com as variáveis: complexidade do estabelecimento (*farm complexity*) e heterogeneidade do cultivo (*crop heterogeneity*), com as quais buscamos acessar mecanismos locais, de manejo mais direto dos estabelecimentos rurais, que afetam a diversidade de interações. Com a construção destas variáveis buscamos sintetizar aspectos da composição e da configuração espacial dos elementos naturais e seminaturais presentes nas duas escalas de observação (Figura 1, Caixa 1). Portanto, cada uma destas variáveis representa uma "meta-métrica", que sumarizam as diferentes nuances que compõem o gradiente ambiental em sistemas agrícolas.

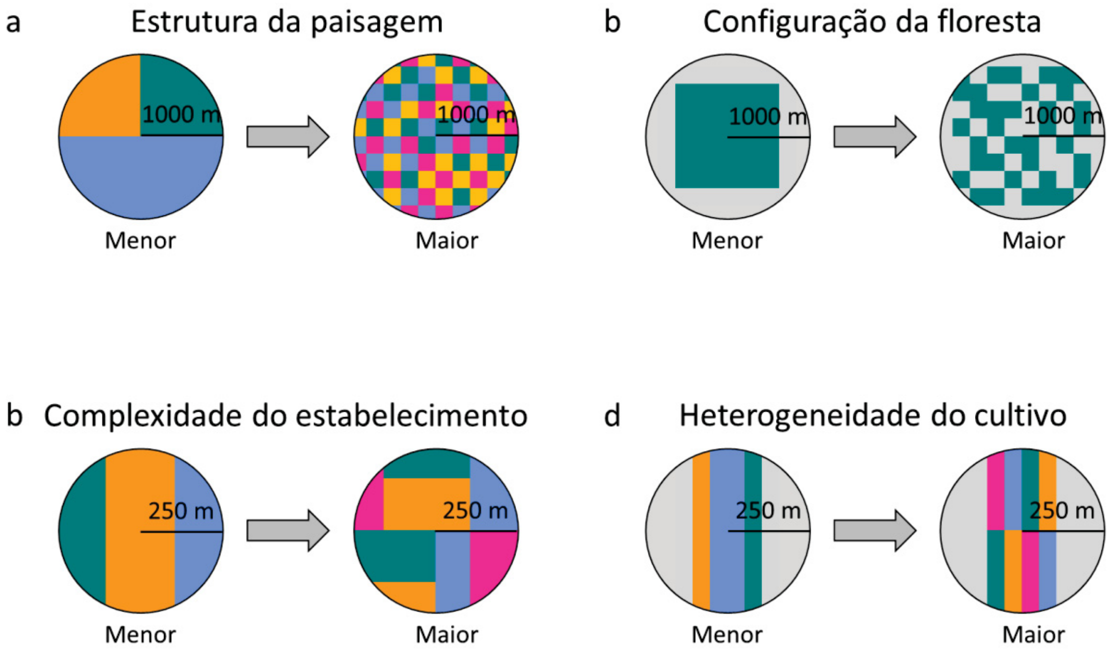


Figura 1 Interpretação visual das variáveis sintéticas utilizadas como preditoras nos três capítulos desta tese (ver também Quadro 1). a: O aumento do valor da estrutura da paisagem representa um incremento em conjunto em métricas que quantificam a complexidade da composição e da configuração das classes de paisagem. Isso implica a presença de mais classes organizadas espacialmente de forma mais complexa, resultando em uma paisagem com aparência de mosaico aleatório. b: O aumento da configuração da floresta representa um incremento em métricas que quantificam a complexidade da configuração da classe de formação florestal. Em geral, isso se traduz em fragmentos menores, distribuídos de maneira espacialmente mais complexa, gerando uma paisagem com vegetação mais fragmentada. c: O aumento da complexidade do estabelecimento representa um incremento em conjunto em métricas que quantificam a complexidade da composição e da configuração das classes presentes no estabelecimento. Esse padrão indica uma maior variedade e intercalação de elementos de diferentes classes de cultivos e outros elementos naturais e antrópicos, resultando em um estabelecimento menos setorizado. d: O aumento da heterogeneidade do cultivo representa um incremento em conjunto em métricas que quantificam a complexidade da composição e da configuração das classes de culturas presentes nos estabelecimentos. Esse aumento está associado à maior riqueza e equitabilidade das culturas, levando à imagem de um cultivo mais diversificado e com organização mais complexa dos talhões de cultivo.

Caixa 1 – Detalhamento das variáveis preditoras

As quatro variáveis utilizadas como preditoras nesta tese são variáveis sintéticas, que correspondem ao primeiro eixo principal obtido em uma análise de componentes principais (mais detalhes em Métodos e Material Suplementar do Capítulo I).

Para a obtenção da estrutura da paisagem (Figura 1a) e da configuração da floresta (Figura 1b), utilizamos um raster de classificação de cobertura e uso do solo (MapBiomas, 2023), com raio de 1000 m a partir do centróide dos estabelecimentos. Para a estrutura da paisagem, as variáveis de entrada foram métricas de paisagem computadas no nível de paisagem e que quantificam a composição e configuração da paisagem, considerando todas as classes de paisagem presentes no buffer analisado (e.g., riqueza de manchas, que quantifica o número de classes presentes na paisagem, e entropia condicional, que quantifica a complexidade da configuração da paisagem). Para a configuração da floresta, as variáveis de entrada foram métricas de paisagem computadas no nível de classe e que quantificam a configuração da classe de Formação Florestal (e.g., percentual de paisagem da classe, que quantifica o percentual da paisagem ocupado por florestas).

Para a obtenção da complexidade do estabelecimento (Figura 1c) e da heterogeneidade do cultivo (Figura 1d), utilizamos um raster de classificação de cobertura e uso do solo feito manualmente no desenvolvimento deste trabalho (ver Capítulo I), com raio de 250 m a partir do centróide dos estabelecimentos. Para a complexidade do estabelecimento, as variáveis de entrada foram métricas de paisagem computadas no nível de paisagem e que quantificam a composição e configuração do estabelecimento, considerando todas as classes de paisagem presentes no buffer analisado (e.g., densidade de manchas, que quantifica a densidade de manchas de todas as classes no estabelecimento). Por fim, para a heterogeneidade do cultivo, as variáveis de entrada foram métricas de paisagem computadas no nível de paisagem e que quantificam a composição e configuração do estabelecimento, considerando apenas as classes correspondentes às culturas amostradas (e.g., índice de diversidade de Shannon, que quantifica a diversidade de culturas produzidas no estabelecimento).

1.2.3. Específicos

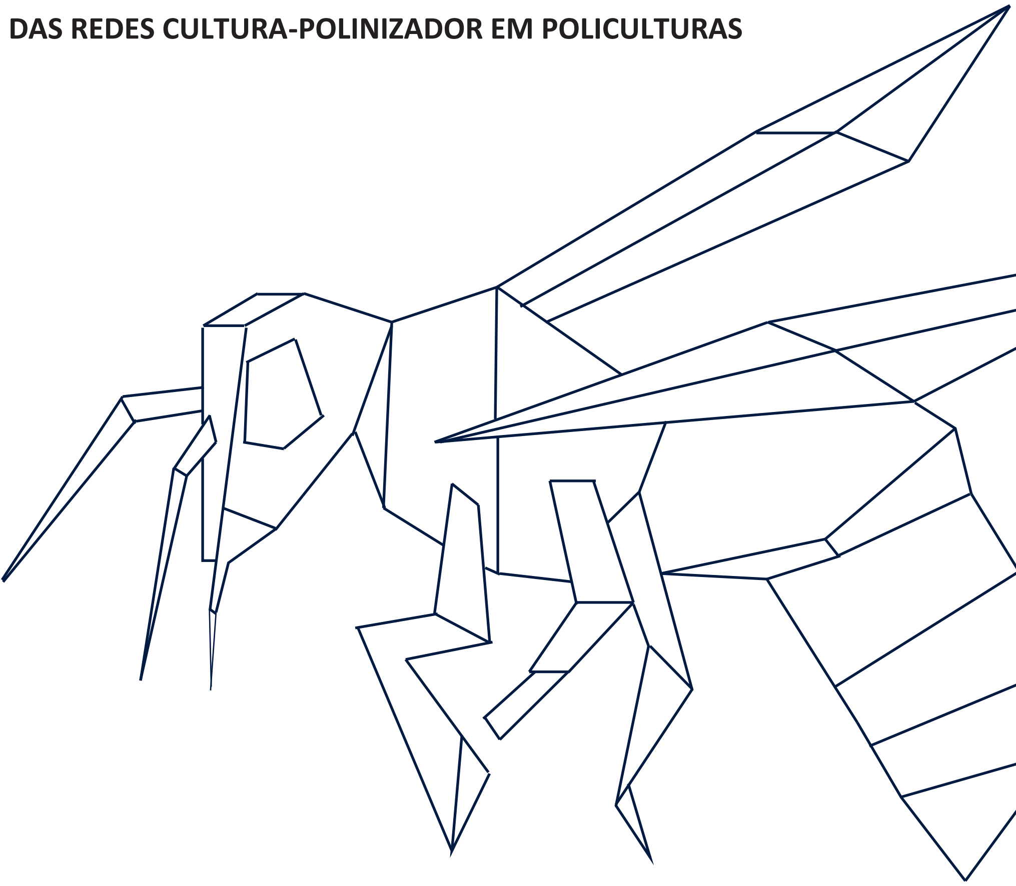
Em cada capítulo nós buscamos observar o efeito destas quatro métricas (estrutura da paisagem, configuração florestal, complexidade do estabelecimento e heterogeneidade do cultivo, em diferentes aspectos das redes cultura-polinizador: composição (Capítulo I); estrutura (Capítulo II); e robustez (Capítulo III). Portanto, cada capítulo foi desenvolvido de forma independente, mas buscando uma construção integrada dos conhecimentos desenvolvidos em cada um. Em cada um deles apresentamos um manuscrito em versão pré-submissão.

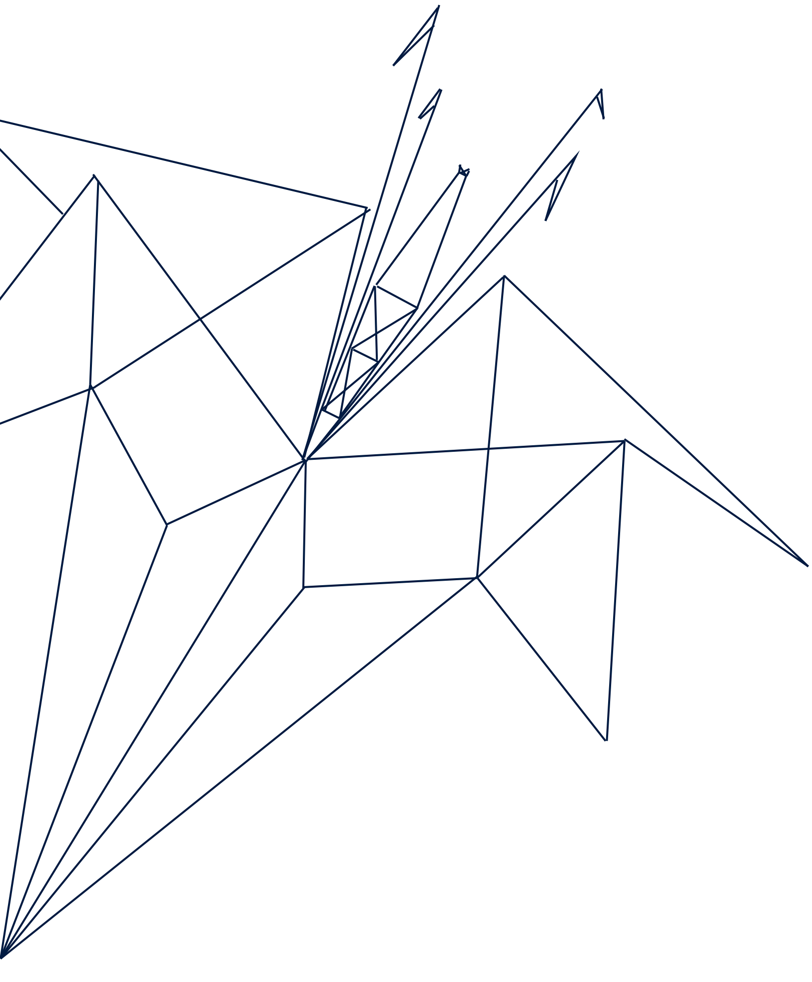
No Capítulo I, intitulado: "*Composição das redes cultura-polinizador em policulturas*" nós investigamos os efeitos da agricultura sobre a composição das redes de interação cultura-polinizador. Para isso nós adotamos um quadro conceitual de β-diversidade, onde comparamos a dissimilaridade de interações observadas nos estabelecimentos em relação à diversidade de interações observada regionalmente. Com isso buscamos entender como a paisagem e o manejo agrícola filtram as interações do *pool* regional de interações nos estabelecimentos.

No Capítulo II, intitulado: "*Estrutura das redes cultura-polinizador em policulturas*" nós investigamos os efeitos da agricultura sobre a estrutura das redes de interação cultura-polinizador. Para isso nós analisamos como as métricas da paisagem e do estabelecimento agrícola afetam as propriedades da rede: assimetria, conectância, modularidade, aninhamento e especialização por intermédio do número de interações, da riqueza de interações e da riqueza de polinizadores. Com isso buscamos entender como a paisagem e o manejo afetam aspectos estruturais que moldam a topologia das redes formadas nos estabelecimentos agrícolas.

No Capítulo III, intitulado "*Robustez das redes cultura-polinizador em policulturas*" nós investigamos os efeitos da agricultura sobre a robustez das redes de interação cultura-polinizador. Para isso nós testamos o efeito das métricas de manejo e paisagem sobre a robustez das redes cultura-polinizador em diferentes cenários de extinção das espécies. Neste capítulo analisamos efeitos diretos e mediados pela topologia das redes. Para a cascata de extinção-coextinção nós modelamos cenários considerando: diferentes alvos de extinção primária; diferentes métodos de ordenamento das extinções primárias; com ou sem possibilidade de religação de interações perdidas. Com isso buscamos entender como as redes formadas nos estabelecimentos devem se comportar mediante a diferentes mecanismos de extinção, além de seus promotores e amortecedores.

2. CAPÍTULO I: COMPOSIÇÃO DAS REDES CULTURA-POLINIZADOR EM POLICULTURAS





COVER PAGE

Title

Interaction β-diversity in farmlands: Effect of agricultural management and landscape features on composition of crop-pollinator networks

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ABSTRACT

Agriculture influences biodiversity through the intensification of land use changes and farm management. Such impacts may vary from local to landscape scales. They influence not only species composition but also their interactions, which can compromise essential ecosystem services, such as pollination. In this study, we investigated how landscape features and farm management affect the composition of crop-pollinator interactions in smallholder polycultures. We sampled interactions between crops and bees on 13 farms. From these interactions, we derived interaction β-diversity indices (β_{WN}: interaction β-diversity, β_{ST}: interaction β-diversity due to species turnover, β_{OS}: interaction β-diversity due to interaction rewiring, and β_{Poll}: interaction β-diversity due to pollinator turnover) based on the dissimilarity of crop-pollinator networks of local farms relative to the regional interaction pool. For these farms, we generated variables for landscape structure and forest configuration at the landscape scale, and farm complexity and crop heterogeneity at the local scale. We tested the effects of these four variables on the β-diversity indices using generalised linear model selection. We found that farm complexity significantly affected β_{WN} and β_{ST}, while crop heterogeneity affected β_{ST}, β_{OS}, and β_{Poll}. Landscape structure influenced only β_{OS}, whereas forest configuration had minimal effects on interaction dissimilarity β_{WN}. Our findings demonstrate that the composition of interactions in smallholder polycultures is primarily determined by management decisions made at the farms. This highlights the farmer's role in conserving important ecosystem services. Such effect is particularly pronounced on dissimilarity arising from species turnover, especially pollinators. Integrating local and regional measures is essential for sustainable land management to conserve biodiversity and ensure food security.

Keywords

Agricultural landscapes, interaction beta-diversity, interaction networks, pollinator conservation, sustainable agriculture.

Highlights

- Farm management is the main driver of crop-pollinator network composition in smallholder farms.
- Crop heterogeneity drives interaction β-diversity and interaction turnover.
- Farm complexity drives interaction rewiring and turnover.
- Landscape structure affects pollination networks through interaction rewiring.
- Farmers management and landscape features are crucial for conserving pollination networks.

2.1. INTRODUCTION

Pollination is one of the most essential ecosystem services for agriculture (IPBES, 2016). Around 75% of plants grown for human consumption have some level of dependence on pollinators (Klein et al., 2007). Production mediated by pollinators can represent a billion-dollar increase in the market price of these crops (Giannini et al., 2015; Lautenbach et al., 2012). However, despite their importance for agriculture, pollinators are strongly threatened by the intensification of agriculture (Kremen et al., 2002). The decline in the abundance and diversity of bees, the most important pollinators, comes mainly from the synergy of pesticide use, pathogen spillover, and the reduction of habitats and resources (Goulson et al., 2015; Potts et al., 2010). These three factors primarily emerge from management decisions made locally on producing farms. Moreover, the effects of agricultural management are scalable and can thwart the entire ecosystem functioning of agricultural matrices (Tscharntke et al., 2012b, 2012a).

The ecological simplification of landscape is a large-scale side-effect of agricultural intensification. The abrupt and fast conversion of large natural areas into simplified farming lands (e.g., monocultures) is a significant threat to biodiversity, including crop pollinators (Tscharntke et al., 2005). Therefore, the quality of the landscape where farms are located can affect the provision of the pollination ecosystem service (e.g., González-Chaves et al., 2020). For pollinators, the structure of the landscape, in terms of composition and configuration, represents the spatial arrangement of habitats and resources of different qualities in natural and semi-natural elements (Kennedy et al., 2013). Therefore, landscape structure can determine the occurrence of pollinators in the agricultural matrix and its permeability (Aguirre-Gutiérrez et al., 2015).

There is strong evidence of the impact of agricultural intensification on the taxonomic (Le Féon et al., 2010), functional (Hass et al., 2018), and phylogenetic (Grab et al., 2019) diversity of pollinators at the landscape level. Noteworthy, there is still a gap in understanding how agricultural intensification at different scales and intensities affects the composition of crop interactions with their pollinators. Most studies on the relationship between pollination and agricultural intensification are focused on impacts on production (e.g., Grab et al., 2019) and are carried out in monoculture systems (e.g., Hipólito et al., 2018). As a rule, these studies treat pollination interactions (generally visitors' frequency and diversity) as production predictors, and as a response to management or the surrounding landscape (Boreux et al., 2013; Grab et al., 2019; Hipólito et al., 2018). Usually, only plants are seen as a resource (e.g., Westphal et al., 2003). The rare studies focusing on the composition of interactions in agricultural environments are more concerned with the effects of environmental gradients (Lázaro and Gómez-Martínez, 2022) or in the network pattern (Hass et al., 2018). There is a considerable knowledge gap on the mechanisms that modulate the composition of interactions in agricultural landscapes.

An objective way to analyse the factors that promote variation in the composition of interactions along environmental gradients is to analyse the interactions' β-diversity (Poisot et al., 2012). Since β-diversity expresses dissimilarity between communities, the interaction β-diversity directly reflect ecological mechanisms shaping communities, varying along environmental gradients (Carstensen et al., 2014; Pellissier et al., 2018; Poisot et al., 2015). This approach has already shown the role of abundance and phenology in the composition of networks (CaraDonna et al., 2017), the maintenance of the interaction composition post-disturbance (Baronio et al., 2021), density-dependent dynamics in the composition of interaction networks (Ceron et al., 2022), and the role of specialisation in the composition of interaction networks (Noreika et al., 2019). However, these studies focus on local-local dissimilarities. Here, we focus on an approach to local-regional interaction dissimilarity to delve into how and why locally realized interactions differ from those present in the regional pool of interactions. We thus explored how agricultural management and landscape features filters the regional interaction pools into local interaction pools.

In this study, we investigated the relationships between agricultural management, landscape structure, and the composition of crop-pollinator interactions in polycultures. Using well-established geoprocessing techniques, we accessed landscape structure and forest configuration through landscape metrics based on land cover and land use (LCLU). With these two variables, we tested the relationships between the interactions' composition and anthropogenic-driven gradients emerging at the landscape scale (Tscharntke et al., 2012b). To represent the spatial management properties of farms, we applied the logic of landscape analysis on a reduced scale at the farm level. In this way, we were able to measure farm complexity and crop heterogeneity, which are expressed through the spatial structure of natural and semi-natural elements of farms. Farm complexity and crop heterogeneity summarise measures of spatial complexity of farms (LCLU configuration and composition) representing an essential part of the management decisions made on farms. With these variables, we assessed the effect that farming management has on the interactions' composition.

Our objective was to investigate the factors shaping the composition of crop-pollinator interactions in polyculture farms. To do this, we tested the effects of landscape structure, forest configuration, farm complexity, and crop heterogeneity on the interaction β-diversity index (β_{WN}) and its components (β_{ST}, $\beta_{ST.h}$, and β'_{OS}). We measured these different β-diversity indexes based on a local-regional comparison between crop-pollinator networks on farms and the regional pool of interactions, i.e, a meta-network aggregating all farm networks. We then discussed the mechanisms that govern the filtering of interactions at a local scale. In addition, we also present a flexible framework for studying the composition of interactions applicable to different environmental gradients.

2.2. METHODS

2.2.1. Study region and sites

We conducted this study in the watersheds of the Miringuava and Miringuava-Mirim Rivers, located in São José dos Pinhais, Paraná, Brazil (Figure 1). The region falls under the Atlantic Forest biome domain (Araucária Forests ecoregion) and has a mixed Atlantic rainforest vegetation physiognomy. The climate in the area is Cfb (Temperate oceanic climate) following the Köppen-Geiger classification.

We sampled the data during the rainy season between October 2020 and March 2021, which historically has an average temperature of 19.3 ºC, total precipitation of 1013 mm (an average of 168.83 mm/month), and an average relative humidity of 86%. The watersheds landscape is composed mostly by forest (45.5%) and farming (44.5%), with a gradient towards the west where the non-vegetated area (e.g., urban areas) is concentrated (7.6% coverage). The remaining 1.3% of LCLU corresponds to water, and < 1.1% of non-forest natural formation (MapBiomas Project, 2023).

We selected 15 sampling units of smallholder farms with an average area of 12.56 ± 6.66 ha to capture the region's LCLU gradient. All farms were polycultures that involved the cultivation of fruits, vegetables, leafy greens, and green manure plants, with either conventional (10 farms) or organic (5 farms) management. We considered farms as organic if they followed certified (4) or non-certified (1) agroecological principles, including the avoidance of synthetic agrochemicals and an emphasis on ecological inputs and biodiversity. At the time of pollinator sampling, the farms had 1 to 13 (6 ± 3) flowering cultivated plants. To ensure the independence of the samples, we choose farms with a minimum distance of 1 km between their centroids. We accessed farms with the owner's authorization after signing an informed consent form approved by Humans Research Ethics Committee (CEP/SD) of the Federal University of Paraná and approved it under CAAE: 55408221.2.0000.0102.

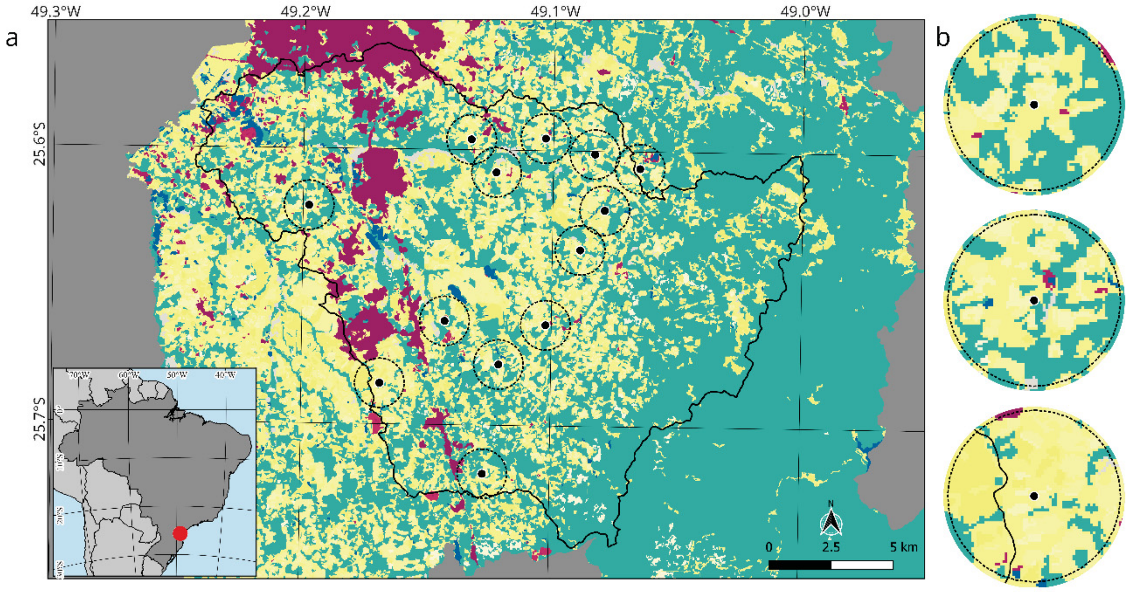


Figure 1a Map of the study region (limits: 25°33′43″S, 49°10′03″W; 25°44′41″S, 49°05′28″W; 25°36′36″S, 48°59′53″W; and 25°36′19″S, 49°14′38″W); and sample unit farms with MapBiomas Project LCLU classification (greens: forest; greys: non-forest natural formation; yellows: farming; purples: non-vegetated area; and blues: water). Black dots: sample unit farms; black dotted circles: 1 km buffers; black solid line: Miringuava and Miringuava-Mirin rivers watersheds; classified area: São José dos Pinhais. In the highlighted map, the red dot indicates the approximate position of the study area in Brazil. 1b Highlight of three sampling units to illustrate the landscape gradient observed surrounding the farms. Map composition generated with QGIS 3.30.0 - ʻs-Hertogenbosch (https://www.qgis.org) using the Global Administrative Areas (GADM; https://gadm.org/) and Hydrographic Divisions of Brazil (https://portaldemapas.ibge.gov.br/) for the base map. Datum EPSG:4326 – WGS 84.

2.2.2. Pollinators sampling

The sampling were based on established protocols for bees sampling (Silveira et al., 2002) and the recommendations for registering interactions (Jordano, 2016). We sampled pollinators during their visits to flowering crops on farms. We considered as pollinators the species that touched the reproductive structures of the flowers (androecium and or gynoecium) at any time during the fieldwork. We only sampled bees because they are the most important pollinators of crops (Kleijn et al., 2015). We sampled between 08:00 a.m. and 04:00 p.m. on sunny or partially cloudy days, with temperatures ranging from 18 ºC to 28 °C. We prioritised days with calm and fresh breezes (winds of 1 to 24 km/h) and moderate relative humidity (30 to 70 %).

We captured the bees with an entomological net and euthanised them in a killing jar with ethyl acetate during free scans through the crop plots. Each scan lasted for 15 minutes without a stopwatch pause for euthanasia. We carried out 40 scans on each farm among the flowering crops. We randomly draw the order of scans to avoid temporal biases in sampling interactions. For crops with morning anthesis, such as *Cucurbita* spp., we scanned only between 08:00 a.m. and 12:00 a.m. To ensure adequate sampling, we scanned each crop at least four times, totalling one hour. We sampled two days in each farm, with an average interval of 47 ± 24 days between each sampling. Therefore, we sampled each farm for 20 hours (15 minutes x 40 scans x two days), totalling a sampling effort of 300 hours (15 farms x 20 hours). On every farm, the same two collectors (FFJ and JLH) captured the pollinators.

We removed one sample unit (#02, Figure 1) because we could not carry out the second campaign due to weather and logistic conditions. We also removed one sample unit (#09, Figure 1) because of the strong presence of urban infrastructure surrounding the farm and due to meliponiculture activity on the farm. Both factors could lead to confounding factors in our analyses.

Crop identification occurred in the field and was confirmed in the laboratory by FFJ. JLH and RBG identified the bees at the lowest possible taxonomic level in the laboratory following Melo and Gonçalves (2005) classification. We deposited the bee’s vouchers in the Padre Jesus Santiago Moure Entomological Collection (DZUP) at the Federal University of Paraná (UFPR).

2.2.3. Interactions β-diversity

We built an adjacency matrix of the frequency of interactions between bee species in the columns and crops in the rows. We did this procedure for the 13 farms, pooling the records made in the two sampling campaigns. We used these matrices to build 13 local bipartite interaction networks. All local matrices were combined in a regional bipartite meta-network. Using these networks, we calculated the interaction β-diversity indices. Here, we considered the interactions from the meta-network as the regional pool of interactions, which includes all potential interactions observed for the species sampled in the region. The interactions we observed locally on the farms represent the realised interactions given the potential interactions in the regional pool.

To assess the interaction β-diversity between the regional interaction pool and local farm networks, we compared the interaction α-diversity of the farm networks with the interaction γ-diversity of the regional meta-network, calculated by combining all farms. To do this, we used integral and partitioned indices of β-diversity of interactions calculated for all farms based on their dissimilarity with the regional meta-network. To verify the differences between farm networks and the regional meta-network we used the β-diversity of interactions (β_{WN}), which measures the dissimilarity of interaction networks depending on the difference in the identity of interactions (each exclusive combination between an interacting pair). Using this metric, we estimated the β-diversity index of farms due to the absence of interactions represented in the meta-network (Poisot et al., 2012).

In addition to this measure of the interaction's β-diversity, we used two indices derived from the partitioning of β_{WN}. This index can be partitioned by the equation: $\beta_{WN} = \beta_{ST} + \beta_{OS}$, where: β_{ST} is the dissimilarity of interactions due to species substitution, that is, represents a turnover when interactions are not realised due to the absence of one of the species in the interacting pair (Poisot et al., 2012). With this measure, we estimated the β-diversity component explained by the absence of species present in the meta-network. β_{OS} is the dissimilarity of interactions established between species common to two of the realisations. In our case, we used a particular case of β_{OS}, called β'_{OS}, which measures the dissimilarity between a local network and its counterpart in the regional pool of interactions, although operationally, the two come from the same equation (Poisot et al., 2012). The substantial difference of β'_{OS} is that the local network will always represent a subset of the interactions observed in the pool of interactions (Poisot et al., 2012). Using this index, we measure the proportion of interactions filtered out at the farm level, despite their presence in the regional pool and the local co-occurrence of species.

We used a second partitioning to decompose the β_{ST} component, following the equation: $\beta_{ST} = \beta_{ST.h} + \beta_{ST.l} + \beta_{ST.lh}$, where: $\beta_{ST.h}$ is the dissimilarity due to the absence of pollinator species; $\beta_{ST.l}$ is the dissimilarity to the absence of crop species; and $\beta_{ST.lh}$ is the dissimilarity due to the absence of both (Novotny, 2009). For this particular case, we chose to use only the $\beta_{ST.h}$ partition (called β_{Poll} from now on, $\beta_{ST.l}$ as β_{Crop} and $\beta_{ST.lh}$ as $\beta_{Crop\text{-}Poll}$), which represents the bees, considering that plants' occurrence is determined by farmers and not by natural environmental mechanisms and processes. With this index, we could specifically verify how much of the dissimilarity observed in β_{ST} on farms is due to the absence of bees that are present on a regional scale, removing the weight of crop richness, mediated by farm management action, on β_{ST}. We calculated all β-diversity indices with the "betalinkr" function from the "bipartite" R-package. We used the "commondenom" partitioning method for better comparison of partition values (Dormann et al., 2008).

2.2.4. Landscapes and farms characterisation

Traditionally, the effect of landscape on biological or ecological aspects has been tested through landscape metrics, which are mathematical abstractions of specialised ecological mechanisms. These metrics can reflect different aspects of landscape structure – such as the diversity, aggregation, and shape of the patches that compose the landscape – with emergent effects at different observational scales (Hesselbarth et al., 2019; McGarigal, 2013). Numerous studies have associated these metrics with bee diversity, plant-pollinator interactions, and pollination ecosystem service (Boscolo et al., 2017; Coutinho et al., 2021; Hipólito et al., 2018; Jeronimo and Varassin, 2023; Quinlan et al., 2021). However, there is still a gap in understanding how the multiplicity of mechanisms embedded in these metrics interact with one another, effectively characterising the landscape and genuinely impacting ecological phenomena, such as pollination. For this reason, in this study, we propose a different methodological approach that seeks to summarise, as much as possible, the aspects that are relevant in structuring the landscape gradient. Through this approach, we aim to observe how the landscape, in its entirety and across different levels, can affect crop-pollinator interaction networks.

To achieve this, we analysed two scales: the first is the landscape level, in which we extracted landscape structure and forest configuration variables that summarise metrics from the classical landscape ecology approach applied to traditional landscape classes (McGarigal, 2013). The second is the farm level, in which we extracted farm complexity and crop heterogeneity variables, applying landscape metrics to compute the composition and configuration of agricultural management elements at a fine scale within farms. With these four metrics, we seek to understand the effects that important facets of agriculture have on the diversity of interactions: the landscape context in which farms are embedded, which may facilitate pollinator foraging; the landscape context of the distribution of natural resources for pollinator species; the spatial management structure within farms, which may facilitate pollinator foraging and permanence; and the crop heterogeneity, which serves both as a resource for pollinators and benefits from their activity.

For landscape structure and forest configuration we computed landscape metrics in buffers of 0.5, 1.0, 1.5 and 2.0 km of radii generated from the centroid of the sampled farms. To measure these landscape metrics, we used the LCLU classification from the 7.0 collection of the MapBiomas Project (2023). This classification is based on remote sensing images from the LANDSAT satellite program and has a resolution of 30 x 30 m per pixel. The classification is computed with the Random Forest and U-Net machine learning algorithms, trained from random samples of pixels with no change in LCLU over the years (Souza et al., 2020). We considered the highest resolution of the five macro classes of the collection, totalling 29 different classes of LCLU. However, in the study region, only 12 of these classes were present, namely: one class of forest, one class of non-forest natural formation, six classes of farming, three classes of non-vegetated area, and one class of water, with no pixel classified as not observed.

To evaluate (1) landscape structure, we computed landscape metrics (more details in section 2.5, and Appendix A Table S1) that quantify configuration and composition at the landscape level. These metrics consider joint variations of all fragments and classes contained in the area. Therefore, this variable refers to variations in the spatial configuration and composition of the landscape around the farms. We measured (2) forest configuration by computing the landscape metrics at the class level, which quantifies the configuration of the forest formation class (subclass of the MapBiomas forest class). These metrics consider joint variations of the patches belonging only to the forest formation class in the area. Therefore, this variable refers to any variation in the spatial configuration of forest fragments around the farms.

For farm complexity and crop heterogeneity, we computed the landscape metrics in 250 m buffer radii generated from the centroid of the sampled farms. To quantify the landscape metrics at the farm level, we used a manual classification of LCLU. We constructed this classification based on remote sensing images from the CBERS 04A satellite program and images obtained on farms using a DJI Phantom 3 Standard® Drone. The drone photographs were always taken from an altitude of approximately 50 m, taking as many frames as necessary to cover the farm area and its immediate surroundings. Additionally, we georeferenced crops, buildings, and forest fragments on farms to help with the accuracy of LCLU classification. From these images and georeferenced points, we vectorised all natural and non-natural elements within the buffer boundary. Finally, we utilised the vectorised polygons to create a raster with 42 LCLU classes with a resolution of 2x2 m per pixel (Table S2). We considered these classes to belong to five macro classes: crops (28 classes corresponding to the sampled crops); other farming elements (eight classes); vegetation (three classes); urban infrastructure (two classes); and water bodies (one class). All vector and raster geoprocessing steps were carried out using the native functions of the QGIS software version 3.30 – ‘s-Hertogenbosch (QGIS Development Team, 2023) and the Semi-Automatic Classification Plugin v.7.10.11 (Congedo, 2021).

To measure the (3) farm complexity, we computed landscape metrics that quantify configuration and composition at the farm level. These metrics also consider joint variations of all fragments and classes in the analysis area. Therefore, this variable refers to all variations in the spatial configuration and composition of farms. For (4) crop heterogeneity, we computed landscape metrics that quantify configuration and composition, measured at the landscape level. These metrics consider joint variations of all fragments of the sampled crop classes. Therefore, this variable refers to all variations in the spatial configuration and composition of crops produced on sampled farms.

To calculate Landscape structure, forest configuration, farm complexity, and crop heterogeneity, we extracted all possible metrics available in the “landscapemetrics” R-package using the “calculate_lsm” function (Hesselbarth et al., 2019). For metrics available in more than one statistical measure (e.g., mn, sd, or cv), we only used the mean (mn). We also discarded metrics that could not be computed (NA values) on one or more farms. We computed these metrics using an edge depth of one pixel and a neighbourhood of eight cells (queen's case contiguity).

2.2.5. Statistical analyses

From landscape metrics computed in each level (landscape and farm) for each predictor (landscape structure, forest configuration, farm complexity, and crop heterogeneity), we performed a principal component analysis (PCA) using the "prcomp" function from the "stats" R-package (R Core Team, 2024). Because the metrics have different scales and measurement units, we standardised them before the PCA. To represent the landscape structure, forest configuration, farm complexity, and crop heterogeneity, we use the first component of the PCA, computed for each level. The eigenvalues for the axes of each predictor and their biplot with the most relevant landscape metrics are reported in the supplementary material Appendix A Figures S1 and S2 respectively, with a list of all landscape metrics used to compute each predictor (Appendix A Table S1).

For landscape structure and forest configuration we extracted the first component from landscape metrics computed in four different buffers (0.5, 1.0, 1.5 and 2.0 km) to detect the scale of effect analyses (Miguet et al., 2016). We determined the scale of effect based on the highest R^2 value among the four radii, using two separate model selections, one for each predictor. In each selection, we built four models consisting of the response variable as a function of each predictor in each radius. After this selection, we modelled landscape structure and forest configuration using only the components resulting from the landscape metrics computed on the 1.0 km buffer, which showed the strongest effect. To select the scale of effect, we considered only the interaction β-diversity (β_{WN}) as a response variable.

To verify which factor is most relevant for the composition of the crop-pollinator network, we performed a model selection. Initially, we built a complete model containing the response variable (an interaction β-diversity index) as a function of the four predictor variables (landscape structure, forest configuration, farm complexity, and crop heterogeneity). We constructed these models with the "glmmTMB" function from the "glmmTMB" R-package (Brooks et al., 2017) using the β distribution family and logit link function. We build only additive models without considering interactions between the predictor variables. The complete model was subjected to a stepwise regression using the “dredge” function from the “MuMIn” R-package (Bartoń, 2024) to compare all possible combinations between the predictor variables. We considered models with ΔAICc ≤ 2 as having substantial empirical support. Akaike weights were used to assess the relative likelihood of each model (Burnham et al., 1998). However, we considered plausible only the models with AICc smaller than the null model (response ~ 1). Besides that, we also computed a global p-value through a likelihood-ratio test, comparing the plausible models with their corresponding null models. To measure the relative importance of the predictor variables we calculated their relative weight by adding the weight of models where they appear (Bartoń, 2024; Burnham et al., 1998). We performed all this model selection procedure for all interaction β-diversity indices (β_{WN}, β'_{OS}, β_{ST}, and β_{Poll}).

2.3. RESULTS

We recorded interactions between 26 species of agricultural plants and 103 species of bees. The regional network (meta-network) comprised 6571 interactions realised between 330 unique crop-pollinator pairs. Local networks had an average 505.5 ± 156.0 interactions, with an average of 11 ± 4 % (51.1 ± 13.0) of different crop-pollinator pairs. On average, local networks had 6.4 ± 2.9 crop species and 28.0 ± 5.4 bee species. The most frequent interactions were between *Apis mellifera* (tribe: Apini) and *Raphanus sativus* (fodder radish, family: Brassicaceae, 1426 interactions), *Trigona spinipes* (Meliponini) and *Cucurbita maxima* (pumpkin, Cucurbitaceae, 407), and *Peponapis fervens* (Eucerini) and *C. maxima* (374). The bee species with higher interaction frequency were *A. mellifera* (2554), *Bombus pauloensis* (832, Bombini), and *T. spinipes* (831). The most visited crops were *R. sativus* (2364), *C. maxima* (1025), and *Cucurbita pepo* (613, courgette, Cucurbitaceae).

We found a high interaction β-diversity (β_{WN}), comparing farms to the regional pool of interactions (0.85 ± 0.04, Figure 2). Most interaction β-diversity was due to species turnover (β_{ST}; 0.77 ± 0.08, Figure 2) instead of rewiring (β'_{OS}; 0.07 ± 0.04, Figure 2). The turnover due to bee replacement (β_{Poll}) was 0.19 ± 0.05, due to crop replacement (β_{Crop}) was 0.32 ± 0.06, and due to bee and crop replacement ($\beta_{Crop\text{-}Poll}$) was 0.26 ± 0.08.

At least one of the predictors variables, landscape structure, forest configuration, farm complexity and crop heterogeneity, explained β-diversity (Table 1). The best model for interactions β-diversity (β_{WN}) was the crop heterogeneity model (ΔAICc = 0.00, w = 0.41, p = 0.01). The model composed of crop heterogeneity + forest configuration (ΔAICc = 1.05, w = 0.24, $p < 0.01$) was also considered plausible. For species turnover (β_{ST}), the best model was the one composed of crop heterogeneity + farm complexity (ΔAICc = 0.00, w = 0.26, $p < 0.01$). Still, the model composed only of crop heterogeneity (ΔAICc = 0.49, w = 0.21, $p < 0.01$) was also considered plausible. For interaction rewiring (β'_{OS}) only the model composed of farm complexity + landscape structure (ΔAICc = 0.00, w = 0.62, p = 0.02) was plausible. For turnover due to bee replacement (β_{Poll}), only the model composed of farm structure (ΔAICc = 0.00, w = 0.43, $p < 0.01$) was plausible.

Finally, crop heterogeneity presented the highest relative weight for β_{WN} (0.79, Figure 3a), β_{ST} (0.65, Figure 3b), while farm complexity presented a relevant relative weight for β_{ST} (0.64, Figure 3b), β'_{OS} (0.98, Figure 3c), and β_{Poll} (0.69, Figure 3d). landscape structure had a relevant weight only for β'_{OS} (0.77, Figure 3c), and forest configuration had a relevant weight only for β_{WN} (0.39; Figure 3).

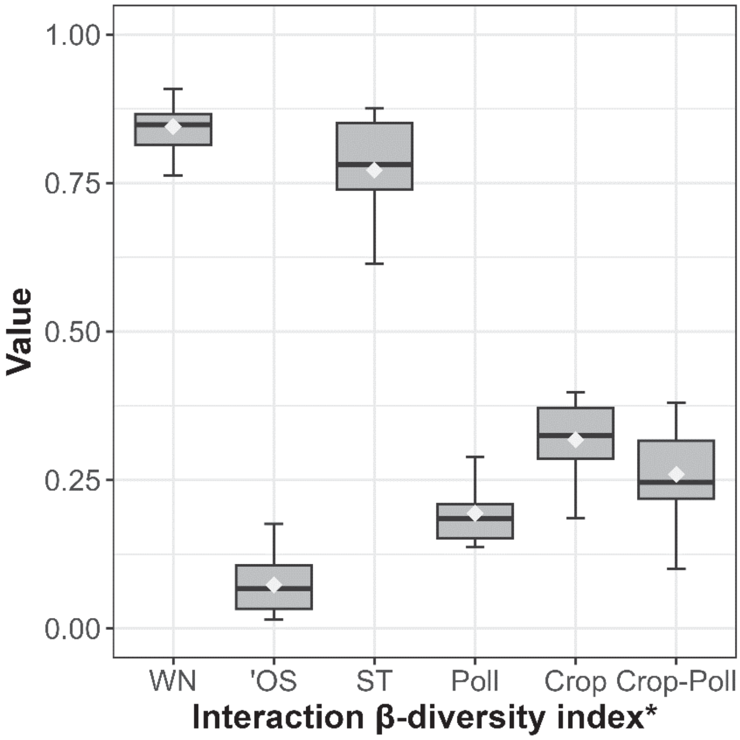


Figure 2 Comparison between interaction β-diversity indices (β_{WN}, β_{ST}, β'_{OS}, β_{Poll}, β_{Crop}, and $\beta_{Crop\text{-}Poll}$) computed between farms networks and the regional poll of interactions. β_{WN} = interactions β-diversity, β_{ST} = interactions β-diversity due to species turnover, β'_{OS} = interactions β-diversity due to interaction rewiring, β_{Poll} = interactions β-diversity due to bee's turnover, β_{Crop} = interactions β-diversity due to crops turnover, $\beta_{Crop\text{-}Poll}$ = interactions β-diversity due to crops and bee's turnover.

Table 1 Plausible models for interaction β-diversity indexes (β_{WN}, β_{ST}, β'_{OS}, β_{Poll}) and species composition β-diversity (β_S). β_{WN} = interactions β-diversity, β_{ST} = interactions β-diversity due to species turnover, β'_{OS} = interactions β-diversity due to interaction rewiring, β_{Poll} = interactions β-diversity due to bee's turnover. Index: β-diversity dissimilarity indexes; Intercept: model intercept. Slope: model estimators of landscape structure, forest configuration, farm complexity, and crop heterogeneity effects on the response variables (Index); df: degrees of freedom; logLink: logarithmic link function; ΔAIC: difference in AIC values between a model and the best model in the set; Weight: relative probability that a model is the best among those compared; p-value: probability value.

		Slope									
Index	**Intercept**	**Landscape Structure**	**Forest Configuration**	**Farm Complexity**	**Crop Heterogeneity**	**df**	**logLink**	**AICc**	**ΔAICc**	**weight**	**p-value**
β_{WN}	1.71				0.05	3	27.91	-47.14	0.00	0.41	0.01
	1.71		0.03		0.04	4	29.55	-46.10	1.05	0.24	0.00
β_{ST}	1.25			0.05	0.05	4	21.88	-30.77	0.00	0.26	0.00
	1.24				0.07	3	19.47	-30.28	0.49	0.21	0.00
β_{OS}	-2.76	0.08		-0.17		4	32.11	-51.22	0.00	0.62	0.02
β_{Poll}	-1.43			-0.05		3	23.78	-38.90	0.00	0.43	0.00

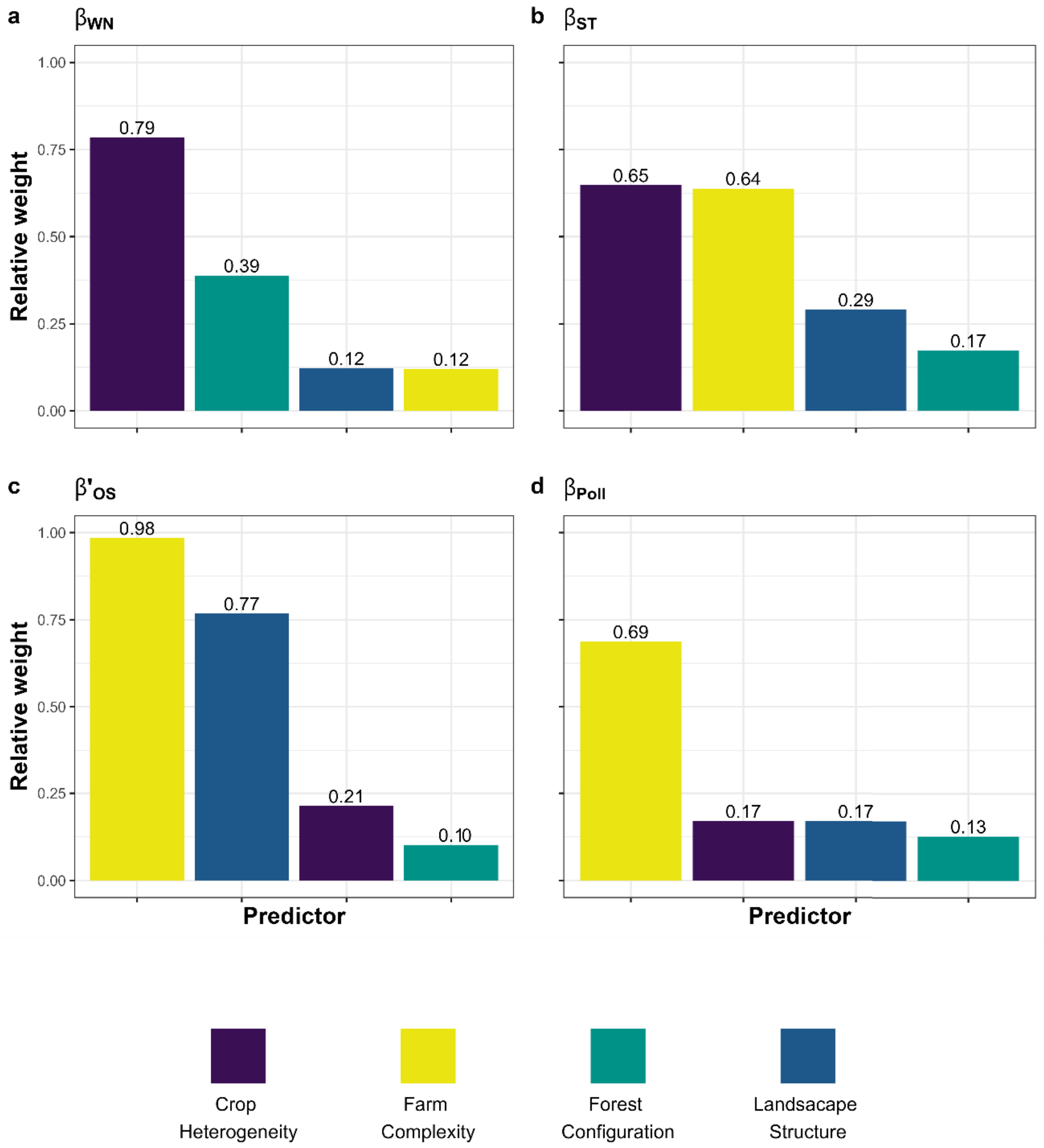


Figure 3 Relative importance (weight proportion) of the predictor variables in models explaining the interaction β-diversity (a: β_{WN}, interaction β-diversity; b: β_{ST}, β-diversity due to species turnover; c: β'_{OS}, β-diversity due to interaction rewiring; and d: β_{Poll}, β-diversity due to pollinator turnover). The weight proportion of each predictor is the sum of the weight of the models in which the variable appears (Table 1).

2.4. DISCUSSION

Our results demonstrate that the agricultural management of the farms affects the composition of crop-pollinator interactions in a polyculture more than the landscape of their surroundings. The effects of farm complexity and crop heterogeneity on interaction dissimilarity highlight how spatial management decisions shape interactions between crops and pollinators. Farmers assume a central role in these relationships, by managing both natural and semi-natural habitats and farm resources. In this context, we demonstrate that farm management constitutes the most critical filter for the realisation of the interactions within farms, even though landscape also affects the composition of farm interaction networks. Therefore, both local management and the landscape context of the farms are important for interactions composition.

The more significant influence of crop heterogeneity on the β_{WN} is not surprising. We calculate crop heterogeneity from landscape metrics that measure the composition and configuration of crops, therefore taking into account the abundance and richness of crops. As crops represent one of the interacting groups, the networks' structure and composition naturally depends on the abundance and richness of crops (Ebeling et al., 2008; Guimarães, 2020). Furthermore, increasing the abundance and richness of plants in the network can increase pollinators' richness (Kral-O'Brien et al., 2021), resulting in higher dissimilarity when comparing farms with different number of crops. Also, it is important to highlight that the functional and taxonomic diversity of plants is also a driver of pollinator diversity, thus representing an important factor in the composition of interactions (Fornoff et al., 2017; Ribeiro et al., 2024). Thus, crop abundance and richness will directly affect the difference between local network interactions and the regional pool, highlighting the role of local management in attracting pollinators. Given our local-pool comparison, bigger local networks (i.e., highly diverse polycultures with more pollinators species and interactions) comprise a greater percentage of the regional pool (Dunne, 2005).

Although with a minor effect, forest configuration also influenced β_{WN}. Forest configuration measures the spatial configuration of forest patches and, thus, can be interpreted as a direct proxy for the spatial distribution of forested habitats and resources driving the differences in pollinator composition among farms (Boscolo et al., 2017). Furthermore, the distribution of the physical forest structure itself can determine the flow of pollinators across the landscape (Krewenka et al., 2011; Nery et al., 2018), increasing or constraining it depending on the configuration. Therefore, forest configuration may affect the local abundance and diversity of floral visitors accessing farms close to these patches. For species dependent on forest resources (e.g., vegetation clumps for *Bombus* spp. and tree trunks for Meliponini bees), the configuration of forest patches represents also the spatial arrangement of resources for feeding and nesting (Krewenka et al., 2011; Montagnana et al., 2021; Nery et al., 2018).

Because bees with different bee traits (e.g., intertegular distance) are sensitive to different landscape characteristics (Coutinho et al., 2021), the forest configuration filter out different bees in the local pool due to the transit of these species through the matrix (Boscolo et al., 2017). For open-field species (e.g., *Apis mellifera*), large forest fragments can be physical barriers that reduce their transit across the landscape (Krewenka et al., 2011). Because we sampled the pollinators in a gradient of crop composition, we should also expect exceptional lower values of β'_{OS} since the crop turnover will inflate β_{ST} (White et al., 2022). Furthermore, plant-centred sampling, estimates higher β-diversity of interactions, but the β'_{OS} is proportionally smaller than that found in pollinator-based sampling (Souza et al., 2021).

We also did not perceive significant phenotypic variations to restrict interactions due to phenological or functional restrictions. We did not expect these restrictions since this study does not have spatial or temporal scales to reach these effects (Peralta et al., 2020). For these reasons, besides the mathematical relationship between β_{ST} and β'_{OS} (Poisot et al., 2012), our local networks are more likely to present an exceptionally small number of species (especially pollinators) than the interactions they perform, compared to the meta-network. Thus, we see β'_{OS} with less proportional importance than β_{ST} in the composition of the β_{WN} value. This is clear by comparing Figure 3 from (Poisot et al., 2012) with Figure S3 in Appendix A.

The interaction dissimilarity due to pollinators turnover in relation to the regional pool (β_{Poll}) was mainly due to farm complexity. This emphasises the importance of factors beyond crop heterogeneity in explaining the interactions β-diversity driven by species turnover. Here, we can see that not only the identity, richness, and proportion of crops planted are drivers of farm interaction diversity but also other management decisions (Bloom et al., 2023). Given the composition and configuration of other farm elements, we can find more deterministic explanations. Farms composed of patches of native vegetation cover and a large diversity of wild plants are more attractive and permeable to pollinators, ensuring greater diversity within their boundaries (Bloom et al., 2023; Gilpin et al., 2022; Warzecha et al., 2021). Furthermore, the abundance of inert cover classes (e.g., built environment and covered surfaces in general) physically reduces the amount of habitat as resource for pollinators (Boscolo et al., 2017). These two factors strongly limit the diversity of pollinators on farms. considering the hypothesis of habitat amount (Fahrig, 2013).

In addition to the amount of suitable and unsuitable areas for pollinators, how the different crops are interspersed, in one or multiple plots, with other natural and non-natural elements present on farms is relevant to interaction composition (Holzschuh et al., 2010; Warzecha et al., 2021). Forest patches, hedgerows, and native fields increase the diversity of habitats and resources for bees (Boscolo et al., 2017; Kremen and Merenlender, 2018), increasing the abundance and diversity of bees in farms (Grab et al., 2019; Hass et al., 2018; Hoehn et al., 2008). Compacted bare soil and fallow areas usually represent poor or inert environments, reducing the farm's attractiveness for bees (Boscolo et al., 2017). These effects on pollinators' diversity will inevitably affect the interaction composition (Guimarães, 2020). Therefore, the proportion and configuration of land designated to native vegetation, hedgerows, gardens, builds, water reservoirs, and others farm elements are also farmers' decisions that can affect the crop-pollinator interaction (Brosi et al., 2008). Still, we found no information about the impact of agricultural infrastructure (e.g., sheds, greenhouses, barns, etc.) on pollinator diversity. It may follow the same pattern found in urban gradients promoted by land uses like roads and buildings (White et al., 2022), but only focused research can answer this question. In the big picture, the effect of management decisions on the interactions' diversity goes beyond direct crop management.

Although β'_{OS} is especially low in networks resulting from plant-centred sampling (Souza et al., 2021), it is still crucial for understanding the dynamics that drive interaction composition. Due to the comparison of local networks with the interactions regional pool, as we did, the β'_{OS} expresses direct and comparable differences between the not-realised interactions in the farms. In this scenario, farms with the highest β'_{OS} value have proportionally fewer interactions present in the interactions regional pool (Poisot et al., 2012). Like β_{Poll}, β'_{OS} was mainly influenced by farm complexity. This pattern indicates that the factors that limit interactions by restricting pollinator diversity (expressed in β_{Poll}) are similar to those that limit interactions by restricting partner choice (expressed in β'_{OS}).

Mass flowering plants in agricultural systems influence pollinators' attraction in different ways (Holzschuh et al., 2016; Kovács-Hostyánszki et al., 2013; Westphal et al., 2003), and can modulate the effect of landscape on pollinators (Fijen et al., 2019). This can place interactions on farms in a dynamic of dense dependence on crops, where mechanisms of competition and facilitation between them can directly affect the interactions (Bergamo et al., 2020; Sponsler et al., 2023). Also, biological and ecological characteristics of pollinators, such as level of specialisation, social level, vibration capacity, and body size, can synergically determine their interactions (Brosi, 2016). Social bee species have larger foraging ranges and tend to forage on plants in a flowering boom, neglecting or ignoring plants in a lower flowering peak (Grüter and Hayes, 2022). This may increase competitive pressure on less abundant pollinators (usually solitary bees) in these blooming plants, marginalising these species for interactions with less abundant resources (Bänsch et al., 2021). Therefore, more representative networks of the regional pool should be expected in polycultures with higher richness and a balanced abundance of crops.

The effect of landscape structure on β'_{OS}, in turn, must be almost entirely related to the morphology and behaviour of pollinators (Coutinho et al., 2021). As landscape structure affect the transit of pollinators across the matrix (Boscolo et al., 2017), the pollinators' foraging decisions are certainly influenced by landscape permeability. However, this permeability is strongly dependent on the morphology and behaviours of the species (Boscolo et al., 2017; Grüter and Hayes, 2022). In this context, the crops closer to pollinator nests should be the most sought-after floral resources (Coutinho et al., 2021). Therefore, species with greater permeability in the matrix would have an advantage in obtaining abundant or favourite resources (Grüter and Hayes, 2022). At this scale, a synergy of pollinator permeability with density-dependent competition effects is also plausible. In more stochastic ways, abundant species would have an advantage in obtaining well-positioned resources as they would be more likely to find them first. In a more deterministic way generated by competition, less abundant species would be displaced to poorly positioned resources.

2.5. CONCLUSIONS

In this study, we present how landscape and agricultural management can affect the composition of crop-pollinator interaction networks in polycultures. Our findings emphasise the key role of agricultural management in shaping crop-pollinator interactions within diversified polycultures. We demonstrate that decisions concerning farm management has a stronger influence on interaction networks than the surrounding landscape. This underscores the direct link between farmers' choices and the diversity of ecological interactions and highlight the central role that farmers can play in conserving pollination interactions and this ecosystem service. Our findings on the effect of landscape structure on the rewiring of interactions highlight the interplay between farm-level management and landscape-scale dynamics, suggesting that multiscale approaches are essential for understanding the composition of crop-pollinator networks.

Here we use a traditional approach in a novel way to delve deeper into the β-diversity patterns of pollination interactions in a system that is particularly important for humanity. In doing so, we aim to clarify how interactions are assembled on farms and how this influences the dynamics of pollination networks, particularly in purely agricultural systems. We emphasize that analysing β-diversity among local networks and the regional pool of interactions can provide powerful insights for the conservation of pollination interactions, whether in natural or agricultural systems. By integrating ecological and agronomic perspectives, we can better promote sustainable agricultural practices that enhances biodiversity, ecosystem services and food security.

APPENDIX

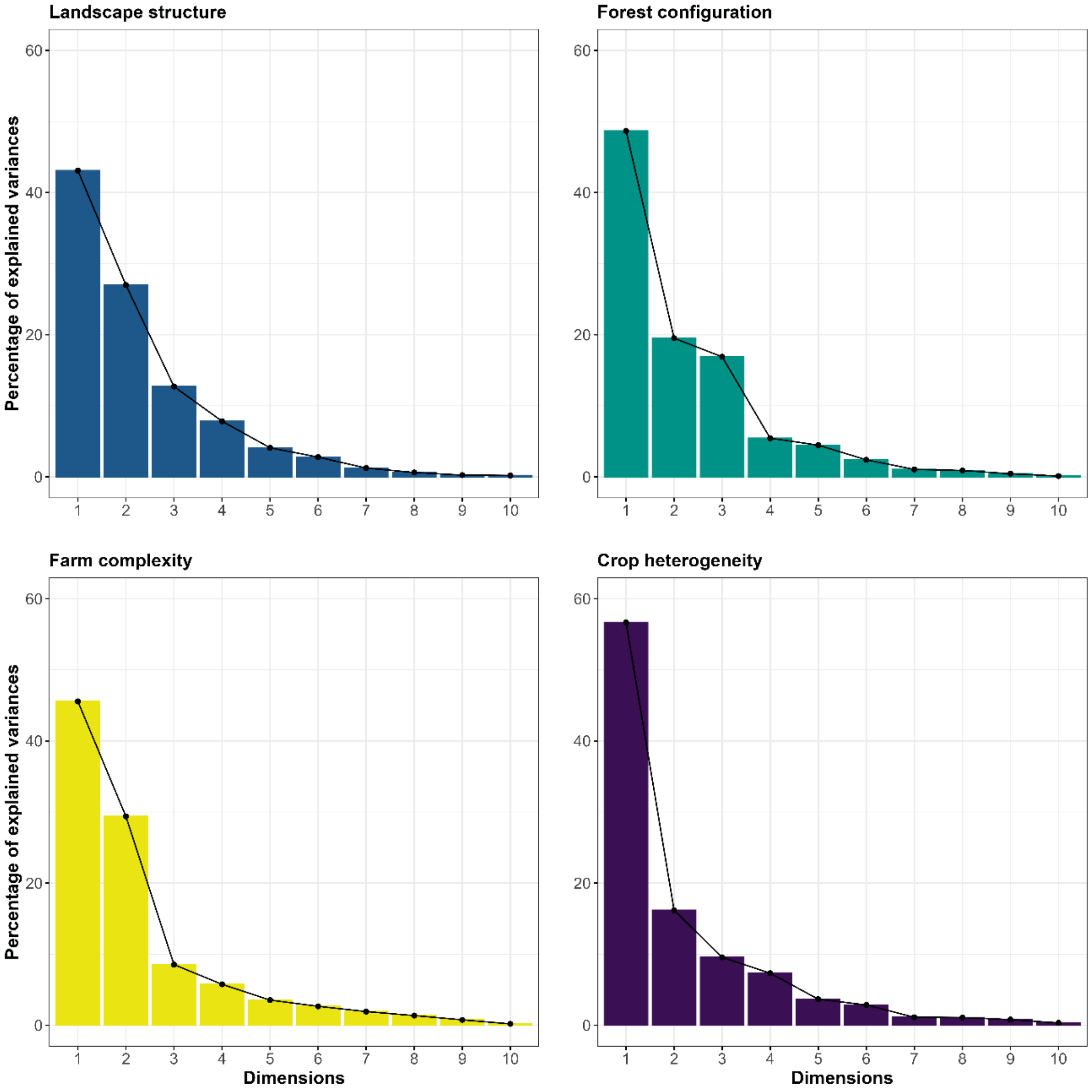


Figure S1 Proportion of variance explained by the principal components (PCA) for the predictor variables. Blue: landscape structure; green: forest configuration; yellow: farm complexity; purple: crop heterogeneity.

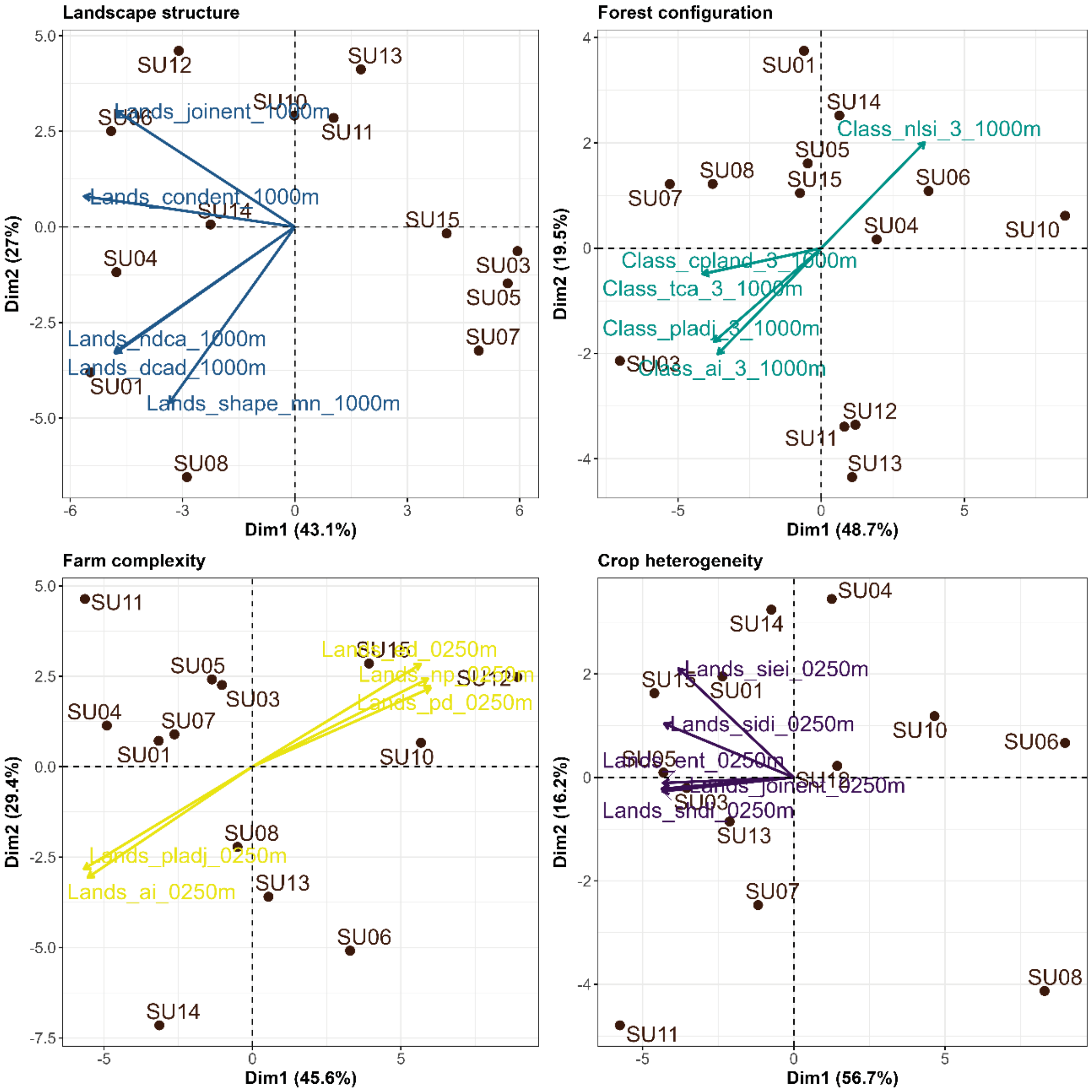


Figure S2 Biplot of PCA for the predictor variables. Blue: landscape structure; green: forest configuration; yellow: farm complexity; purple: crop heterogeneity. Only the five variables with the highest total contribution to PC1 and PC2 are displayed in the biplot. Brown dots represents the sample units (farms).

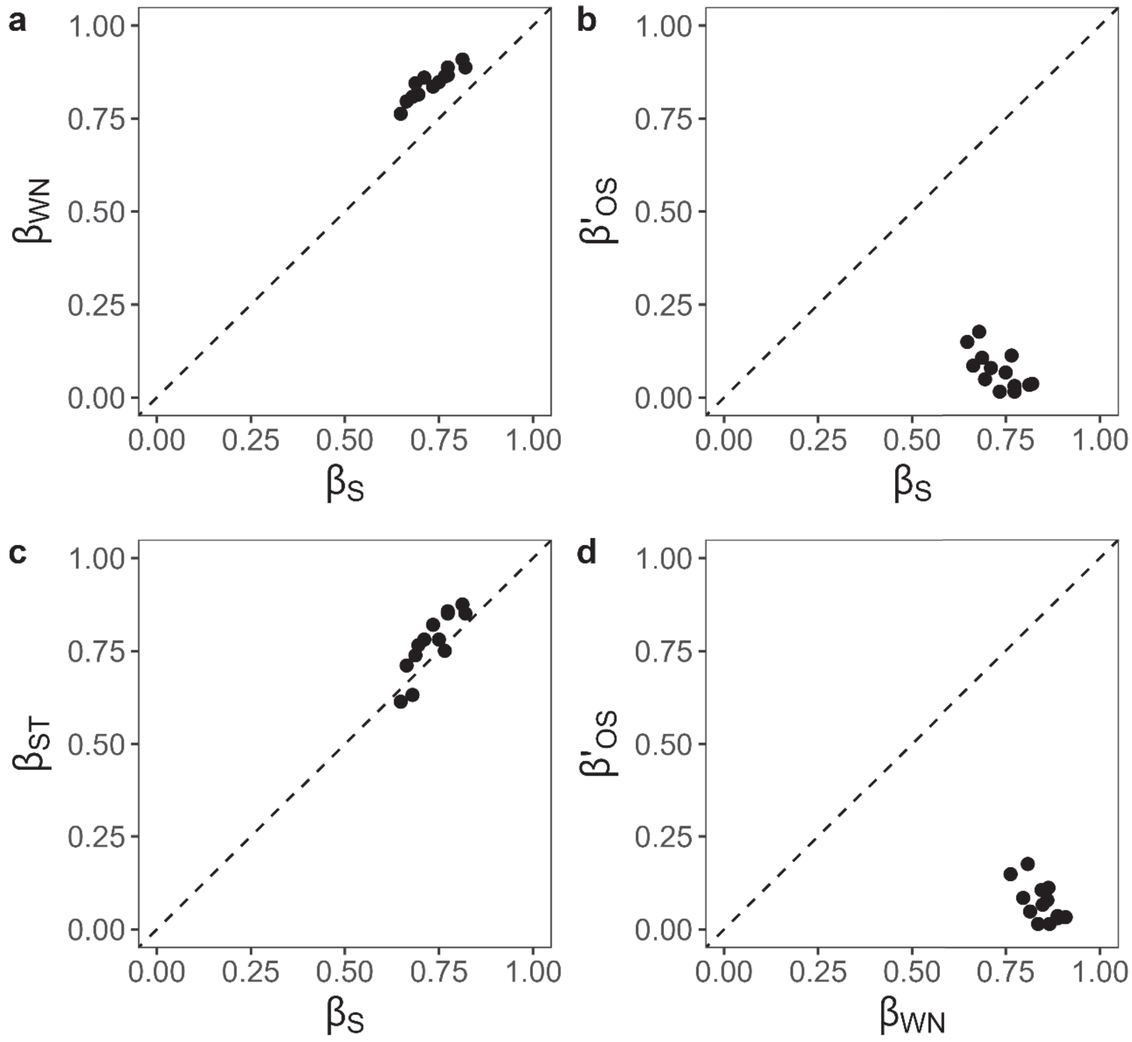


Figure S3 Correlation between a: β_{WN} with β_S; b: β'_{OS} with β_S; c: β_{ST} with β_S; and d: β'_{OS} with β_{WN} for the dissimilarity values observed in this study. β_{WN}: interaction β-diversity; β_{ST}: β-diversity due to species turnover; β'_{OS}: β-diversity due to interaction rewiring. This figure is a replication of figure 3 from Poisot et al. (2012) for comparison purposes.

Table S1 Table of landscape metrics used to generate the predictor variables: landscape structure, forest configuration, farm complexity, and crop heterogeneity. Predictor: corresponding predictor variable for PC1; Landscape metric: landscape metric computed using the "landscapemetrics" R-package (Hesselbarth et al., 2019). Type: Type of the corresponding metric. Acronym: abbreviation of the metric name in the "landscapemetrics" package. Description: Brief description of the landscape metrics extracted from Hesselbarth et al., 2019. Only the top ten landscape metrics with the highest scores for each PC1 axis corresponding to each predictor variable are presented.

Predictor	**Landscape metric**	**Type**	**Acronym**	**Description**
Landscape structure	Conditional entropy	Complexity	condent	Complexity of a landscape pattern configuration. It measures only a geometric intricacy (configurational complexity) of a landscape pattern.
	Effective mesh size	Aggregation	mesh	The effective mesh size is an 'Aggregation metric'. Because each patch is squared before the sum is calculated and the sum is standardized by the total landscape area, MESH is a relative measure of patch structure.
	Landscape division index	Aggregation	division	It can be in as the probability that two randomly selected cells are not located in the same patch.
	Mean of core area	Core area	core_mn	Equals the mean of core areas of all patches in the landscape. The core area is defined as all cells that have no neighbour with a different value than themselves.
	Landscape shape index	Aggregation	lsi	It is the ratio between the actual landscape edge length and the hypothetical minimum edge length. The minimum edge length equals the edge length if only one patch would be present.
	Total edge	Area and edge	te	Total edge includes all edges. It measures the configuration of the landscape because a highly fragmented landscape will have many edges.

	Edge density	Area and edge	ed	The edge density equals all edges in the landscape in relation to the landscape area. The metric describes the configuration of the landscape, e.g. because an overall aggregation of classes will result in a low edge density.
	Total core area	Core area	tca	Equals the sum of core areas of all patches in the landscape.
	Percentage of like adjacencies	Aggregation	pladj	It calculates the frequency how often patches of different classes i (focal class) and k are next to each other, and following is a measure of class aggregation.
	Aggregation index	Aggregation	ai	It equals the number of like adjacencies divided by the theoretical maximum possible number of like adjacencies for that class summed over each class for the entire landscape.
Forest configuration	Core area percentage of landscape	Core area	cpland	It is the percentage of core area of class i in relation to the total landscape area.
	Total core area	Core area	tca	Equals the sum of core areas of all patches in the landscape.
	Percentage of landscape of class	Area and edge	pland	It is the percentage of the landscape belonging to class i. It is a measure of composition and because of the relative character directly comparable among landscapes with different total areas.
	Total (class) area	Area and edge	ca	The total (class) area sums the area of all patches belonging to class i. It shows if the landscape is e.g. dominated by one class or if all classes are equally present.
	Mean of core area	Core area	core_mn	Equals the mean of core areas of all patches in the landscape. The core area is defined as all cells that have no neighbour with a different value than themselves.
	Mean of patch area	Area and edge	area_mn	The metric summarises each class as the mean of all patch areas belonging to class i. The metric is a simple way to describe the composition of the landscape.

	Effective mesh size	Aggregation	mesh	The effective mesh size is an ’Aggregation metric’. Because each patch is squared before the sum is calculated and the sum is standardized by the total landscape area, MESH is a relative measure of patch structure.
	Landscape division index	Aggregation	division	It can be in as the probability that two randomly selected cells are not located in the same patch.
	Largest patch index	Area and edge	lpi	It is the percentage of the landscape covered by the corresponding largest patch of each class i. It is a simple measure of dominance.
	Percentage of like adjacencies	Aggregation	pladj	It calculates the frequency how often patches of different classes i (focal class) and k are next to each other, and following is a measure of class aggregation.
Farm complexity	Patch density	Aggregation	pd	It describes the fragmentation the landscape (number of patches per 100 hectares), however, does not necessarily contain information about the configuration or composition of the landscape.
	Conditional entropy	Complexity	condent	Complexity of a landscape pattern configuration. It measures a only a geometric intricacy (configurational complexity) of a landscape pattern.
	Number of patches	Aggregation	np	Number of patches within landscape. It describes the fragmentation of the landscape, however, does not necessarily contain information about the configuration or composition of the landscape.
	Mean of core area	Core area	core_mn	Equals the mean of core areas of all patches in the landscape. The core area is defined as all cells that have no neighbour with a different value than themselves.
	Mean of patch area	Area and edge	area_mn	The metric summarises the landscape as the mean of all patch in the landscape. The metric is a simple way to describe the composition of the landscape.

	Percentage of like adjacencies	Aggregation	pladj	It calculates the frequency how often patches of different classes i (focal class) and k are next to each other, and following is a measure of class aggregation.
	Edge density	Area and edge	ed	The edge density equals all edges in the landscape in relation to the landscape area. The metric describes the configuration of the landscape, e.g. because an overall aggregation of classes will result in a low edge density.
	Landscape shape index	Aggregation	lsi	It is the ratio between the actual landscape edge length and the hypothetical minimum edge length. The minimum edge length equals the edge length if only one patch would be present.
	Aggregation index	Aggregation	ai	It equals the number of like adjacencies divided by the theoretical maximum possible number of like adjacencies for that class summed over each class for the entire landscape.
	Total edge	Area and edge	te	Total edge includes all edges. It measures the configuration of the landscape because a highly fragmented landscape will have many edges.
Crop heterogeneity	Joint entropy	Complexity	joinent	Complexity of a landscape pattern. An overall spatio-thematic complexity metric.
	Shannon’s diversity index	Diversity	shdi	It is a widely used metric in biodiversity and ecology and takes both the number of classes and the abundance of each class into account.
	Marginal entropy	Complexity	ent	It measures a diversity (thematic complexity) of landscape classes.
	Simpson’s diversity index	Diversity	sidi	It is widely used in biodiversity and ecology. It is less sensitive to rare class types than lsm_l_shdi. It can be interpreted as the probability that two randomly selected cells belong to the same class.

Mutual information	Complexity	mutinf	It disambiguates landscape pattern types characterize by the same value of an overall complexity.
Patch cohesion index	Aggregation	cohesion	The Patch Cohesion Index measures the physical connectedness of patches within the same land cover class. Higher values indicate more spatially cohesive and less fragmented patches.
Modified Simpson's diversity index	Diversity	msidi	Measures landscape diversity by considering the proportion of area occupied by each class. Higher values indicate more evenly distributed land cover types.
Conditional entropy	Complexity	condent	Complexity of a landscape pattern configuration. It measures a only a geometric intricacy (configurational complexity) of a landscape pattern.
Percentage of like adjacencies	Aggregation	pladj	It calculates the frequency how often patches of different classes i (focal class) and k are next to each other, and following is a measure of class aggregation.
Edge density	Area and edge	ed	The edge density equals all edges in the landscape in relation to the landscape area. The metric describes the configuration of the landscape, e.g. because an overall aggregation of classes will result in a low edge density.

Table S2 Classification of LULC for farms (250 m buffer), grouped into macro categories. Each class represents a distinct landscape element manually classified using drone images following its description. The code indicates the classification value in the raster image.

Code	**Macro**	**Class**	**Description**
1	Vegetation	Trees	Woody/Late vegetation
2	Vegetation	Shrub	Vegetation with multiple stems / mid vegetation
3	Vegetation	Grass	Land covered by herbaceous vegetation, mostly grass or pasture
5	Urban Inf.	Buildings	Constructed structures for human use
11	Urban Inf.	Other anthropogenic structures	Other man-made features (mostly roads, trails and waste dump sites)
4	Farm Elements	Exposed soil	Agricultural bare ground with little to no vegetation
6	Farm Elements	Silviculture	Managed tree plantations (*Eucaliptus* spp. or *Pinus* spp.)
7	Farm Elements	Non-flowering crops	Cultivated plants harvested before flowering (mostly herbs, leaves and roots)
8	Farm Elements	Flowering crops without flowers	Crops that normally flower but are not flowering at the time
10	Farm Elements	Greenhouse crops	Plants grown under controlled conditions in greenhouses
9	Water	Water bodies	Lakes, rivers, ponds, and other surface water
20	Crop	Pumpkin	*Cucurbita maxima*
21	Crop	Courgette	*Cucurbita pepo*
22	Crop	Aubergine	*Solanum melongena*
23	Crop	Calabash	*Lagenaria siceraria*
24	Crop	Chayote	*Sechium edule*
25	Crop	Common bean	*Phaseolus vulgaris*
26	Crop	Adzuki bean	*Vigna angularis*
27	Crop	Sunflower	*Helianthus annuus*
28	Crop	Scarlet eggplant	*Solanum aethiopicum*
29	Crop	Cucumber	*Cucumis sativus*
30	Crop	Groundcherry	*Physalis pubescens*
31	Crop	Strawberry	*Fragaria* × *ananassa*

32	Crop	Bishop's crown pepper	*Capsicum baccatum* var. *pendulum*
33	Crop	Okra	*Abelmoschus esculentus*
34	Crop	Bell pepper	*Capsicum annuum*
35	Crop	Pole bean	*Phaseolus vulgaris* - treated differently from common beans due to the vertical cultivation method
36	Crop	Tomato	*Solanum lycopersicum*
37	Crop	Chicory	*Cichorium intybus*
38	Crop	Broccoli	*Brassica oleracea* var. *italica*
39	Crop	Potato	*Solanum tuberosum*
40	Crop	Mustard greens	*Brassica juncea*
41	Crop	Parsley	*Petroselinum crispum*
42	Crop	Sweet potato	*Ipomoea batatas*
43	Crop	Dandelion	*Taraxacum officinale*
44	Crop	Fennel	*Foeniculum vulgare*
45	Crop	Apple-of-Peru	*Nicandra physalodes*
46	Crop	Fodder radish	*Raphanus sativus* var. *oleiformis*
47	Crop	Nasturtium	*Tropaeolum majus*
48	Crop	Soybean	*Glycine max*
49	Crop	Corn	*Zea mays*
50	Crop	Citrus fruits	*Citrus* spp.

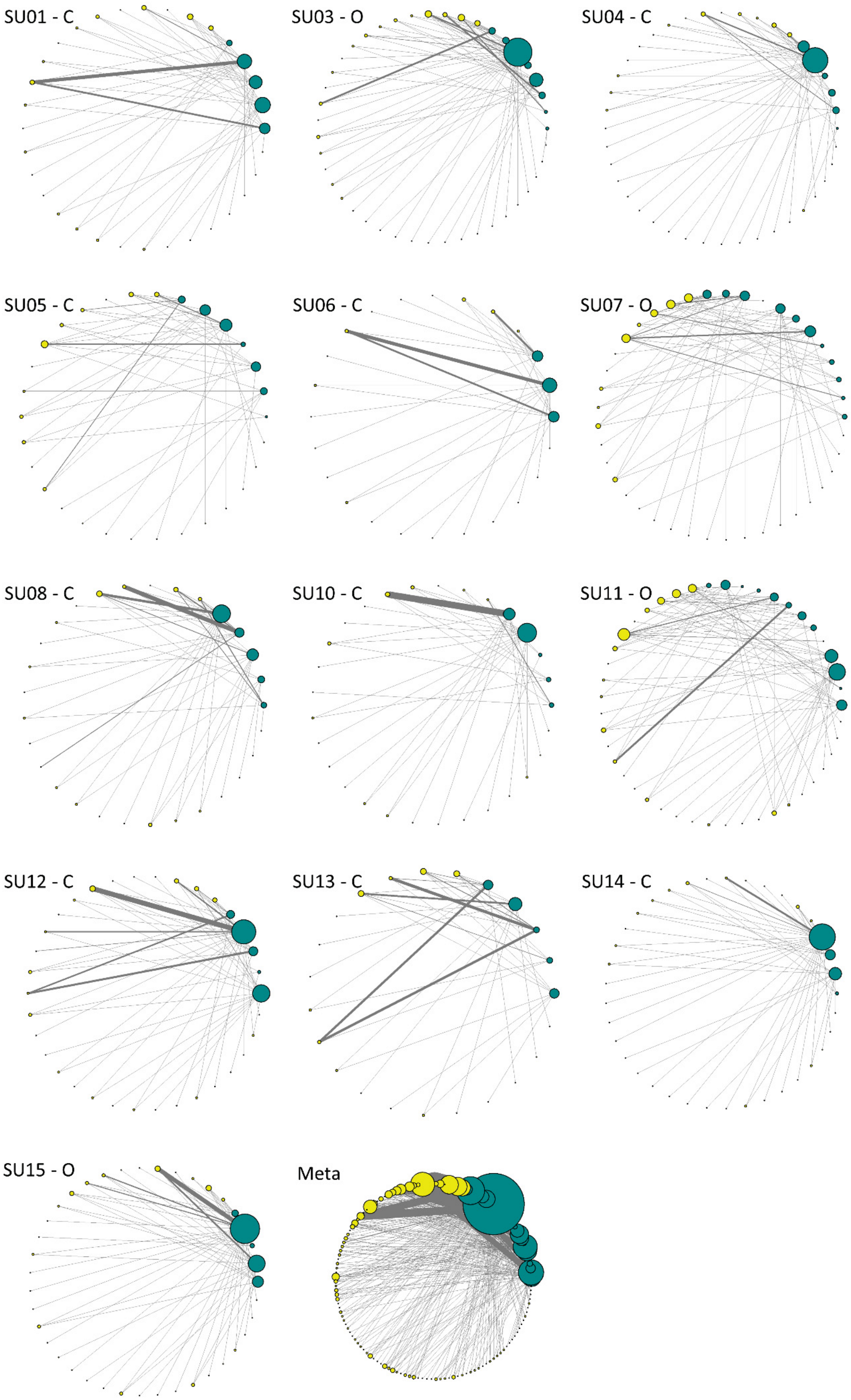
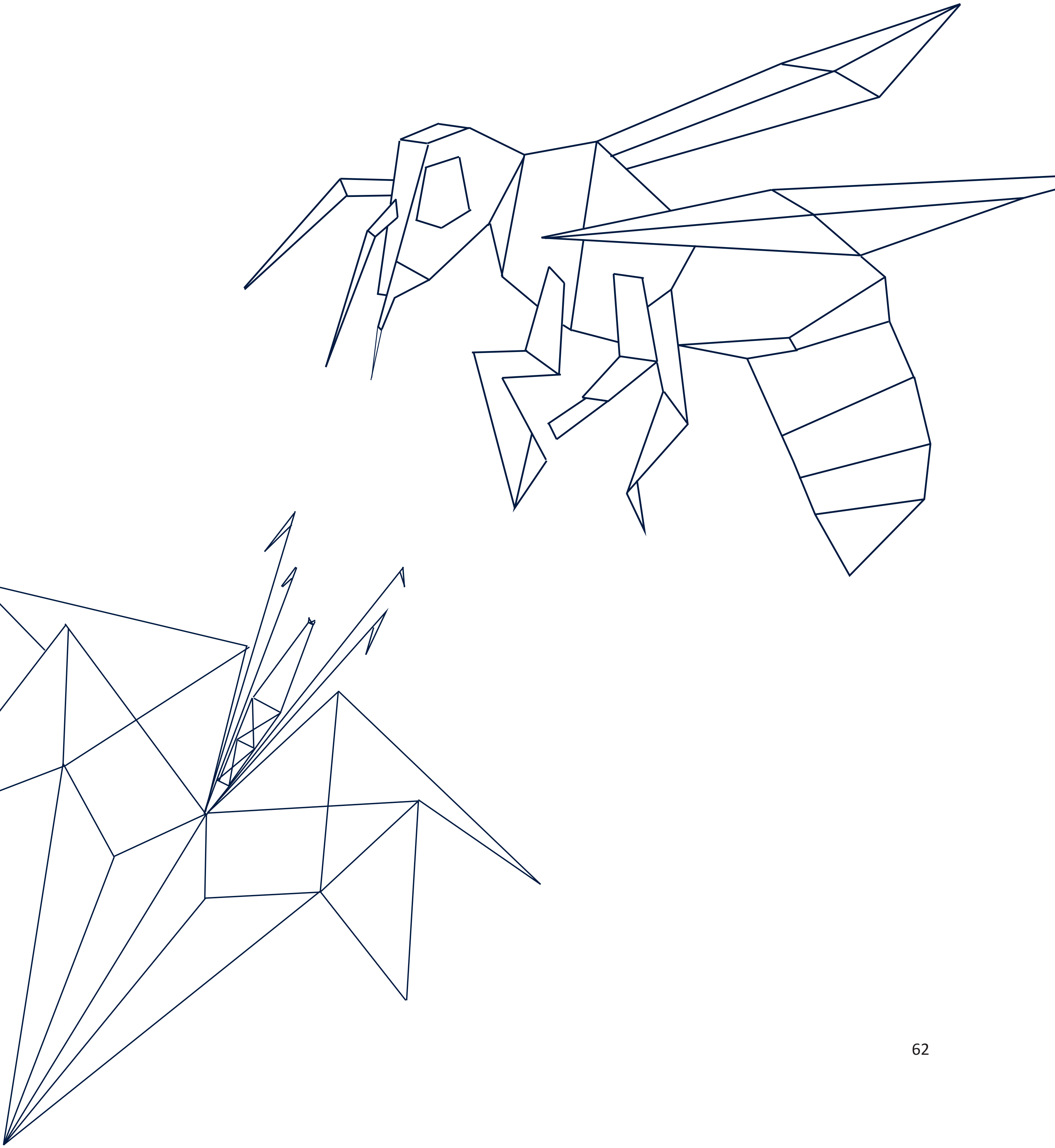

SU01 - C
SU03 - O
SU04 - C
SU05 - C
SU06 - C
SU07 - O
SU08 - C
SU10 - C
SU11 - O
SU12 - C
SU13 - C
SU14 - C
SU15 - O
Meta

Figure S4 Crop–pollinator interaction networks of the smallholding farms. Green circles: crops; yellow circles: bees; grey lines: interactions. The size of the nodes (circles) is weighted by species degree. The width of the edges is weighted by the number of links between species. From SU01 to SU15 are shown the crop–pollinator networks of the sample units (except SU02 and SU09, which were removed from the analyses, see 2.2. Methods). In Meta, the meta-network is shown, constructed from the union of the adjacency matrices of the analysed sample units. C: indicates farms with conventional management; and O: indicates farms with organic management.

3. CAPÍTULO II: ESTRUTURA DAS REDES CULTURA-POLINIZADOR EM POLICULTURAS



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Title

Network topology of crop–pollinator interactions in smallholder polycultures: The role of landscape and agricultural management

Authors

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ABSTRACT

Pollination services are critical for agricultural productivity but are increasingly threatened by land-use changes and agricultural intensification. This study examines how land-scape structure and farm management shape the structure of crop-pollinator interaction networks in smallholder polycultures. Using data from 13 farms, we analysed 6571 inter-actions between crops and bee species to assess the effects of landscape structure, forest configuration, farm complexity, and crop heterogeneity on network metrics, including the number of links, interaction richness, pollinator richness, asymmetry, connectance, modularity, nestedness, and specialization. Results from piecewise structural equation models (PSEM) showed that crop heterogeneity reduced specialization, and connectance by enhancing interaction richness. Also, possibly enhances asymmetry through enhancing pollination richness. By contrast, forest configuration reduced interaction richness, enhancing asymmetry and connectance. Farm complexity positively affected nestedness by increasing the number of links. These findings showed that network structure is primarily modulated at the local scale, although regional-scale effects were also present. This highlights the importance of local management decisions in conserving farm interactions, while also emphasizing that farms are not isolated from the broader regional context. Our findings highlight the need for integrated conservation strategies that combine local farm management with landscape-scale planning to safeguard pollination services.

Key-words

Agricultural landscapes, ecosystem services, interaction networks, pollinator conservation, sustainable agriculture.

Highlights

- Crop-pollinator network structure was primarily shaped by local-scale factors.
- Crop heterogeneity was the main driver of crop-pollinator network structure.
- Crop heterogeneity and forest configuration effects were mediated by interaction richness and farm complexity by the number of links.
- Only network asymmetry and connectance were influenced by regional-scale factors.
- Integrated farm and landscape management is key for sustainable pollination services.

3.1. INTRODUCTION

Pollination by animals plays a fundamental role in agriculture, as most crops exhibit some level of dependence on pollinators for their production (Klein et al., 2007; Ollerton et al., 2011). As the most important group of crop pollinators, bees can enhance agricultural yield in terms of both quantity (e.g., increased fruit set; Garibaldi et al., 2013) and quality (e.g., longer shelf life; Klatt et al., 2014). The contribution of bees to crop production is amplified by their abundance (Garibaldi et al., 2013) and diversity across different dimensions – taxonomic (Klein, 2009), functional (Martins et al., 2015), and phylogenetic (Grab et al., 2019). Therefore, the interactions between crops and their pollinators are essential for ensuring a stable and sustainable ecosystem service.

Despite its evident importance for agriculture, pollination is under intense negative pressure from the environmental changes characteristic of the Anthropocene (IPBES, 2016; Potts et al., 2010). Among these, drastic shifts in land cover and land use (LCLU) – primarily driven by agricultural intensification – stand out for their impact on pollinators ((Dainese et al., 2019; Kennedy et al., 2013; Klein et al., 2007). The widespread conversion of natural habitats into farmland has led to a severe ecological simplification of ecosystems (Andersson et al., 2021; Tscharntke et al., 2012a). This simplification reduces the availability of food and nesting resources for pollinators, making them scarcer in more degraded landscapes (Kennedy et al., 2013; Potts et al., 2010; Winfree et al., 2009). Additionally, this large-scale effect not only emerges but is further intensified by local management practices such as the excessive and illegal use of pesticides, monoculture planting, and the removal of ruderal plant species (Goulson et al., 2015; Sánchez-Bayo and Wyckhuys, 2019).

Given the importance of pollination for agriculture and its vulnerability to the effects of agricultural intensification (Klein et al., 2007; Potts et al., 2010), crop-pollinator interactions represent a critical subject from both ecological and economic perspectives (Dainese et al., 2019; Garibaldi et al., 2013). Understanding crop-pollinator dynamics is thus imperative for a future with food security (IPBES, 2016). One of the most effective ways to study crop-pollinator interactions is through the analysis of pollination network structure (Bascompte and Jordano, 2007; Tylianakis et al., 2010). The topological structure of these networks provides information about interaction dynamics, which influences ecosystem stability and resilience (Memmott et al., 2004; Thébault and Fontaine, 2010).

Basic network proprieties, such as network size, interaction richness, and species richness at a specific trophic level, provide insights into the factors shaping interacting communities (Bascompte and Jordano, 2007; Tylianakis et al., 2010). Moreover, network properties give insight for processes such as trophic-level interdependence for resource acquisition (asymmetry), flexibility in resource use (connectance and specialization), partner redundancy (nestedness), and partner selectivity (specialization and modularity) (Bascompte et al., 2003; Blüthgen et al., 2008; Burgos et al., 2007; Olesen et al., 2007). These metrics are crucial for understanding the resilience of crop-pollinator networks to environmental changes (Memmott et al., 2004; Tylianakis et al., 2010). For instance, the distance from natural areas can influence partner choice, affecting pairwise interactions between species (Garibaldi et al., 2013; Kennedy et al., 2013). Moreover, the network structure is highly responsive to both regional and local-scale changes driven by agricultural intensification (Klein et al., 2007; Tylianakis and Morris, 2017). Therefore, topological metrics are valuable not only for studying the ecological dynamics of crop-pollinator interactions but also for assessing factors that may impact crop production and agricultural productivity.

Although numerous studies have explored network structure in agricultural systems (e.g., Gay et al., 2024; Hass et al., 2018; Morrison et al., 2020), it is still unclear how crop-pollinator network structure is affected by agricultural intensification across different scales (Kennedy et al., 2013). Most studies focus on monocultures (Giannini et al., 2015; Hipólito et al., 2018; Quinlan et al., 2021) or networks that include wild and ruderal plant species on farms (Gilpin et al., 2022; Hass et al., 2018; Kovács-Hostyánszki et al., 2013). In contrast, in our study we focused on managed plants, examining interactions exclusively between cultivated plants and their pollinators within smallholder polycultures. By focusing our analysis on a purely agricultural system, we believe this approach can provide valuable insights into the "pure" impacts of agricultural intensification on pollination services it depends on. Additionally, it offers a unique perspective on the isolated responsiveness of pollinator dynamics within strictly agricultural structures.

Therefore, in this study, our objective was to understand how landscape structure and farm spatial management influence crop-bee network structure in smallholder polycultures. To achieve this, we analysed the relationships between four landscape and management metrics based on LCLU – landscape structure (measuring the complexity of the surrounding landscape), forest configuration (assessing the complexity of forest arrangement around farms), farm complexity (evaluating the spatial complexity of farms), and crop heterogeneity (quantifying the structural diversity of crop planting) – and eight network topology metrics: number of links, interaction richness, pollinator richness, asymmetry, connectance, nestedness, modularity, and specialization. We predefined hypotheses regarding the relationships between these variables (Figure S1), addressing the following questions:

(1) Which aspects of crop-pollinator network topology (asymmetry, connectance, modularity, nestedness and specialization) are influenced by agriculture, at different scales (landscape structure, forest configuration, farm complexity and crop heterogeneity)? (2) Does agricultural intensification, at different scales (e.g., high fragmented landscapes, low crop diversity), reduce the structural complexity of plant-pollinator networks?

3.2. METHODS

3.2.1. Study area and sampling units

We conducted this study on 13 smallholder polycultures managed either conventionally (nine farms) or organically (four farms). The farms covered an area of 12.56 ± 6.66 ha, with 6 ± 3 flowering crops present simultaneously during the sampling period (min = 3, max = 13). The farm owners granted access to their properties by signing an informed consent form, approved by the Human Research Ethics Committee (CEP/SD) of the Federal University of Paraná (CAAE: 55408221.2.0000.0102).

The farms are located in the Miringuava and Miringuava-Mirim river basins, in São José dos Pinhais, Paraná, Brazil. The study area lies within the Araucaria Forest ecoregion in the Atlantic Forest biome and experiences a Temperate Oceanic climate (Cfb in the Köppen-Geiger classification). It has an average temperature of 19.3 ºC and annual precipitation of 1013 mm. LCLU is characterised by a predominance of Forest (45.5 %) and Farming class (44.5 %), with a concentration of Non-vegetated area class (7.6 %) in the western region (MapBiomas Project, 2023). For further details on the study area and sampling units, refer to *Capítulo I*.

3.2.2. Crop-pollinator data

In this study, we are using data on pollination interactions between crops and bees, previously collected by members of the Ecosystem Services for Resilient and Sustainable Agriculture Project (*Capítulo I*). The interactions were collected during the rainy season between October 2020 and March 2021, following protocols for bee sampling (Silveira et al., 2002) and recommendations for interaction recording (Jordano, 2016). Bee vouchers were deposited in the Padre Jesus Santiago Moure Entomological Collection (DZUP) at the Federal University of Paraná (UFPR).

The data correspond to records of 6571 interactions between 26 crop species and 103 bee species. The farm networks consist of 505 ± 162 interactions between 6 ± 3 crop species and 28 ± 6 bee species. Of these interactions, 330 are unique crop-pollinator pairwise interactions (interaction richness), with 51 ± 14 (11 ± 4% of the interactions) per farm.

The crop species with the highest number of interactions were *Raphanus sativus* (2364 interactions, common name: fodder radish, family: Brassicaceae), *Cucurbita maxima* (1025, pumpkin, Cucurbitaceae), and *Cucurbita pepo* (613, courgette, Cucurbitaceae). The bee species with the highest number of interactions were *Apis mellifera* (2554, tribe: Apini), *Bombus pauloensis* (832, Bombini), and *Trigona spinipes* (831, Meliponini). The most frequent crops on the farms were *R. sativus* (13 farms), *Capsicum annuum* (8, bell pepper, Solanaceae), *C. pepo* (6), *Solanum lycopersicum* (6, tomato, Solanaceae), and *Solanum melongena* (6, aubergine, Solanaceae). The most frequent bee species on the farms were *A. mellifera* (13 farms), *Bombus morio* (13, Bombini), *B. pauloensis* (13), *T. spinipes* (13), *Dialictus* sp. (12, Halictini, morphotype nº 12), *Augochlora daphnis* (11, Augochlorini), and *Dialictus* sp. (11, morphotype nº 11). The most frequent interactions were: 1426 between *A. mellifera* and *R. sativus*, 407 between *T. spinipes* and *C. maxima*, and 374 between *Peponapis fervens* (Eucerini) and *C. maxima*.

3.2.3. Landscape and management variables

Here, we used landscape structure, forest configuration, farm complexity, and crop heterogeneity as predictor variables for the topology of crop-pollinator interaction networks. These variables represent the first principal component (PC1) obtained from independent principal component analyses (PCA) conducted for four sets of landscape metrics. Detailed descriptions of these variables, the original landscape metrics, and the data on landscape and farm characterisation based on LCLU are available in *Capítulo I*.

Landscape structure and forest configuration summarise landscape metrics calculated based on LCLU within a 1000 m radius buffer from the farm centroids. To compute the landscape metrics summarised in these variables, we used raster images of the MapBiomas Project, Collection 8.0 (MapBiomas Project, 2023). For landscape structure, we used metrics calculated at the landscape level, considering all LCLU classes present within the buffer. For forest configuration, we used metrics calculated at the class level, focusing solely on the Forest Formation subclass within the Forest macroclass (MapBiomas Project, 2023). We used these variables to quantify landscape features that may influence the structure of crop-pollinator interaction networks.

Farm complexity and crop heterogeneity summarise landscape metrics calculated based on LCLU within a 250 m radius buffer from the farm centroids. To compute the landscape metrics summarised in these variables, we used raster images of LCLU generated from drone images, georeferenced points, and satellite images (*Capítulo I*). For farm complexity, we used metrics calculated at the landscape level, considering all LCLU classes within the buffer. For crop heterogeneity, we used metrics calculated at the landscape level, focusing exclusively on the LCLU classes corresponding to the sampled crops. We used farm complexity and crop heterogeneity to quantify the spatial management of farms, which may affect the structure of crop-pollinator interaction networks.

3.2.4. Network analyses

From the pollination interaction data obtained for each farm, we constructed 13 independent weighted adjacency matrices, with crops represented in rows and bees in columns. For each farm, we built a weighted crop-pollinator interaction network. For each of these networks, we calculated network-level metrics, including the number of links, interaction richness, pollinator richness, asymmetry, connectance, modularity, nestedness, and specialisation.

We used the number of links, interaction richness, and pollinator richness as mediating variables, as they may represent more direct responses of network structure to the effects of landscape features and farm management. The number of links is defined as the total number of interactions occurring between all individuals involved on the farms, accounting for redundant interactions that occurred multiple times between the same species pair. This metric quantifies network size and interaction abundance and is directly related to the number of bees sampled on the farms. Interaction richness refers to the number of unique pairwise interactions between crop and pollinator species. This metric serves as an estimator of interaction diversity on the farms. Pollinator richness directly corresponds to the number of pollinator species observed on each farm, making it an estimator of bee diversity.

Asymmetry, connectance, modularity, nestedness, and specialisation were used as response variables, as they may represent more complex responses of network structure to the effects of landscape features and farm management. We computed the raw network metrics using the "networklevel" function from the R-package "bipartite" (Dormann et al., 2008). Web asymmetry is calculated as the ratio between crop richness and pollinator richness. Positive values indicate a higher proportion of pollinators, negative values indicate a higher proportion of crops, and a value of zero represents a 1:1 ratio (Dormann et al., 2009), and can indicate the degree of dependence between trophic levels (Blüthgen et al., 2007). Connectance is determined as the ratio of observed interaction richness to the total possible interactions, calculated based on all possible combinations of crops and pollinators (Dormann et al., 2009). This metric expresses the proportion of realised interactions in the network (Blüthgen et al., 2007). Modularity quantifies the network's division into modules using Newman's *Q* modularity measure (Dormann et al., 2009). To compute modularity, we used the function "metaComputeModules" from the R-package "bipartite." This metric evaluates the degree to which interactions in the network are compartmentalised into groups of species that preferentially interact (Dormann et al., 2009). Nestedness measures the extent to which the network is organised into a nested pattern. We employed the *NODF* metric, which is considered more consistent for nestedness assessment (Almeida-Neto et al., 2008; Dormann et al., 2008). This metric reflects how interactions involving rare species are subsets of those involving the most abundant species (Almeida-Neto et al., 2008). Finally, we measured network specialisation using the H_2' metric, which evaluates the deviation of observed interactions from expectations based on the marginal totals of the matrix. This metric quantifies the network's complementary specialisation, that is, the degree to which species in a network interact selectively, complementing each other in their interactions and reducing interaction redundancy (Blüthgen et al., 2008, 2006).

For all crop-pollinator networks, we constructed a rarefaction curve and calculated sampling completeness to assess the quality of interaction sampling on farms (Chacoff et al., 2012). To perform rarefaction, we transformed the adjacency matrices into a one-dimensional vector, indicating the number of interactions between each unique pairwise interaction in the network. We then removed zero-interaction pairs and computed the observed interaction richness. Using the "estimateR" function from the R-package "vegan" (Oksanen et al., 2024), we estimated the expected interaction richness for each farm. Next, we used the "rarefy" function from the same package to rarefy the interactions (Oksanen et al., 2024). Finally, we calculated the sampling completeness of the networks by dividing the observed interaction richness by the expected interaction richness (Chacoff et al., 2012; Vizentin-Bugoni et al., 2016).

3.2.5. Statistical analyses

To analyse the effect of landscape features and farm management on the structure of crop-pollinator interaction networks, we used the piecewise framework for structural equation modelling (PSEM – Lefcheck, 2016). For each response variable (asymmetry, connectance, modularity, nestedness, and specialisation), we fitted a PSEM. The model fitting process incorporated the best model for the response variable and the best models for intermediate variables identified as significant predictors in the best model of the respective response variable. The structural models were fitted using the "psem" function from the R-package "piecewiseSEM" (Lefcheck, 2016). In this framework, we were able to comparatively assess the direct effects of predictor and mediator variables on the response variables using standardized beta values (βStd.), as well as the indirect effects of predictor variables on the response variables. The indirect effect is determined by multiplying the standardized beta of the predictor's effect on the mediator by the standardized beta of the mediator's effect on the response.

In this framework, we build full base models for each intermediate variables and for each response variables. These models were constructed with the "glm" function from the R-package "stats" (R Core Team, 2024). They are subjected to an exhaustive model selection considering all possible combinations of variables using the “dredge” function from the package “MuMIn” (Bartoń, 2024). Only additive combinations were allowed, excluding interactions between variables, ranging from 0 (null model, ~1) to the maximum possible number of predictors (four predictors for intermediate variables and eight predictors for response variables).

The best model was determined by the lowest AICc value. Although we considered models with ΔAICc ≤ 2.0 and similar weight equally plausible to the best model, we only included the best models during PSEM construction. To assess the relative importance of variables in each model, we used the “sw” function from the R-package “MuMIn,” which computes the sum of model weights across all models containing each explanatory variable.

For the number of interactions, interaction richness, and pollinator richness, used as intermediate variables, we built complete base models using landscape structure, forest configuration, farm complexity, and crop heterogeneity as predictor variables. Models for interaction richness and pollinator richness were fitted using a Poisson distribution family with a log link function. Although the number of links is a discrete variable, we fitted its model using a Gaussian distribution family with an identity link function.

For asymmetry, connectance, modularity, nestedness, and specialisation, used as response variables, we built complete base models using landscape structure, forest configuration, farm complexity, crop heterogeneity, number of links, interaction richness, and pollinator richness as predictor variables. Since sampling completeness can affect network structure, we added it as a predictor variable. All these models were fitted using a Gaussian distribution family with an identity link function.

We validated the models using tests for uniformity, dispersion, and outliers in model residuals, performed with the “testResiduals” function from the R-package “DHARMa.” When applicable, and to avoid collinearity, we also checked the variance inflation factor (VIF) using the “vif” function from the R-package “car.” None of the best-fitting final models failed residual tests or exhibited variables with VIF ≥ 10. No missing relationships among predictor variables were detected using the “fisherC” function from the R-package “piecewiseSEM” (Lefcheck, 2016).

3.3. RESULTS

3.3.1. Network's structure

The number of interactions showed an intermediate variation across farms, while interaction richness and pollinator richness exhibited high variation (Table 1). Among the topology metrics, only asymmetry showed intermediate variation, whereas connectance, modularity, nestedness, specialization, and sampling completeness displayed high variation across farm networks (Table 1). Asymmetry ranged from moderate to high, always skewed towards pollinators (i.e., pollinator richness > crop richness, Table 1). The connectance range indicates networks with very low to moderate connectance, but low on average (Table 1). The modularity range suggests networks with very low to moderate modularity (Table 1). The nestedness range reflects a weakly to moderately nested pattern (Table 1). The specialisation range presents networks from weakly to highly specialised, with an intermediate average specialisation (Table 1). Finally, network sampling completeness was intermediate on average but exhibited a large range (Table 1).

Table 1 Summary statistics of network metrics across farms. The table shows the minimum (Min), maximum (Max), mean, standard deviation (SD), and coefficient of variation (CV, %) for each metric, including the number of links, interaction richness, pollinator richness, asymmetry, connectance, modularity, nestedness, specialization, and sampling completeness. S’ after the terms 'pollination' and 'interactions' refers to richness.

Metric	**Min**	**Max**	**Mean**	**SD**	**CV (%)**
Number of links	288	817	505	62	12.28
Interaction S	30	78	51	14	27.45
Pollinator S	18	35	28	6	21.43
Asymmetry	0.415	0.784	0.635	0.119	18.74
Connectance	0.181	0.476	0.319	0.088	27.59
Modularity	0.167	0.582	0.421	0.111	26.37
Nestedness	24.7	52.9	39.3	8.2	20.87
Specialization	0.254	0.830	0.544	0.151	27.76
Sampling completeness	22.2	79.9	55.3	15.1	27.31

3.3.2. Structural models

The number of links was positively affected only by farm complexity (Table 2). Interaction richness was positively affected by crop heterogeneity and negatively affected by forest configuration (Table 2). Pollinator richness was marginally affected by crop heterogeneity (Table 2). Asymmetry was positively affected by pollinator richness and negatively affected by interaction richness (Table 2). Connectance was negatively affected by interaction richness (Table 2). Modularity was not affected by any of the predictors tested. Nestedness was positively affected by the number of links (Table 2). Finally, specialization was negatively affected by crop heterogeneity (Table 2). More information about the models' summaries on Table 2. The relative importance (cumulative weight) of the predictors in each model is shown in Figure 1. We found no effects of sampling completeness on any response variable.

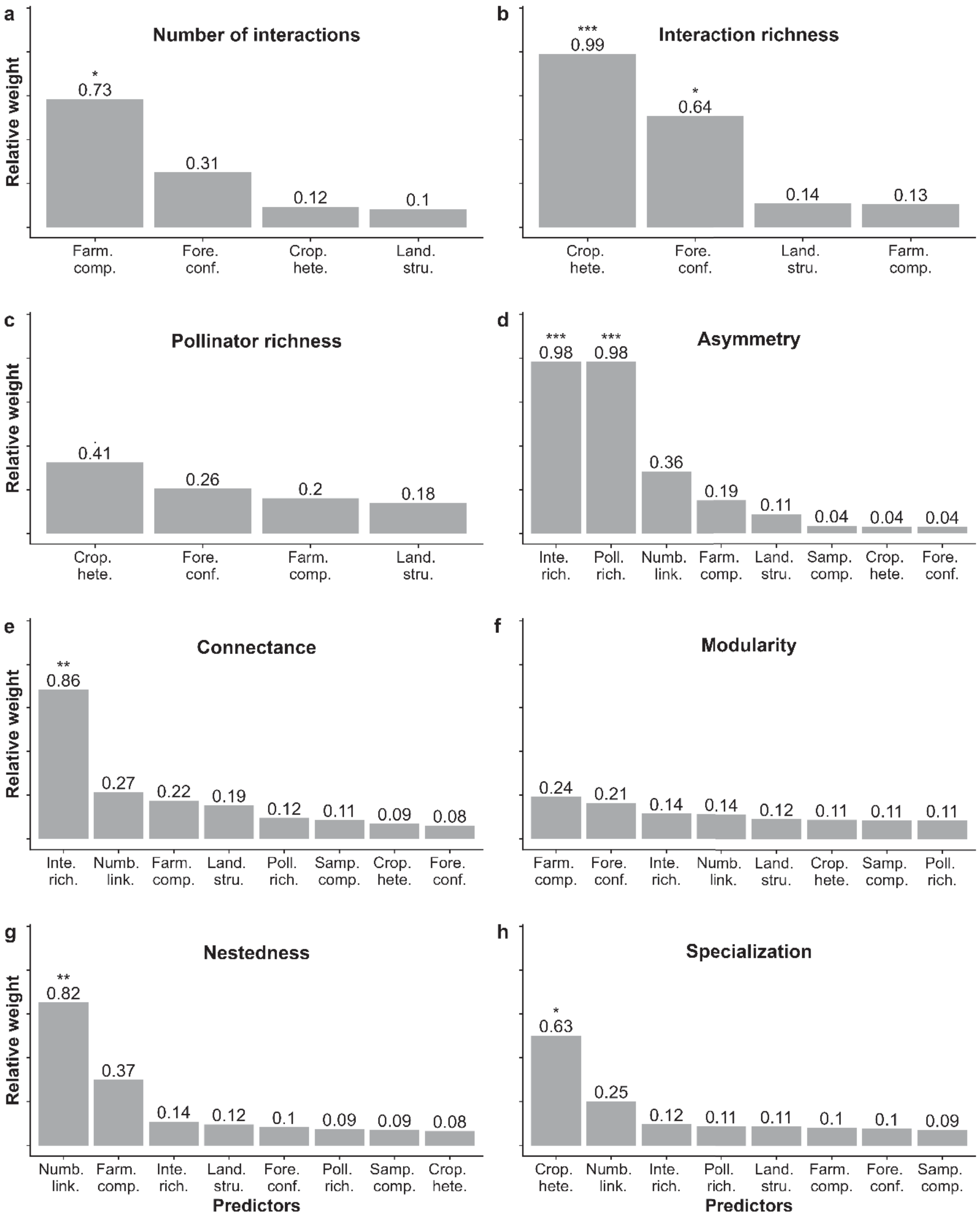


Figure 1 Relative importance (cumulative weight) of predictors in the structural equation models for different network properties. Each panel represents a response variable: (a) number of interactions, (b) interaction richness, (c) pollinator richness, (d) asymmetry, (e) connectance, (f) modularity, (g) nestedness, and (h) specialization. Bars indicate the cumulative weight of each predictor across all selected models in which the respective variable appears. Predictors include farm composition (Farm. comp.), forest configuration (Fore. conf.), crop heterogeneity (Crop. hete.), landscape structure (Land. stru.), interaction richness (Inter. rich.), pollinator richness (Poll. rich.), number of links (Numb. links), sample completeness (Samp. comp.), and habitat cover (Habi. cov.). Asterisks indicate statistical significance (. $p < 0.10$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

Table 2 Results of the generalized linear models (GLMs) fitted for the analyzed response variables. The columns show: the dependent variable (Response), the independent variables (Predictors), the family distribution with the link function used for each model, the intercept estimate (Intercept), the standard error (SE), the t-value or z-value (t/Z value), the p-value (p-value), the Akaike Information Criterion (AIC), and the model weight. A lower AIC indicates a better model fit. S’ after the terms 'pollination' and 'interactions' refers to richness.

Response	**Predictor**	**Family distribution (link function)**	**Intercept**	**β**	**SE**	**t/Z value**	**p-value**	**AIC**	**Weight**
Number of links	Farm complexity	Gaussian (identity)	505.462	21.242	9.343	2.274	0.044	169.180	0.352
Interaction S	Crop heterogeneity	Poisson (log)	3.913	0.034	0.010	3.498	0.000	98.002	0.491
	Forest configuration	Poisson (log)		-0.025	0.011	-2.201	0.028		
Pollinator S	Crop heterogeneity	Poisson (log)	3.328	-0.011	0.012	1.665	0.096	82.289	0.233
Asymmetry	Pollinator S	Gaussian (identity)	0.565	0.023	0.005	4.642	0.001	-29.581	0.327
	Interaction S	Gaussian (identity)		-0.011	0.002	-5.446	0.000		
Connectance	Interaction S	Gaussian (identity)	0.566	-0.005	0.001	-3.750	0.003	-32.188	0.237
Modularity		Gaussian (identity)	0.421					-17.339	0.182
Nestedness	Number of links	Gaussian (identity)	20.357	3.647	0.010	3.647	0.004	86.333	0.250
Specialization	Crop heterogeneity	Gaussian (identity)	0.544	-2.436	0.008	-2.436	0.033	-12.967	0.249

3.3.3. PSEM models

Overall, all proposed models exhibited a good fit (Table 3). Asymmetry was significantly explained ($R^2 = 0.75$; Figure 2) by a direct positive effect of pollinator richness (βStd. = 1.103; SE = 0.005; t = 4.642, p = 0.001) and a direct negative effect of interaction richness (βStd. = -1.294; SE = 0.002; t = -5.446, p < 0.001). Thus, asymmetry was influenced by an indirect positive effect of crop heterogeneity (βStd. = 0.495 mediated by pollinator richness) and forest configuration (βStd. = 0.446) mediated by interaction richness, and by an indirect negative effect of crop heterogeneity (βStd. = -0.735). Connectance was significantly explained ($R^2 = 0.56$; Figure 2) by a direct negative effect of interaction richness (βStd. = -0.749; SE = 0.001; t = -3.750, p < 0.003). Therefore, it was influenced by an indirect positive effect of forest configuration (βStd. = 0.258), and an indirect negative effect of crop heterogeneity (βStd. = -0.426). Nestedness was significantly explained ($R^2 = 0.55$; Figure 2) by a direct positive effect of the number of links (βStd. = 0.740; SE = 0.010; t = 3.647, p = 0.004). Thus, it was influenced by an indirect positive effect of farm configuration (βStd. = 0.418). Finally, specialization was significantly explained ($R^2 = 0.35$; Figure 2) solely by a direct negative effect of crop heterogeneity (βStd. = -0.592; SE = 0.008; t = -2.436, p = 0.033).

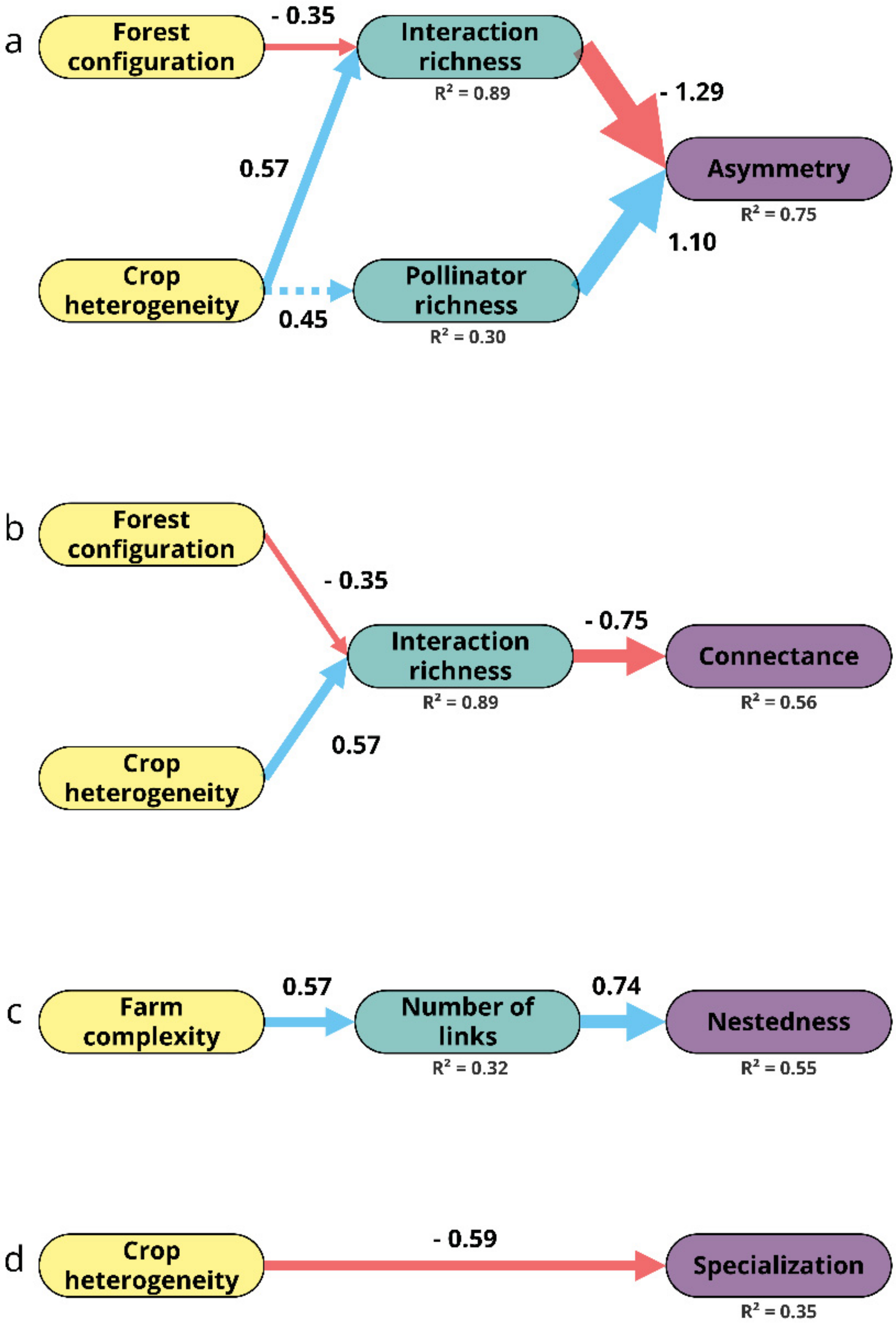


Figure 2 Piecewise structural equation models (PSEM) schema illustrating the relationships between landscape management variables, mediator variables, and interaction patterns. Each panel represents a different response variable: (a) Asymmetry, (b) connectance, (c)

nestedness, and (d) specialization. Arrows indicate significant relationships (p-values ≤ 0.05), red for negative effects and blue for positive effects. Dashed arrows indicate partially significant relationships (p-values > 0.05 and ≤ 0.10). Numbers along the arrows denote standardised path coefficients (βStd.). The R^2 values below the response variable boxes indicate the proportion of variance explained by the model. Yellow: predictor variables; green: intermediate predictor variables; purple: response variables.

Table 3 Results of the piecewise structural equation models (PSEM) fitted for the analysed response variables. The columns show: the dependent variable (Response), the independent variables (Predictors), the chi-squared statistic (χ^2) for global fit, the degrees of freedom (df χ^2) and p-value (p χ^2), Fisher's C statistic (C_{Fisher}) with its degrees of freedom (df C_{Fisher}) and p-value (p C_{Fisher}), and the Akaike Information Criterion (AIC), which helps compare models, with lower values indicating better fit and simplicity. S' after the terms 'pollination' and 'interactions' refers to richness.

Response	**Predictor**	**χ^2**			**CFisher**			
		χ^2	**df**	**p**	**C_{Fisher}**	**df**	**p**	**AIC**
Connectance	Interaction S	0.077	2	0.962	0.555	4	0.968	65.814
Asymmetry	Pollinator S + Interaction S	4.932	4	0.294	8.618	8	0.376	150.71
Nestedness	Number of links	3.222	1	0.073	4.168	2	0.124	255.51
Specialization	Crop heterogeneity	0	0	1	NA	NA	NA	-12.967

3.4. DISCUSSION

We found that crop-pollinator interaction networks in smallholder polycultures present strong asymmetry, low connectance, and intermediate nestedness, and low to high specialisation. The wide variation in network properties suggests that individual farm contexts strongly influence network structure. We found that the underlying structure of networks is primarily shaped at the local scale. We observed that heterogeneity in crop composition played a key role in determining interaction richness on farms and possibly influenced pollinator species richness as well. This confirms that a greater diversity of floral resources, both in variety and proportion, attracts a higher richness of pollinators, thereby enhancing the potential for unique pairwise interactions (Ebeling et al., 2008; Fowler et al., 2016).

3.4.1. Crop heterogeneity

In this study, we found that crop-pollinator interaction networks in smallholder polycultures exhibit a fragile structure. This results from their strong asymmetry, low connectance, and intermediate nestedness (Bascompte and Scheffer, 2023; Dunne et al., 2002; Pastor et al., 2012). Highly asymmetric networks are particularly vulnerable to the loss of key species in the less abundant or rich trophic level (Pastor et al., 2012). With high asymmetry, the loss of key species may trigger a "rivet-like" extinction pattern. Networks with low connectance show reduced interaction sharing among species, which lowers interaction redundancy. Redundancy plays a crucial role in maintaining interaction networks (Dunne et al., 2002; Thébault and Fontaine, 2010). Without redundancy in their interactions, species are more likely to be extirpated from networks when they lose their preferred partners. Pollination networks are typically nested (Bascompte et al., 2003; Thébault and Fontaine, 2010), which enhances their resistance to species loss by buffering extinction cascades (Memmott et al., 2004). Low nestedness may therefore indicate networks that are more vulnerable to disturbances, especially when highly connected species are lost (Memmott et al., 2004; Solé and Montoya, 2001).

Here, we also found that crop-pollinator networks in smallholder polycultures can exhibit heterogeneous structures. This pattern is evident in the wide variation in network modularity and specialisation (Blüthgen et al., 2008; Olesen et al., 2007). Contrary to our expectations, we did not observe consistently modular networks. We anticipated higher modularity on farms, as some Solanaceae crops (e.g., *S. melongena*, aubergine) are visited exclusively by specialised buzz-pollinating bees (e.g., *Thygater analis*) (Mesquita-Neto et al., 2018). Moreover, all farms contained crops dependent on buzz pollination, albeit with varying species richness and proportions. Agricultural systems are generally composed of generalist species (Gay et al., 2024), which is reinforced by a pollinator-skewed network, leads to networks with lower complementary specialisation (Blüthgen et al., 2007). This wide variation in both, modularity and specialisation, suggests that individual farm contexts, inside the 250 m buffer and/or surrounding, strongly influence network structure.

We found that the underlying structure of networks is primarily shaped at the local scale. We observed that heterogeneity in crop composition and proportions played a key role in determining interaction richness on farms and possibly influenced pollinator species richness as well. This confirms that a greater diversity of floral resources, both in variety and proportion, attracts a higher richness of pollinators, thereby enhancing the potential for unique pairwise interactions (Ebeling et al., 2008; Fowler et al., 2016).

The negative relationship between asymmetry and interaction richness indicates that an increase in unique pairwise interactions is associated with a more balanced species richness across the crop/pollinator trophic levels. Thus, greater interaction richness may enhance the stability of crop–pollinator networks by mitigating species extinction–coextinction dynamics in highly asymmetric networks (Pastor et al., 2012).

Crop heterogeneity may increase interaction richness through two main pathways. First, greater crop heterogeneity corresponds to higher plant species richness due to the landscape metrics that constitute this axis (*Capítulo* I, Appendix A – Table S1, Figures S1 and S2). Second, increased crop heterogeneity, particularly in terms of species richness, is expected to enhance pollinator richness (Ebeling et al., 2008; Gómez-Martínez et al., 2022; Kral-O'Brien et al., 2021). Given these mechanisms, crop heterogeneity should lead to higher interaction richness, by increasing species richness.

Therefore, by increasing species and interaction richness, farms with greater crop diversity should exhibit lower network asymmetry, as they promote pairwise interactions that would not occur in farms with low crop heterogeneity, that is dominated by a few crops that occupy large areas. These crops are visited by a limited number of abundant pollinators, which monopolise plant interactions (Fowler et al., 2016; Sponsler et al., 2023). However, if crop heterogeneity increases with little or no corresponding rise in crop richness (e.g., through greater fragmentation of crop plots), , there could still be an effect on pollinator richness (Sponsler et al., 2023)., and crop heterogeneity might reinforce network asymmetry.

A high diversity of plants, in terms of variety and abundance and both in this study expressed by crop heterogeneity, promotes preferential interactions by pollinators (Fowler et al., 2016; Gómez-Martínez et al., 2022). Because of the relief of competitive pressures given by the greater availability of resources, pollinators tend to visit crops with which they have a greater affinity (Gómez-Martínez et al., 2022), reducing interaction redundancy while also alleviating resource competition (Sponsler et al., 2023). Alternatively, some species may shift their foraging to less abundant crops that face lower competition (Sponsler et al., 2023). In both cases, there should be a reduction in connectance in response to crop heterogeneity. It is worth noting that the reduction in connectance is a direct consequence of increasing interaction richness. This pattern is fundamentally mathematical, as interaction richness tends to grow quadratically, while the number of realised interactions does not increase at the same rate (Blüthgen et al., 2006; Valdovinos et al., 2009).

Crop diversity may also play an important role in regulating network specialisation, because most of interactions arises from non-selective interactions, driven in part by the high proportion of exotic species, which must meet their resource demands while bypassing coevolutionary constraints (Corcos et al., 2020; Montero-Castaño and Vilà, 2017). Thus, In general, agricultural networks tend to be more generalist, exhibiting mid-low complementary specialisation (Gay et al., 2024). This high generalism in interactions is particularly evident for crops – none of the 26 studied here are native to the region – and for pollinators that are globally widespread as alien species, such as *A. mellifera*. However, in this study, we observed networks with a wide range of specialisation levels. Nonetheless, farms with fewer crop species, especially those arranged in homogeneous plots, exhibited higher interaction selectivity.

3.4.2. Farm complexity

The effect of farm complexity over interaction richness does not contradict the crop heterogeneity in enhancing interaction richness by reducing competition. Rather, it suggests that farms with low crop diversity and homogeneous plots tend to be dominated by abundant pollinators that exhibit mass foraging (Montero-Castaño and Vilà, 2017; Rollin et al., 2013). As a result, relatively generalist crops (e.g., *C. annuum* and *S. lycopersicum*) and pollinators (e.g., *B. pauloensis* and *A. mellifera*) may form networks with specialized structures. Taken together, the effects of crop heterogeneity on specialization and the effect of farm complexity on interaction richness can explain the high selectivity of interactions on farms with few abundant crops. Thus, complementary specialisation on farms may not arise from species' inherent selectivity but rather from their dominance over resources due to density-dependent processes.

Farms with greater spatial complexity – considering their natural elements, crops, and other components – exhibited a higher number of links, resulting in larger networks. This effect likely arises because a more complex arrangement of microhabitats increases interaction opportunities for pollinator species (Fahrig et al., 2011; Moreira et al., 2015). Moreover, since areas with greater farm complexity tend to an increased mix of forest and grassland patches, abundant social species adapted to this type of landscape (e.g., *A. mellifera*) may benefit, increasing their number of links (Quinlan et al., 2021).

By increasing the number of interactions within networks, farm complexity enhances a key feature for the resilience of crop-pollinator networks: their nestedness (Bascompte and Scheffer, 2023). This finding is particularly relevant given that crop-pollinator networks observed here are less nested than networks observed in natural areas (Bascompte et al., 2003). Thus increasing farm complexity may potentially make them less susceptible to background extinction-coextinction cascades (Burgos et al., 2007; Gaiarsa and Guimarães, 2019).

Because, farms with higher complexity values exhibit greater spatial heterogeneity in the arrangement of their elements (e.g., more land-use classes, divided into smaller, interspersed fragments). Our results indicate that nestedness is influenced not only by the spatial distribution of resources but also by elements that may either hinder or facilitate pollinator movement across the farm, as well as the exposure of crops to pollinators (Boscolo et al., 2017; Quinlan et al., 2021).

3.4.3. Forest configuration

Beyond local farm factors, the surrounding landscape context also influenced network structure. The configuration of native vegetation is a well-established factor influencing interactions on farms of different sizes and management practices (Hass et al., 2018; Hipólito et al., 2018; Nery et al., 2018; Rahimi et al., 2022). Here we found specifically that farms located in landscapes with higher forest configuration values, that is, a greater number of smaller, more irregularly shaped fragments exhibited lower interaction richness. This suggests that high natural habitat fragmentation can create a considerable impermeable matrix, likely acting as a barrier to the movement of some pollinators (Hadley and Betts, 2012) and for the establishment of nests due to the lack of forest resources and habitat (Kennedy et al., 2013). Even if farm pollinator richness remains unaffected, fragmentation likely alters which resources these pollinators can access on the farms, probably due to the energy expended spent traveling from the nest to the resource sources (Jha and Kremen, 2013; Pioltelli et al., 2024). Another possibility is that reduced interaction richness reflects the dominance, or even monopolisation, of interactions by pollinator species better adapted to foraging in fragmented landscapes (e.g., *Bombus* spp., *A. mellifera*) (Coutinho et al., 2021; Quinlan et al., 2021).

Conversely, forest configuration enhanced network asymmetry, likely due to fragmentation effects. Farms in more fragmented landscapes tend to receive fewer floral visitors (Boscolo et al., 2017; Moreira et al., 2015), directly reducing interaction richness, once lower pollinator abundance promotes lower pollinator richness leading to fewer interaction possibilities. Additionally, a smaller pool of pollinators is likely to interact with more abundant or familiar resources (Bascompte et al., 2003), optimising foraging by avoiding rarer plants or not favourite plants. This effect may be particularly pronounced on farms with low crop diversity, as it amplifies asymmetry already driven by management decisions (e.g., growing few and abundant crops).

As increased forest fragmentation reduces the connectance of crop-pollinator networks by decreasing interaction richness, it counterbalances the positive effect of crop heterogeneity on connectance. Ultimately, this demonstrates that crop-pollinator network structure is not only shaped across multiple scales but also that both landscape context and on-farm management can influence the same network properties in varying intensities and directions. Thus, in contrasting scenarios (e.g., an ecologically intensive farm within a highly degraded landscape, or vice versa), sustainable management at one scale may have its positive effects on biodiversity diminished or nullified by intensive management by negative impacts at another scale (Brittain et al., 2010), or even make them more relevant in specific scenarios (Kennedy et al., 2013; Tscharntke et al., 2012b). In more extreme cases, the negative effects of both scales may impose increased threat to pollinator biodiversity and essential pollination services for crops (Tscharntke et al., 2012b). This highlights the fundamental importance of integrated sustainable management at both local and regional levels for conserving interaction diversity and the ecosystem services it provides (Kremen and Merenlender, 2018; Steffan-Dewenter and Westphal, 2008).

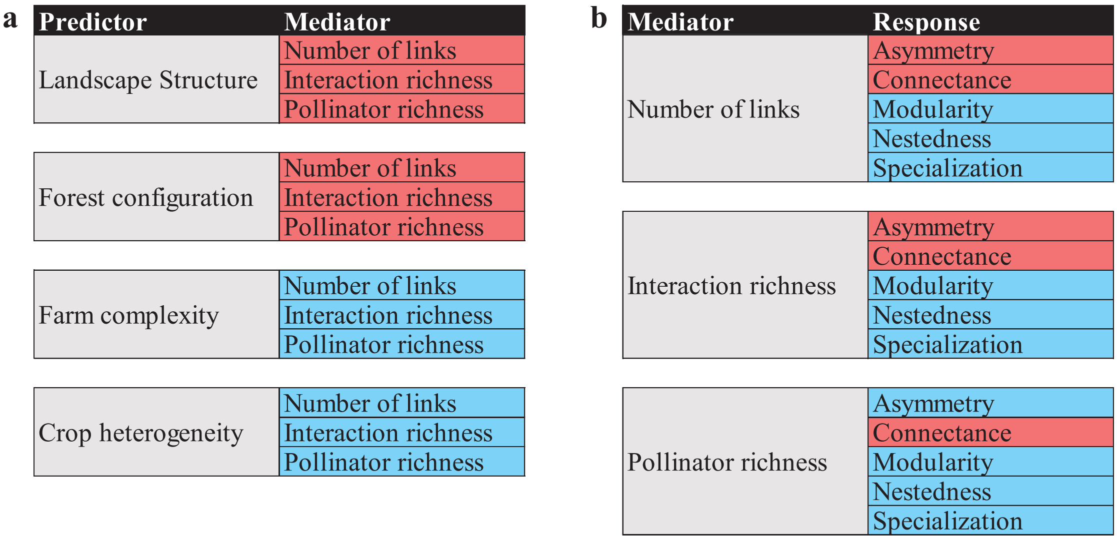
While our study provides valuable insights, certain limitations must be recognised. Since our analysis focuses exclusively on smallholder polycultures, comparative studies across different farming systems are necessary to determine the broader applicability of our findings. Addressing these gaps will be essential for developing comprehensive strategies that promote pollinator-friendly agriculture and safeguard ecosystem services.

3.5. CONCLUSIONS

Our findings underscore the role of farm management in shaping crop-pollinator networks. From a conservation perspective, these results demonstrate that decisions made at the farm level directly affect the pollination services provided to the crops in polycultures.

Beyond farm management, the broader landscape context also plays a crucial role in structuring interaction networks, highlighting the multiscale nature of pollination networks. This underscores the importance of integrating both local farm management and landscape-scale planning to enhance pollination services across agricultural systems.

APPENDIX



a

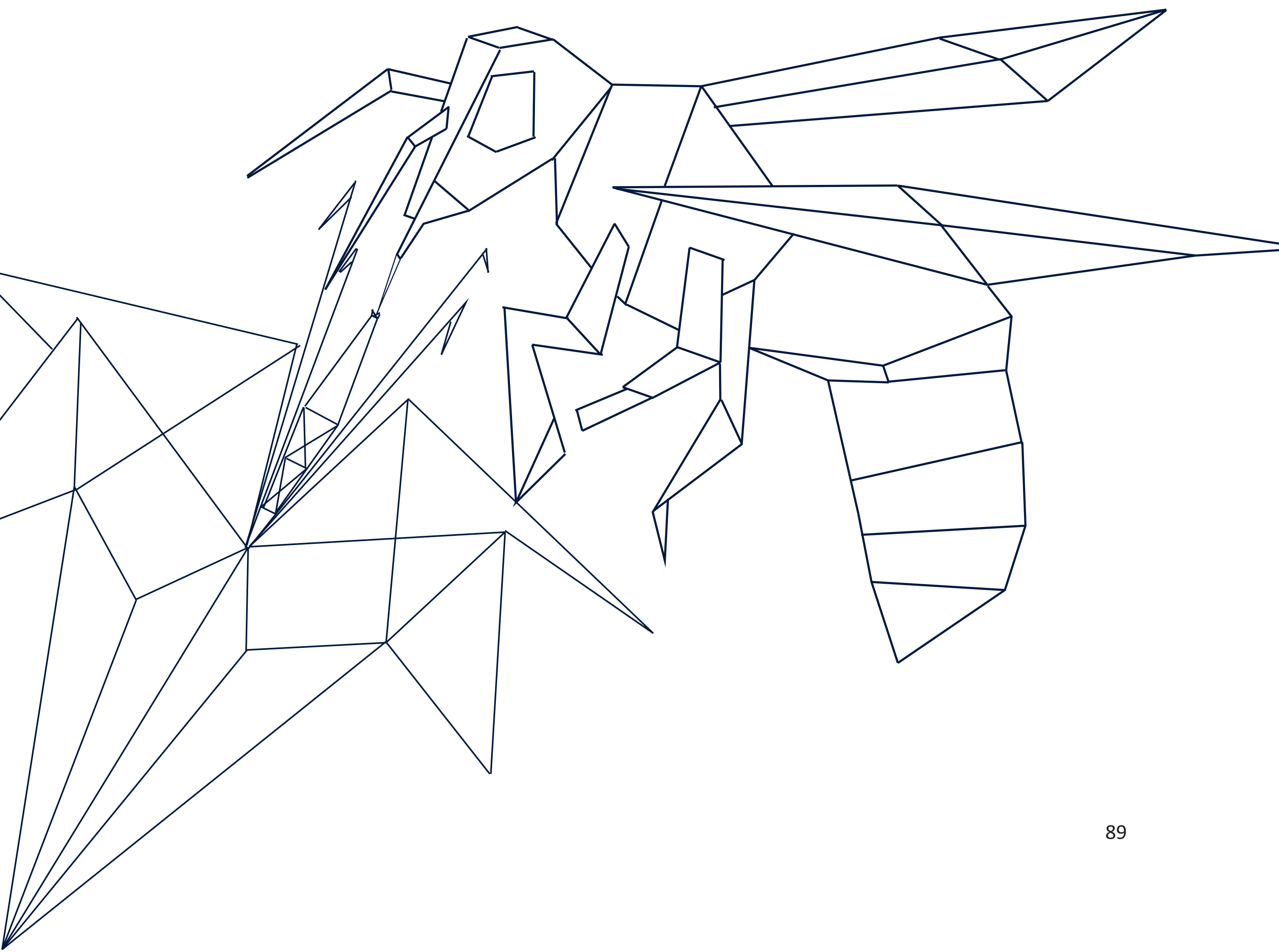
Predictor	Mediator
Landscape Structure	🟥 Number of links
	🟥 Interaction richness
	🟥 Pollinator richness
Forest configuration	🟥 Number of links
	🟥 Interaction richness
	🟥 Pollinator richness
Farm complexity	🟦 Number of links
	🟦 Interaction richness
	🟦 Pollinator richness
Crop heterogeneity	🟦 Number of links
	🟦 Interaction richness
	🟦 Pollinator richness

b

Mediator	Response
Number of links	🟥 Asymmetry
	🟥 Connectance
	🟦 Modularity
	🟦 Nestedness
	🟦 Specialization
Interaction richness	🟥 Asymmetry
	🟥 Connectance
	🟦 Modularity
	🟦 Nestedness
	🟦 Specialization
Pollinator richness	🟦 Asymmetry
	🟥 Connectance
	🟦 Modularity
	🟦 Nestedness
	🟦 Specialization

Figure S1 Hypothesised direct relationships between predictor, mediator, and response variables in our piecewise structural equation model (PSEM). Panel (a) illustrates the expected effects of predictors (landscape structure, forest configuration, farm complexity, and crop heterogeneity) on mediators (number of links, interaction richness, and pollinator richness). Panel (a) illustrates the expected effects of mediators on response variables (asymmetry, connectance, modularity, nestedness, and specialization). Blue represents expected positive relationships, whereas red indicates expected negative relationships. We hypothesized that predictors would not have a direct effect on responses for all variables involved.

4. CAPÍTULO III: ROBUSTEZ DAS REDES CULTURA-POLINIZADOR EM POLICULTURAS



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Title

Resilient agriculture: Effect of agricultural management and landscape features on the robustness of crop-pollinator networks

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ABSTRACT

The robustness of pollination networks represents their resilience to species loss across different scenarios that trigger extinction-coextinction cascades. In agricultural environments, this parameter functions as a proxy for the stability of pollination ecosystem service provision while ensuring resources for pollinator conservation. Integrating network analyses with landscape ecology techniques, we aim to understand which local and regional agricultural factors contribute to the robustness of crop-pollinator networks in smallholder polycultures under different extinction-coextinction scenarios. To assess this, we modelled robustness considering different combinations of primary extinction targets, extinction methods, and interaction rewiring. Through structural equation modelling, we examined how aspects of landscape structure and agricultural management affected robustness in these different scenarios, mediated by network topology. The results showed that crop-pollinator network robustness is more sensitive to crop than pollinator extinctions due to network asymmetry, as many pollinators rely on only a few crops. However, nestedness can buffer extinction cascades in random crop loss scenarios. Meanwhile, higher connectivity can amplify cascades when crops are lost but buffer them when pollinators are lost. Robustness was strongly related to the primary extinction order, with networks being most sensitive to extinctions ranked by interaction degree, followed by random extinctions, and least sensitive to those ranked by abundance. In random removal scenarios, landscape structure and farm complexity drove the network topology's effect on robustness, while forest configuration could reduce robustness under random crop loss. In other scenarios, conventional management, by lowering pollinator richness compared to organic management, also weakened crop-pollinator network robustness. Overall, the study highlights that strategic landscape and farm management can enhance agroecosystem sustainability by fostering robust crop-pollinator networks. Strengthening these interactions promotes pollinator ecological health, increases agricultural productivity, and supports biodiversity conservation. Integrating ecological features into agricultural planning is crucial for building resilient systems that benefit both farmers and the environment.

Keywords

Agricultural landscapes, ecosystem services, interaction networks, pollinator extinction, sustainable agriculture.

Highlights

- Farm management practices shape crop-pollinator network robustness in smallholder polycultures.
- Crop diversity enhances pollinator network stability and interaction efficiency.
- Landscape structure influences pollinator networks through interaction dynamics.
- Sustainable agricultural practices foster robust interactions between crops and pollinators.
- Landscape and farm level mechanisms affects pollinator health and ecosystem services in agriculture.

4.1. INTRODUCTION

The robustness of interaction networks might be understood as the relationship between the extinctions at a given trophic level and the cascading secondary extinctions at another trophic level (i.e., the proportion of surviving interactors) (Dunne et al., 2002; Memmott et al., 2004; Solé and Montoya, 2001). A stronger directly proportional relationship between primary and secondary extinctions indicates a faster network collapse, thus implying lower robustness (Memmott et al., 2004). The robustness is a network-level metric sensitive to the methods applied in models estimating extinction and co-extinction curves. The trophic level targeted for primary extinction (CaraDonna and Waser, 2020; Schleuning et al., 2016), the rules for ordering its extinctions (Memmott et al., 2004), the possibility of rewiring and the rules governing its occurrence (Kaiser-Bunbury et al., 2010; Vizentin-Bugoni et al., 2020), and the type of secondary extinction cascade propagation are parameters and choices that may result in varying robustness values for the same network (Bane et al., 2018). This approach thus provides many options for simulating extinctions and co-extinctions, offering insights into what these different patterns could imply for various ecological interaction systems.

In pollination ecology research, the robustness concept can represent a proxy for the resilience of plant-pollinator interaction networks in response to disturbances that drive species extirpation within the network. The robustness measure, therefore, operationalises the level of structural stability of a pollination network and the interaction's functional integrity (Kaiser-Bunbury et al., 2017). A well-developed body of knowledge assesses the robustness of ecological networks in natural systems. Overall, these studies demonstrate consistent patterns regarding the dependence of robustness on network topology, such as network asymmetry (Okuyama and Holland, 2008; Pastor et al., 2012; Santamaría et al., 2016), connectance (Dunne et al., 2002; Vieira and Almeida-Neto, 2015), nestedness (Morrison et al., 2020; Neff et al., 2021; Ramos-Jiliberto et al., 2012) and modularity (Morrison et al., 2020). Additionally, some studies indicate that the specialisation of species and interactions (which may reflect the degree of network specialisation) can also affect the robustness of mutualistic networks (Gaiarsa and Guimarães, 2019; Maia et al., 2021). In addition through the topology of the networks, the effect of environmental and ecological variables such as elevation, latitude (Wang et al., 2024), habitat amount (Evans et al., 2013), phenology (Ramos–Jiliberto et al., 2018), alien species or agricultural intensification (Morrison et al., 2020) influences network robustness. However, there is a gap in exploring the effects that anthropogenic gradients, such as agricultural gradients, may have on the robustness of pollination networks. In this study, we use robustness to species loss within the network as a proxy for the stability of pollination ecosystem service in crop-pollinator networks. Here, we examined whether and how surrounding landscape features and agricultural management can affect the network topology and the robustness of crop-pollinator networks formed in smallholder systems.

Intensive land cover and land use changes due to agricultural intensification have severely affected biodiversity patterns(Tscharntke et al., 2012b, 2005). In this context, ecosystem simplification, has led to a decline in pollinators' diversity and interaction (Bennett et al., 2020; Millard et al., 2021). In a local scale, farms employing intensive management practices (e.g., monocultures with pesticide application) exhibit lower pollinator richness and diversity (Hass et al., 2018; Mogren et al., 2016). Thus, agricultural intensification affects the structure of pollination interaction networks (Morrison et al., 2020), with potential consequences for the provision of pollination service. Despite that, there is evidence that more ecologically intensive management improves the diversity of pollinators, the stability of their interactions and the service provided (Bloom et al., 2023; Happe et al., 2018; Scheper et al., 2023). Thus, unrestrained agricultural intensification risks undermining agricultural functioning itself. Since most of crops depend, to some degree, on pollination (Allen-Perkins et al., 2022; IPBES, 2016), agricultural intensification at different scales can compromise crop yields and, consequently, food security (Tscharntke et al., 2012a). Considering future scenarios marked by substantial environmental changes, it is key to understanding how more sustainable agricultural management at local and regional scales can contribute to pollinators' conservation and pollination services.

Our objective in this study was to understand how landscape and agricultural management influence the robustness of crop-pollinator interaction networks in polyculture farms. To achieve this, we addressed three questions. (1) Which landscape factors (landscape structure and forest configuration) and management factors (farm complexity, crop heterogeneity, and farm management) impact the robustness of crop-pollinator networks? (2) Are these effects mediated by network topology (asymmetry, connectance, modularity, nestedness, and specialisation)? Finally, (3) does the rewiring of interactions mitigate secondary extinction cascades, thereby enhancing the resilience of crop-pollinator networks?

4.2. METHODS

4.2.1. Interaction data

For this study, we used data previously collected during the execution of the Ecosystem Services for Resilient and Sustainable Agriculture 2020/2024 project (CP 07/2019 Biodiversidade do Paraná number 212/2019).

We used interaction networks from 13 smallholder farms in the Miringuava and Miringuava-Mirim watersheds, São José dos Pinhais, Paraná, Brazil. We sampled this data during the rainy season between October 2020 and March 2021. This dataset resulted from 260 hours of sampling effort (20 h per farm) of active pollinator capture on crops during their flowering periods. Details of the experimental design and sampling method are in *Capítulo I*.

Together, the 13 interaction networks comprise 6571 interactions between 23 species of agricultural plants (including 22 crops and one green manure plant), and 103 species of pollinating bees. Bees belong to all five subfamilies that occur in Brazil: Andreninae, Apinae, Colletinae, Halictinae, and Megachilinae. We observed 330 unique pairwise crop-pollinator interactions. The networks observed on farms had 505.5 ± 156.0 interactions, consisting of 6.4 ± 2.9 crop species and 28.0 ± 5.4 bee species.

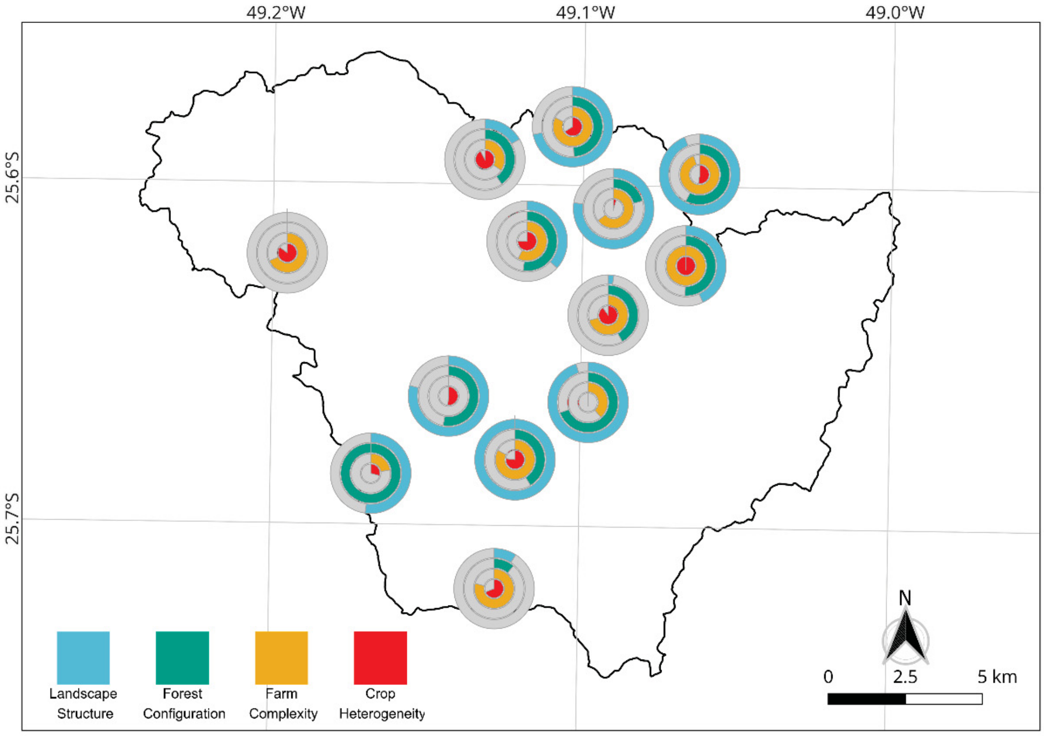

Figure 1. Map of sampling units with gradients of landscape and management variables. The filling of the rings corresponds to the standardised value along the PC1 axis, i.e., the standardised position of the sample unit on the x-axis; units with more filled rings are more distinct from those with less filled rings for each respective variable. Colors represent different variables: blue for Landscape Structure, green for Forest Configuration, yellow for Farm Complexity, and red for Crop Heterogeneity. The black line represents the Miringuava and Miringuava-Mirim watersheds boundaries, located in São José dos Pinhais, Paraná, Brazil. We slightly shifted the farm centroids for better visualisation. See Figure 1 in *Capítulo I* for the exact location of sample unit points. Map composition generated with QGIS 3.30.0 - 's-Hertogenbosch (https://www.qgis.org) using Hydrographic Divisions of Brazil (https://portaldemapas.ibge.gov.br/) for the base map. Datum EPSG:4326 – WGS 84.

4.2.2. Landscape and farm predictors

We used landscape structure, forest configuration, farm complexity, and crop heterogeneity as predictors of robustness in crop-pollinator interaction networks. These predictors correspond to the first axis of four principal component analyses (PCA) carried out independently (see *Capítulo I* for more details). Additionally, we used farm management, as a predictor variable, considering 1 for conventional farm management and 0 for organic management.

We generated landscape structure and forest configuration from landscape metrics computed from the MapBiomas land cover and use classification for the study region (MapBiomas Project, 2023). We computed the metrics for each sampling unit in a 1 km radius buffer from the farms' centroid. For landscape structure, we used landscape-level metrics considering all landscape classes in the buffer. For forest configuration we used class-level landscape metrics considering only the forest formation class.

We generated farm complexity and crop heterogeneity from landscape metrics computed from a land use and cover classification handmade (see *Capítulo I* for more details). For each sampling unit, we computed the metrics in a 250 m radius buffer considering the farms' centroid. For farm complexity we, used landscape-level metrics, considering all landscape classes in the buffer. For crop heterogeneity, we used landscape-level metrics that considered only the landscape classes corresponding to the sampled crops.

We perform the previous geoprocessing steps using the R-package "terra" (Hijmans, 2024) functions and the QGIS software, v.3.30 - 's-Hertogenbosch (QGIS Development Team, 2023). We calculated the landscape metrics with functions from the R-package "landscapemetrics" (Hesselbarth et al., 2019).

4.2.3. Robustness modelling

We used the function "robustness" implemented in the "bipartite" R-package to compute the robustness of crop-pollinator networks. This function calculates the area below the extinction curve generated by the function "second.extinct" (Dormann et al., 2009, 2008). However, to generate the extinction curve, we used an adaptation of "second.extinct", the "one.second.extinct.mod" function (Vizentin-Bugoni et al., 2020). The "second.extinct" function implements the secondary-only knockout models, where primary extinctions of a target guild lead to species extinction in the interacting guild (Bane et al., 2018; Memmott et al., 2004). From the relationship between the number of extinct species of the target guild and the number of surviving species of the interacting guild throughout the model interactions, we computed the robustness of the network with the "robustness" function (Bane et al., 2018; Dunne et al., 2002; Memmott et al., 2004). Using the "one.second.extinct.mod" we set all parameters included in the "second.extinct" function, in addition to the specific implementations of this modified function to control the rules for interaction rewiring.

To calculate robustness, we used the algorithm comprising four stages: (1) primary extinction; (2) rewiring (2.1 new partner's choice + 2.2 rewiring tries); (3) computation of survivors. The algorithm exited the loop when no target species remained for the primary extinction step. At this point the (4) robustness value was computed. If there were still targets for primary extinction, a loop was repeated from the third step to the first. When multiple partner choice were allowed, an internal loop between the partner's choice and rewiring tries steps during rewiring could occur (see Figure 1 in Vizentin-Bugoni et al., 2020 for deeper details). Here we considered different combinations of primary extinction targets, extinction orders, and opportunities for rewiring interactions, as explained below. We analysed 18 different robustness scenarios, and each one simulated 1000 times.

We separately modelled crops and pollinators as target guilds of primary extinction. Through the primary extinction of crop species in these simulations, we accessed the impacts that management decisions concerning the maintenance or removal crop diversity had on the robustness of crop-pollinator networks. Through the primary extinction of pollinator species, we assessed the effects of the loss of pollinator diversity on the robustness of these networks.

Regarding the extinction order of the target guild, we used three rules: (1) random, (2) abundance (less abundant species being extinct first), and (3) degree (more connected species being extinct first). Here, we used random extinction scenarios as a benchmark, as they are mathematically neutral and were expected to represent common agricultural scenarios (e.g., management decisions). Through the simulation of extinctions based on species abundance, we aimed to represent the effects of agriculture-driven, density-dependent mechanisms on the loss of less abundant species, such as crops with smaller planting areas and/or lower economic interest, as well as rarer pollinators (Memmott et al., 2004). Through the simulation of extinctions by degree, we explored the effect that extinctions of central species have on the robustness of crop-pollinator networks, considering that agricultural species central in networks might be more sensitive to crop pests (McDonald and Stukenbrock, 2016) or to mortality in important bee species (Goulson et al., 2015). We thus used this last scenario to prospect for relevant patterns for the conservation of these species.

To model interaction rewiring, we specified the probabilities of partners' choice, the rewiring probabilities, and the number of attempts and potential partners to rewire. In the new partner's choice phase (step 2.1), the algorithm allowed species that have lost their partners during the primary extinction phase to select new partners. We used abundance as a parameter to determine the choice of new partners, considering it is an important mechanism to influence interactions (Vázquez et al., 2009). Rewiring probabilities are probability matrices that control the chances of rewiring with each new possible partner in the network in the new partner's choice step. Here, we also used abundance as the mechanism to determine the rewiring chances, as it is the most frequent in pollination networks (Vázquez et al., 2009; Vizentin-Bugoni et al., 2020). Finally, for the number rewiring attempts, we allowed either single or multiple attempts: in one, the algorithm restricted the possibility of rewiring to a single attempt with a partner; in the other, the algorithm allowed multiple rewiring attempts with each possible partner. In both cases, the number of trials was equivalent to the number of interactions lost with the extinct partner during the primary extinction stage.

4.2.4. Statistical analyses

To evaluate the effect of landscape structure, forest configuration, farm complexity, crop heterogeneity and farm management on the robustness of crop-pollinator networks, we used a Piecewise Structural Equation Modeling (PSEM) approach (Lefcheck, 2016). We added pollinator richness as a predictor variable since species richness influences the robustness of pollination network (Morrison et al., 2020). To avoid redundancy and collinearity, we decided not to include crop richness or global richness (crops + pollinators), as crop richness is included in the metric that compose the crop heterogeneity axis.

We checked the relationship between robustness and the type of primary extinction target (crop or pollinator), extinction order methods (random, abundance and degree) and interaction rewiring methods (single or multiple attempts) to verify the relevance of applying SEM for the different robustness scenarios. For this, we used simple linear models, function "lm" from the "stats" R-package (R Core Team, 2024). As expected, we found a relationship between robustness and the type of primary extinction target ($F_{1, 310} = 596.9$, $p < 0.001$, Figure 2) as well as the extinction order methods ($F_{2, 309} = 52.37$, $p < 0.001$, Figure 2), but surprisingly not the number of attempts in interaction rewiring ($F_{2, 309} = 0.22$, $p = 0.803$, Figure 2). Since robustness did not vary based on the occurrence or type of interaction rewiring, we modelled only the scenarios without rewiring (six scenarios, purple dots in Figure 2) using SEM, as these are the most straightforward robustness scenarios.

As the topology of interaction networks can directly or indirectly affect the robustness of interaction networks (Pimm, 1984), we chose five network topology metrics as intermediate predictors of our model (Morrison et al., 2020; Neff et al., 2021; Okuyama and Holland, 2008; Vieira and Almeida-Neto, 2015). Intermediate variables are those that, in addition to having a direct effect on the response, can also mediate the effect of the predictor variables on the response variable (Lefcheck, 2016). The metrics were network asymmetry, connectance, nestedness (NODF), modularity (Q), and specialisation (H_2'), all metrics that summarize important aspects of network topology and can affect robustness (Dunne et al., 2002; Memmott et al., 2004; Morrison et al., 2020; Okuyama and Holland, 2008; Pastor et al., 2012). We calculated all network topology metrics using the "networklevel", except for modularity that we used the "metaComputeModules" function, both from the "bipartite" R-package (Dormann et al., 2008).

For each one of the network metrics (asymmetry, connectance, nestedness, modularity, and specialisation), we built a complete model where landscape structure, forest configuration, farm complexity, crop heterogeneity, farm management, and pollinator richness were its predictors. We built the complete model for pollinator richness using landscape structure, forest configuration, farm complexity, crop heterogeneity, and farm management as predictors. For the network metrics, we generated the models using a Gaussian distribution family with an identity link function. We only used the Poisson distribution family with the log link function exclusively for pollinator richness. We built the models using the "glm" function from the "stats" R-package (R Core Team, 2024).

From the full models, we generated models considering all possible combinations between the predictor variables, with between zero and four predictor variables ("dredge" function from the "MuMIn" R-package; (Bartoń, 2024). Only additive combinations were allowed, with no interaction between the variables. The best model for each network metric was determined based on the Akaike information criterion, with the best model being the one with the lowest AIC value. We consider models with ΔAIC ≤ 2.0 equally plausible. We considered plausible models only those with a weight ≥ 0.20 and an AIC value higher than the empty model (containing only the transect, ~1). We checked all models by evaluating the model residuals' uniformity, dispersion, and outliers. We performed this step with the "testResiduals" function from the "DHARMa" R-package (Hartig, 2022).

For each robustness scenario, we built complete models using landscape structure, forest configuration, farm complexity, crop heterogeneity, asymmetry, connectance, nestedness, modularity, specialisation, pollinator richness, and farm management. We built all models using a Gaussian distribution family with an identity link function. We submitted all robustness models using the same model selection and validation steps mentioned in the previous paragraph. The only difference was that we allowed combinations between zero and ten predictor variables in the models generated from the full model.

Finally, for each robustness scenario, we composed the structural models: robustness model for the given scenario + the models corresponding to the network metrics that were significant in the robustness model for the given scenario. We use the "psem" function from the "piecewiseSEM" R-package for this step (Lefcheck, 2016). From this stage, we observed each variable's standardised estimated effect value that acted as a predictor of another. To check the goodness-of-fit of the models, we used the "fisherC" function from the "piecewiseSEM" R-package (Lefcheck, 2016). This function tests the variables' conditional independence, checking unobserved relationships between them. With this modelling, we estimated the direct, indirect, and total effects that landscape structure, forest configuration, farm complexity, crop heterogeneity, pollinator richness, and farm management had on the robustness of crop pollinator networks. Furthermore, we evaluated if network topology metrics mediate these effects.

The estimated β between a given variable and robustness represents the direct effect of a variable. To measure the partial indirect effect of a variable on robustness, we multiplied the estimated β of the relationship between the given variable and an intermediate variable by the estimated β of the relationship between the intermediate variable and robustness. The total indirect effect of a predictor variable was computed as the sum of all indirect effects of the given variable. The total effect of a variable on robustness was computed as the sum of its indirect and direct effects (Lefcheck, 2016). Since direct and indirect effects can have opposite signs, we also computed the absolute values of the indirect and total effects. We used these measures to observe the absolute effect magnitude of the predictors of robustness. To obtain the absolute indirect effect of the variables on robustness, we summed the absolute values of all their indirect effects. To obtain the total absolute effect, we added the absolute values of the indirect effects to the absolute value of the direct effect (Lefcheck, 2016).

4.3. RESULTS

Network topology mediated the impact of the robustness of crop-pollinator networks. Network asymmetry and connectance were the most frequent predictors of robustness, appearing in four of the six scenarios we tested (Table 1). Network nestedness was a predictor only in crop species removal scenarios (Table 1). Pollinator richness emerged as a predictor in the scenarios of crop species removal by degree and pollinator species removal by abundance (Table 1). Landscape structure explained network asymmetry and connectance; farm complexity explained connectance and nestedness and farm management explained pollinator richness (Table 1).

Table 1 Summary of models imputed in the SEM flow. The models presented are those with the lowest AIC value for each respective response variable. β = estimated effect value, SE = standard error, RD = residual deviance, df = degrees of freedom, and AIC = Akaike information criterion. t/z = t or z value, only for the Pollinator Richness model, due to modelling with the Poisson distribution, the z statistic is used and not t.

		Predictor Summary Stats					**Model Summary Stats**		
Response	**Predictor**	**β**	**SE**	**t/z**	**p**		**RD**	**df**	**AIC**
Asymmetry	Landscape structure	-0.02	0.01	-2.23	0.048	*	0.12	11	-18.29
Connectance	Farm complexity	0.01	0.00	2.33	0.042	*	0.04	10	-29.23
	Landscape structure	-0.01	0.00	-2.28	0.046	*			
Nestedness	Farm complexity	1.29	0.42	3.06	0.011	*	438.18	11	88.62
Pollinator Richness	Farm management	-0.24	0.11	-2.15	0.031	*	9.58	11	80.61
Robustness (crop-random)	Connectance	-0.55	0.10	-5.71	< 0.001	***	0.00	9	-62.46
	Asymmetry	-0.36	0.06	-6.01	< 0.001	***			
	Nestedness	0.00	0.00	5.37	< 0.001	***			
Robustness (pollinator-random)	Asymmetry	0.17	0.03	5.84	< 0.001	***	0.00	9	-81.41
	Connectance	0.23	0.04	5.83	< 0.001	***			
	Forest configuration	0.00	0.00	-4.12	0.003	**			
Robustness (crop-abundance)	Connectance	-1.68	0.16	-10.61	< 0.001	***	0.01	9	-49.29
	Asymmetry	0.49	0.10	4.98	0.001	***			
	Nestedness	0.01	0.00	4.85	0.001	***			
	Asymmetry	0.08	0.02	3.14	0.012	*	0.00	9	-80.56

Robustness (pollinator-abundance)	Farm Complexity	0.00	0.00	2.69	0.025	*			
	Pollinator Richness	0.00	0.00	4.91	0.001	***			
Robustness (crop-degree)	Forest Configuration	-0.01	0.00	-3.03	0.013	*	0.02	10	-41.08
	Pollinator Richness	-0.01	0.00	-3.63	0.005	**			
Robustness (pollinator-degree)	Connectance	0.69	0.21	3.34	0.008	**	0.03	10	-34.76
	Landscape Structure	-0.01	0.00	-2.32	0.043	*			

The models presented an adequate global fit with conditional independence between the predictors for the robustness of crop-pollinator networks considering: the random removal of crop species ($C_{14} = 20.85$, $p = 0.106$; $R^2 = 0.95$); the random removal of pollinator species, ($C_{12} = 10.72$, $p = 0.553$; $R^2 = 0.96$); the removal by abundance order of crop species $C_{14} = 14.61$, $p = 0.405$; $R^2 = 0.93$); the removal by abundance order of pollinator species ($C_{14} = 14.57$, $p = 0.409$; $R^2 = 0.88$); the removal by degree order of crop species ($C_4 = 1.41$, $p = 0.843$; $R^2 = 0.63$); and the removal by degree order of crop species ($C_2 = 0.37$, $p = 0.833$; $R^2 = 0.77$). We did not find any missing relationship among unconnected variables.

For random removal of crop species, the robustness was affected by landscape structure, mediated by asymmetry and connectance ¸also by farm complexity, mediated by connectance and nestedness (Figure 2b, Table 2). For random removal of pollinator species, the robustness was affected by landscape structure mediated by asymmetry and connectance, also by farm complexity, mediated by connectance, and directly by forest configuration (Figure 2c, Table 2).

For removal by crop abundance, the robustness was affected by landscape structure, mediated by asymmetry and connectance, also by farm complexity, mediated by connectance and nestedness (Figure S1a, Table 2). For removal by pollinator abundance, the robustness was affected by landscape structure, mediated by asymmetry, directly by farm complexity, also by farm management, mediated by pollinator richness (Figure S1a, Table 2).

For removal by crop degree, the robustness was affected directly by forest configuration, and by farm management, mediated by pollinator richness (Figure S2a, Table 2). For removal by pollinator degree, the robustness was affected directly by landscape structure, also by farm complexity, mediated by connectance (Figure S2b, Table 2).

To see the complete results of all the robustness scenarios, see Appendix: Additional Results, and Figures S1-S4 for visualize the pathways for extinction by abundance and degree scenarios.

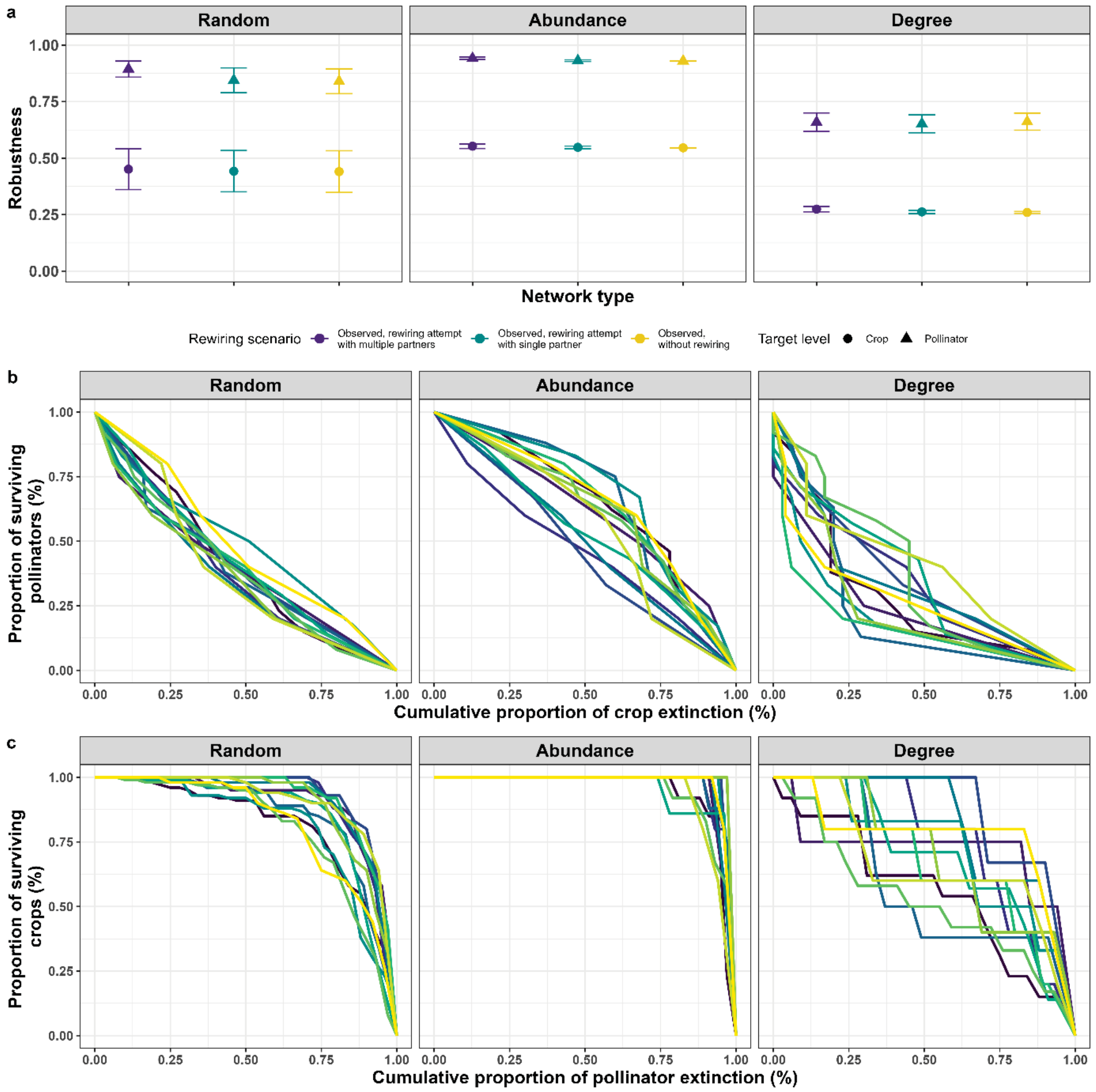

Figure 2a Robustness of crop-pollinator interaction networks across different modelled scenarios. Dots represent the mean robustness values, and bars show the corresponding standard deviation. Shapes indicate the primary extinction targets: circles represent crops, and triangles represent pollinators. Colours differentiate the interaction rewiring scenarios: purple for simulations without rewiring, green for scenarios with a single rewiring attempt, and yellow for scenarios with rewiring attempts with each potential partner. 2b and 2c represent the extinction-coextinction curves of the 13 farms (each line, each colour, for a farm) for the extinction of pollinators (b) and crops (c).

Table 2 Loadings for robustness scenarios in structural equation modeling (SEM). Direct represents the direct effects of predictors on robustness. Columns labeled “Indirect by” indicate effects mediated by the respective variable. Indirect (sum) is the sum of all indirect effects mediated by network metrics or pollinator species richness (S). Indirect (abs) is the sum of the absolute values of these indirect effects. Total (sum) is the sum of all indirect effects mediated by network metrics or pollinator species richness (S) plus the direct predictor effect on robustness. Total (abs) is the sum of the absolute values of indirect effects mediated by network metrics or pollinator species richness (S), combined with the absolute value of the direct predictor’s effect on robustness.

Scenario	**Predictor**	**Direct**	**Indirect by asymmetry**	**Indirect by connectance**	**Indirect by nestedness**	**Indirect by pollinator's S**	**Indirect (sum)**	**Indirect (abs)**	**Total (sum)**	**Total (abs)**
Crop random extinction ($R^2 = 0.95$)	Farm complexity	0.00	0.00	-0.36	0.38	NA	0.02	0.74	0.02	0.74
	Landscape structure	0.00	0.35	0.35	0.00	NA	0.70	0.70	0.70	0.70
Pollinator random extinction ($R^2 = 0.96$)	Landscape structure	0.00	-0.32	-0.29	NA	NA	-0.60	0.60	-0.60	0.60
	Farm complexity	0.00	0.00	0.29	NA	NA	0.29	0.29	0.29	0.29
	Forest configuration	-0.31	0.00	0.00	NA	NA	0.00	0.00	-0.31	0.31
Crop abundance extinction ($R^2 = 0.93$)	Landscape structure	0.00	-0.34	0.76	0.00	NA	0.42	1.10	0.42	1.10
	Farm complexity	0.00	0.00	-0.78	0.40	NA	-0.38	1.18	-0.38	1.18
Pollinator abundance extinction ($R^2 = 0.86$)	Farm complexity	0.39	0.00	NA	NA	0.00	0.00	0.00	0.39	0.39
	Farm management	0.00	0.00	NA	NA	-0.38	-0.38	0.38	-0.38	0.38
	Landscape structure	0.00	-0.25	NA	NA	0.00	-0.25	0.25	-0.25	0.25

Crop degree extinction ($R^2 = 0.63$)	Forest configuration	-0.63	NA	NA	NA	0.00	0.00	0.00	-0.63	0.63
	Farm management	0.00	NA	NA	NA	0.44	0.44	0.44	0.44	0.44
Pollinator degree extinction ($R^2 = 0.77$)	Landscape structure	-0.41	NA	-0.29	NA	NA	-0.29	0.29	-0.70	0.70
	Farm complexity	0.00	NA	0.30	NA	NA	0.30	0.30	0.30	0.30

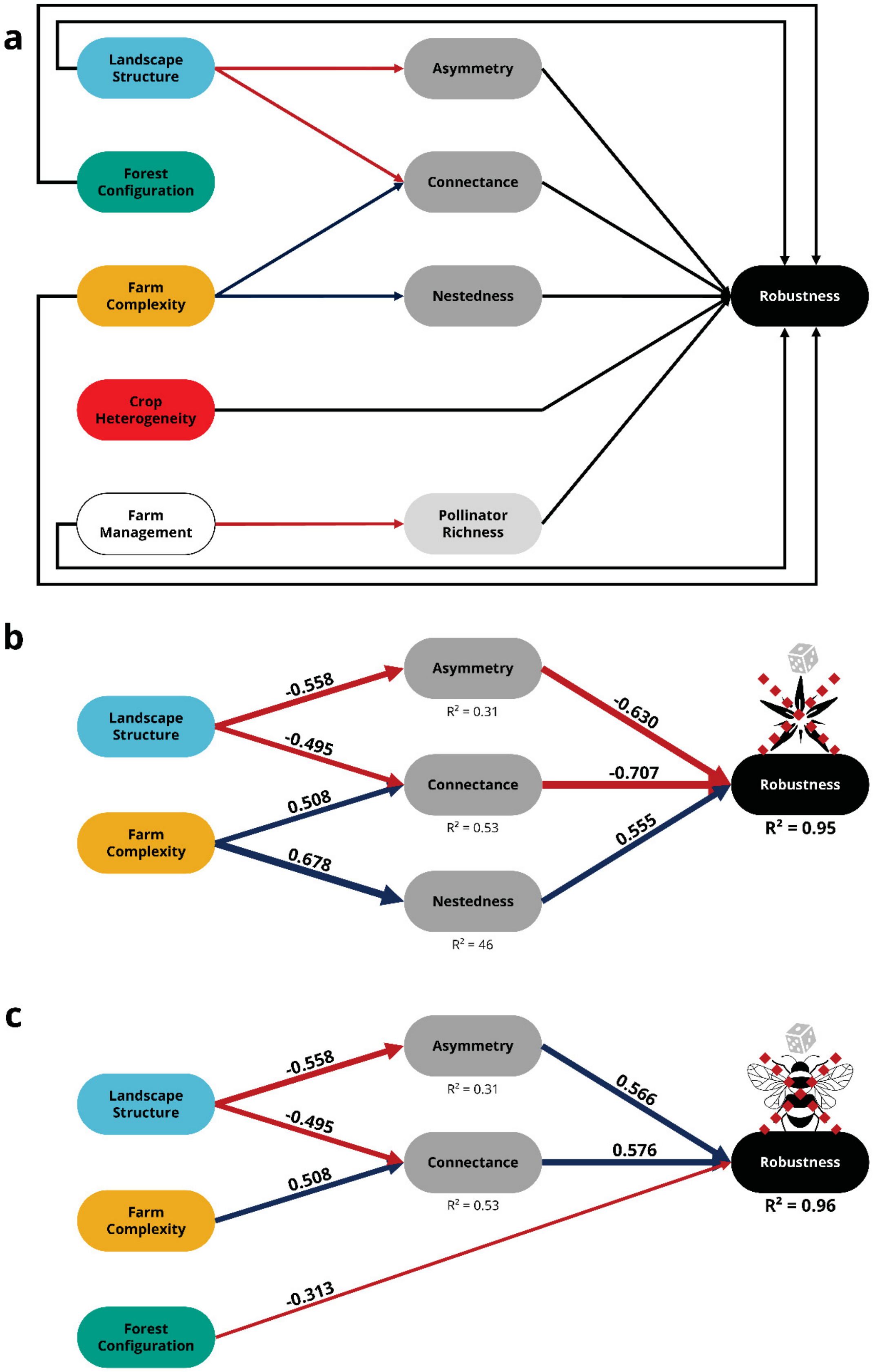

Figure 2a Possible paths after model selection for network metrics, pollinator richness (S), and robustness. The paths shown correspond to all possible paths for the six scenarios modelled

with structural equation modelling (SEM). 2b Paths observed for the robustness scenario considering the random removal of crops. 2c Paths observed for the robustness scenario considering the random removal of pollinators. Arrows indicate relationships between variables in the predictor-response direction. Blue arrows represent positive relationships, while red arrows represent negative relationships. The values on the arrows indicate the standardised β values of the relationships between the variables. The R^2 values indicate the coefficient of determination for the variables used as responses at some point in the SEM flow. The coloured boxes represent landscape and management variables obtained by *Capítulo I* and the white box the Farm Management variable. The grayscale boxes represent network topology metrics and pollinator richness. Black boxes represent robustness.

4.4. DISCUSSION

4.4.1. Rewiring, primary extinction targets and extinction methods

We found that networks were less resilient to plant removal, and we argue that network robustness does not arise from the taxonomic identity of the primary extinction target itself but rather from the occurrence and interaction pattern of the removed guild. Indeed, plant-pollinator networks may show different robustness patterns concerning the target trophic level of primary extinction, with some networks more resilient to plant removal (Kaiser-Bunbury et al., 2010), while others to the removal of pollinators (CaraDonna and Waser, 2020; Schleuning et al., 2016). We discuss that the reason for sensitivity to the removal of one or another trophic level is related to its proportion in the network (its share in the web asymmetry) and the realisation (web connectance) and organisation (nestedness) of its interactions.

Also, because of species proportion and interaction patterns, the interaction rewiring does not buffer the extinction cascades. The absence of the effect of rewiring across all scenarios (considering both primary extinction targets and extinction order rules) strongly suggests that almost all feasible interactions are being realised. Besides that, there is a strong web asymmetry observed in our networks (≈ 1:5, crop for pollinator), indicating that pollinators had already interacted with crop they could. Although rewiring did not buffer the extinction cascade within an intra seasonal period, the topological plasticity of the network over time may enhance network robustness (Ramos-Jiliberto et al., 2012). However, through inter-seasonal land-use changes on farms (i.e., considering crop rotation and its respective interactions), rewiring may support robustness since temporal dynamics are fundamental for the stability of these networks (CaraDonna and Waser, 2020; Ramos-Jiliberto et al., 2012).

As expected, we observed a power-law distribution pattern (Jordano et al., 2003; Memmott et al., 2004) – or at least a strong tendency toward this pattern – across crop and pollinator interactions in all farms. This interaction distribution tends to buffer extinction cascades in scale-free networks (Memmott et al., 2004). However, our system seems exceptionally sensible in some scenarios because of the high concentration of interactions in a few highly connected crop species, facilitating network collapse (Pastor et al., 2012; Vieira and Almeida-Neto, 2015). Therefore, the removal of each crop species represents a significant impact on the networks that reach very low robustness values.

From the pollinators' perspective, a strong web asymmetry represents a strong dependence on crops (Pastor et al., 2012), where the removal of almost any crop represents a "rivet-like" loss pattern (Dunne et al., 2002). Many pollinators lose their interactions when we remove a crop from the network. This may be particularly true when crops are highly connected, causing a higher proportion of pollinator co-extinction (Vieira and Almeida-Neto, 2015). Because there are few crop species, when the pollinators lose a partner, they have few options to rewire their interactions. Of the few possibilities for rewiring with crops, some are unfeasible because they represent forbidden links (Olesen et al., 2011; e.g., non-buzzing bee species x crops with poricidal anthers) or are highly improbable based on their abundance (Vizentin-Bugoni et al., 2020; e.g., rare solitary species x less abundant crops). At first, this likelihood increases the failure rate of rewiring attempts. Even when rewiring occurs, the new partner (crop) will be removed in a few steps during the extinction sequence. This may be the reason why we did not see the enhancing effect of rewiring on robustness in this study.

When the rewiring fails to increase the network robustness, other aspects of the network topology may be relevant. In this scenario, greater network nestedness can increase robustness by favouring interaction redundancy (Morrison et al., 2020). For example, usually, rare pollinator species interacting with few crops become co-extinct in the first stages of primary extinction due to their low occurrence proportion in the network. But, the lost interactions of rare and specialist species are, in general, a subset of the interactions of generalist species in a nested network (Almeida-Neto et al., 2008; Bascompte et al., 2003). So the buffering effect of nestedness should be particularly powerful in larger and more nested networks, where the power-law distribution of interactions is more consistent (Jordano et al., 2003; Memmott et al., 2004).

As observed in natural systems, crop-pollinator interaction networks exhibit greater resilience to removing rarer crops and pollinators. Rarer species typically engage in fewer interactions proportionally and thus assume less interactions within the networks (Olesen et al., 2007). Consequently, it is plausible that these networks demonstrate higher tolerance to removing such species, particularly in nested network structures that buffer against secondary extinction responses. In agriculture, this scenario may reflect the loss of pollinator species that visit the farms sporadically or opportunistically while foraging on non-crop species in the farm's surroundings. However, pollinators that are crucial and regionally associated with specific crops (e.g., *Thygater analis* and *Solanum lycopersicum*, the tomato, as we observed in this study) may be naturally rare and occupy peripheral positions within the network. In this case, removing species such as *T. analis* may have a minimal impact on network structure, its significance for tomato production could be substantial.

Generalist and abundant pollinator species (e.g., *Apis mellifera* and *Bombus pauloensis*) have experienced significant population declines on a global scale (Goulson et al., 2015; Potts et al., 2010). This trend primarily results from the synergistic effects of pathogens, shortages of floral resources, widespread pesticide use, and the lack of nesting resources, compounded by intense competition with alien species (e.g., *A. mellifera* and *Bombus terrestris*) (Goulson et al., 2015; Sánchez-Bayo and Wyckhuys, 2019). Although the loss of keystone pollinators in agroecosystems does not necessarily equate to the extinction of crop species, it can impact the loss of pollination services. Consequently, while most crops may still manage to produce fruit through autogamy, they will likely yield smaller harvests of lower nutritional quality and reduced economic value. This situation could lead to severe economic repercussions for farmers, the agricultural sector, and food security (Tscharntke et al., 2012a). Therefore, the scenario we present here, involving the priority removal of significant pollinators, raises urgent concerns regarding the dynamics of these species in complex agricultural systems, as analysed in this study.

Removing more connected crops, on the other hand, appears less likely but can also result from routine agricultural practices. The connectivity of a species typically correlates with its abundance within the community, which is reinforced by floral abundance for plants. Since high floral abundance often corresponds to larger planting areas, more connected crops may become frequent targets for pests (Lindell et al., 2023). Another potential cause is the spontaneous removal of crops that cover extensive areas (therefore highly connected) due to management practices such as soil rotation, production decline, or the conclusion of a planting cycle.

From the crops' perspective, since crops are scarce and generalists, they are likely to interact with almost all viable partners, leaving no probable alternatives for rewiring. However, unlike what happens with crop removal, we have a higher pollinator diversity, which promotes an insurance or portfolio effect for the crops (Lázaro and Gómez-Martínez, 2022; Solé and Montoya, 2001). Therefore, in this scenario, it is expected that a greater asymmetry of the network, given by a greater proportion of pollinators per crop, will increase the robustness of the network (Santamaría et al., 2016). Likewise, a greater realisation of interactions (network connectance) will buffer the extinction cascade (Dunne et al., 2002) . The more visitors a crop receives, the lower the chance of its secondary extinction with each primary extinction step, and the more primary extinction steps it will take for its extinction to occur.

Ultimately, the pattern observed in this study may indicate that rewiring is, in fact, unlikely in agricultural systems considering short seasonal intervals. We observed a similar pattern when analysing the composition of the same networks other study (*Capítulo I*). On that occasion, we found that the interaction beta-diversity component due to rewiring was extremely low compared to beta-diversity resulting from species turnover (*Capítulo I*; Figure 2 and S1). This is consistent with the fact that we did not observe any effect of rewiring, either when considering single attempt or multiple attempts to rewire.

In the context of a polyculture farm, tolerance to extinctions requires careful examination, as it may be understood in at least three ways that do not necessarily represent "errors" within these networks (Albert et al., 2000; Memmott et al., 2004). In crop systems, a random removal may result from management decisions, whether arbitrarily or strategically made by farmers. These decisions typically stem from socio-economic factors (e.g., production cost infeasibility), environmental considerations (e.g., unsuitable land or climate, pest control measures), or market dynamics (e.g., a decline in market value) that farmers face throughout the production season (Touch et al., 2024). Additionally, crop removals can occur due to more stochastic factors, which are generally climatic (e.g., intense rainfall or severe droughts) (Traveset et al., 2017). Such factors can either directly eliminate crops by localised mortality or disrupt anthesis cycles, interrupting phenological overlap and interactions with pollinators (Memmott et al., 2004). For pollinators, the most likely cause of random removal is linked to stochastic environmental mechanisms, whether of natural origin (e.g., emergence of predators or natural pathogens) or anthropogenic (e.g., removal or management of natural and semi-natural areas at farm boundaries or surrounding regions) (Memmott et al., 2004; Traveset et al., 2017).

The planting and removal of rarer crops (in terms of interactions) likely stem from intrinsic market-driven reasons in agriculture. Crops with limited commercial appeal, challenges in large-scale cultivation, off-season production, or undergoing viability testing often occupy more peripheral positions within farm networks. As we observed in the field, such crops are commonly found in smallholder farms, and farmers may replace them with economically more viable crops. Although removing these crops results in a smaller decrease in network robustness compared to removing more abundant crops, they still play an essential role in network structure. Given the plant-scarce system we observed, even removing less abundant crops already significantly impacts secondary pollinator loss. This pattern suggests that even crops holding less interactions in networks can function as keystone species within the agricultural system.

Pollination networks in natural and semi-natural systems are generally tolerant to random species removals, because random extinctions tend to remove first species with fewer interactions, which trigger weaker extinction–coextinction cascades. (Bastazini et al., 2019; Kaiser-Bunbury et al., 2010; Memmott et al., 2004; Vizentin-Bugoni et al., 2020). We show here for the first time the same pattern within agrosystems, specifically in networks constructed solely from human-managed crop species. While the occurrence of this pattern in agrosystems is unprecedented, we identified that the mechanisms enhancing the robustness of crop-pollinator networks against random removals align with those seen in natural systems. As our networks display a regular power-law distribution of interactions, the losses of keystone species, that is, species with more interactions, are diluted throughout the random primary extinction simulations (Kaiser-Bunbury et al., 2017; Memmott et al., 2004; Pastor et al., 2012).

Therefore, more steps of random removal are needed to extirpate species that significantly impact network structure and, in general, more abundant and connected species (Bastazini et al., 2019). This pattern arises from the low proportion of keystone species relative to those occupying peripheral roles (Jordano et al., 2003; Olesen et al., 2007). Consequently, this lower probability of keystone species extirpation in each removal step substantially diminishes the spread of extinction cascades, lowers the rate of secondary extinctions, and enhances the overall robustness of the networks.

Finally, the simulation of species removal based on the order of interaction degree, employing an attack tolerance approach, serves to understand the resilience of plant-pollinator networks when facing the loss of keystone species (Dunne et al., 2002). We observed that crop-pollinator networks formed in polyculture farms display low resilience under these scenarios. As seen in natural and semi-natural plant-pollinator systems, crop-pollinator networks show limited tolerance to the loss of keystone species that hold a substantial proportion of interactions. Thus, similar to natural systems, generalist and abundant species play a critical role in maintaining community stability within agroecosystems.

4.4.3. Local and regional effects

We showed that factors operating across both local and regional scales regulate the robustness of crop-pollinator interaction networks in polyculture farms. Farm complexity and farm management adopted at the local level influenced the robustness of these networks, highlighting that decisions made at the farm level have significant impacts. Conversely, landscape structure and forest configuration surrounding the farms suggest that the robustness also depends on processes and mechanisms emerging at regional scales, both natural and anthropogenic, including agricultural activities. These patterns indicate that agricultural management and landscape governance are critical for conserving crop-pollinator interactions, particularly in species extinction scenarios. Furthermore, the observed patterns may enhance our understanding of how crop rotation affects crop-pollinator dynamics.

Landscape structure and farm complexity emerged as the most ubiquitous factors for the robustness of crop-pollinator networks, regardless of the extinction pattern these networks face. It means that the composition and configuration that define landscape structure directly affect pollinators' biodiversity within its matrix. However, we observed that greater spatial complexity in landscape structure decreases the proportion of pollinators per plant and the realisation of interactions, thereby reducing network asymmetry and connectance. Thus, excessively heterogeneous landscape may result in landscapes with low permeability for pollinators, consequently impacting their interactions.

The indirect negative effect of landscape structure on robustness when considering the random removal of crops was due reduced network asymmetry and connectance which diminished the impact of rivet-like removals of plants (Dunne et al., 2002). In other scenarios (i.e., random pollinator removal and the removal of abundant crops and pollinators), as expected, the negative effect of landscape structure more directly reflects the difficulty pollinators face in accessing the farms. This situation aligns with the direct negative effect of landscape structure on robustness in the pollinator degree removal scenario.

While habitat quantity emerges as a critical factor in the distribution of species within the landscape, the spatial configuration of these habitat elements is also crucial for species dynamics (Boscolo et al., 2017; Fahrig, 2013; Fahrig et al., 2011; Moreira et al., 2015), as we found in this study. The negative effect of forest configuration on robustness, given crop degree removal and random pollinator removal, may be linked to a reduction in pollinator richness or the realisation of their interactions (Fahrig, 2017; Pioltelli et al., 2024). We expected this effect, as forest configuration represents the distribution of habitat and resources for the majority of the pollinator species collected in this study (e.g., species that nest in tree cavities, such as bees from the Meliponini and Halictini tribes, or in soil, typically covered, such as *Bombus* spp.). However, the effect of forest configuration on robustness were not mediated by pollinator richness or connectance in the effect of forest configuration on robustness. Therefore, the mechanisms that induce this direct effect of forest configuration on robustness remain unclear.

In this study, we observed that farm complexity promoted greater realisation of interactions (increased connectance) and higher nestedness in networks. Farm with greater crop diversity may be more attractive to pollinators due to the promotion of increased availability and variety of floral resources (Ebeling et al., 2008; Gómez-Martínez et al., 2022; Kral-O’Brien et al., 2021). When these resources are embedded within an environment that also provides nesting sites and other necessities as conserved landscapes with wide forest cover (Kennedy et al., 2013), the relationship between crops and their pollinators is further enhanced. Farm complexity can reduce network robustness in scenarios involving random or abundance-based crop removal, as it reinforces the rivet-like removal effect of well-connected crops. Conversely, farm complexity can mitigate the onset of secondary extinctions, generating greater interaction redundancy. This mechanism is clearly demonstrated by farm complexity’s direct effect on robustness in the pollinator abundance removal scenario.

Management type also exerted a strong influence on the diversity present on farms. Ecologically more intensive systems (e.g., organic farming and agroforestry), generally more diverse in crops, tend to attract more pollinators (Bergamo et al., 2025; Kral-O’Brien et al., 2021). This increased diversity in organic farms from the non-use of non-specific pesticides, which can directly and indirectly affect pollinators, promoting their mortality and subsequent reduction in diversity (Goulson et al., 2015; Krupke et al., 2012). In this study, we observed that pollinator richness enhanced robustness when pollinators are removed in order of abundance. This is primarily, but not exclusively, due to the increase in richness, which required more steps for network collapse. The increase in pollinator richness may also be associated with a more even distribution of interactions within the networks, distributing interactions among species and reducing the average rivet-like effect of these species. From a mathematical perspective, pollinator richness may reduce network robustness in removing crops by interaction degree (Memmott et al., 2004; Pastor et al., 2012). This generates an ecologically contradictory effect, as conventional management enhances network robustness in this scenario by reducing pollinator richness. Given the loss of well-connected crops, we interpret that the impact on robustness will be less pronounced with fewer pollinators in the network, reducing the spread of secondary extinctions. Within this framework, conventional farms with high crop richness would exhibit greater robustness due to more stages required for crop removal with reduced secondary extinction spread of pollinators, owing to other management factors (e.g., pesticide application).

4.5. CONCLUSIONS

In this paper, we demonstrated that mechanisms at both local and regional scales regulate the robustness of crop-pollinator interaction networks. Locally, management decisions made by farmers can either enhance or undermine the resilience of the networks formed on their farms. The type of management employed and the spatial arrangement of farms are fundamental in determining pollinator richness and the realisation and patterns of their interactions with crops. Regionally, the management of landscape structure and, consequently, the forest patches within agricultural matrices can also regulate proportion pollinator richness and their consequences for network robustness. Therefore, we conclude that maintaining the stability of crop-pollinator networks across various potential scenarios for species loss on farms depends on local and regional agricultural management. Associating sustainable management of farms with that of the surrounding landscapes is crucial for preserving stable interaction networks capable of providing ecosystem services that ensure food security.

The robustness of plant-pollinator networks in polyculture farms exhibits patterns similar to natural networks, even when considering only interactions with crop plants. However, we observed that in this system, networks are consistently more sensitive to removing plants than to removing pollinators. As rewiring does not mitigate the cascade of secondary extinctions, stability depends on management decisions and crop diversity maintenance.

Finally, our study is limited by a short temporal scope without considering temporal dynamics. The spatial and qualitative evolution of farms over agricultural cycles certainly affects the robustness and stability of crop-pollinator networks. Studies focused on the robustness of crop-pollinator networks over time will be essential for a deeper understanding of the role of landscape and agricultural management in the recurring interactions on farms that produce our food.

APPENDIX

Additional results

For the scenario considering random removal of crop species, the robustness was affected by Farm Complexity (absolute std. β = 0.74 and cumulative std. β = 0.02) and by Landscape Structure (absolute and cumulative std. β = 0.70). Only the network metrics connectance (std. β = -0.71), asymmetry (std. β = -0.63), and nestedness (std. β = 0.56) were related to robustness for this scenario. Farm Complexity had its effect mediated by network nestedness (std. β = 0.38) and connectance (std. β = - 0.36). Network asymmetry (std. β = 0.35) and connectance (std. β = 0.35) mediated the Landscape Structure effect over robustness. Additionally, Landscape Structure and Farm Complexity did not directly impact robustness. For the scenario considering the random removal of pollinator species, we found the effect of Landscape Structure (absolute std. β = 0.60, cumulative std. β = -0.60), Farm Complexity (absolute and cumulative std. β = 0.29), and Forest Configuration (absolute std. β = 0.31 and cumulative std. β = -0.31). Among the network metrics, only connectance (std. β = 0.58) and asymmetry (std. β = 0.57) showed a relationship with robustness in this scenario. Landscape Structure was mediated by network asymmetry (std. β = - 0.32) and connectance (std. β = - 0.29). Farm Complexity had its effect mediated only by network connectance (std. β = - 0.29). Forest Configuration presented only a direct effect, while Landscape Structure and Farm Complexity presented only indirect effects on the robustness.

The robustness considering the removal by abundance order of crop species was affected by Landscape Structure (absolute std. β = 1.18 and cumulative std. β = -0.38) and by

Farm Complexity (absolute std. β = 1.10 and cumulative std. β = 0.42). The network metrics asymmetry (std. β = 0.61), connectance (std. β = -1.53), and nestedness (std. β = 0.59) were related to robustness for this scenario. Farm Complexity had its effect mediated by network connectance (std. β = 0.76) and asymmetry (std. β = - 0.34). Landscape Structure had its effect mediated by network connectance (std. β = - 0.78) and nestedness (std. β = 0.40). Landscape Structure and Farm Complexity did not present direct effects on robustness.

For the robustness considering the removal by abundance order of pollinator species, we observed the effect of Farm Complexity (absolute and cumulative std. β = 0.39), Farm Management (absolute std. β = 0.38 and cumulative std. β = - 0.38), and Landscape Structure (absolute std. β = 0.25 and cumulative std. β = - 0.25). In addition, Pollinator Richness (std. β = 0.66) and the network asymmetry metric (std. β = 0.44) showed a relationship with robustness in this scenario. Farm Management influenced robustness through Pollinator Richness (std. β = -0.38), while Landscape Structure affected robustness through asymmetry (std. β = -0.25). Farm Complexity only had a direct effect, while Farm Management and Landscape Structure did not directly affect robustness.

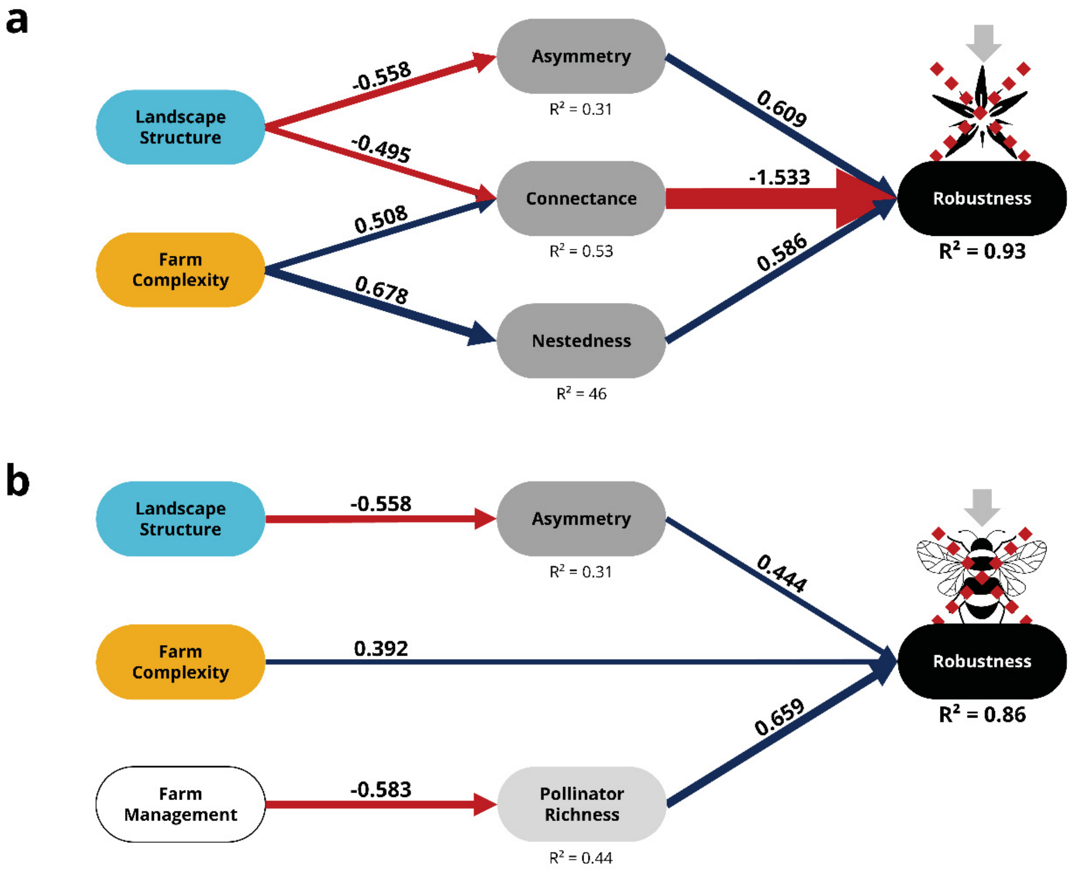

Figure S1a Graph of the paths observed for the robustness scenario considering the removal of crops by their abundance. S1b Graph of the paths observed for the robustness scenario considering the removal of pollinators by their abundance. In both cases less abundant species being removed first. Arrows indicate relationships between variables in the predictor-response direction. Blue arrows represent positive relationships, while red arrows represent negative relationships. The values on the arrows indicate the standardized β values of the relationships between the variables. The R^2 values indicate the coefficient of determination for the variables used as responses at some point in the SEM flow. The colored boxes represent landscape and management variables obtained by *Capítulo I* and the white box the Farm Management variable. The grayscale boxes represent network topology metrics and pollinator richness. Black boxes represent robustness.

The robustness of crop-pollinator networks, considering the removal in order of degree of crop species, was affected by Forest Configuration (absolute std. β = 0.63) and Farm Management (absolute std. β = 0.44). Pollinator Richness entirely mediated the effect of Farm Management (std. β = -0.75). Forest Configuration only had a direct effect.

Finally, for the robustness considering the removal in order of degree of pollinator species, we observed the effect of Landscape Structure (absolute std. β = 0.70) and Farm Complexity (absolute std. β = 0.30). Among the network metrics, only network connectance (std. β = 0.59) showed a relationship with robustness in this scenario. Landscape Structure directly influenced robustness (std. β = -0.41) and was mediated by network connectance (absolute std. β = 0.29). Farm Complexity did not exhibit any direct effects.

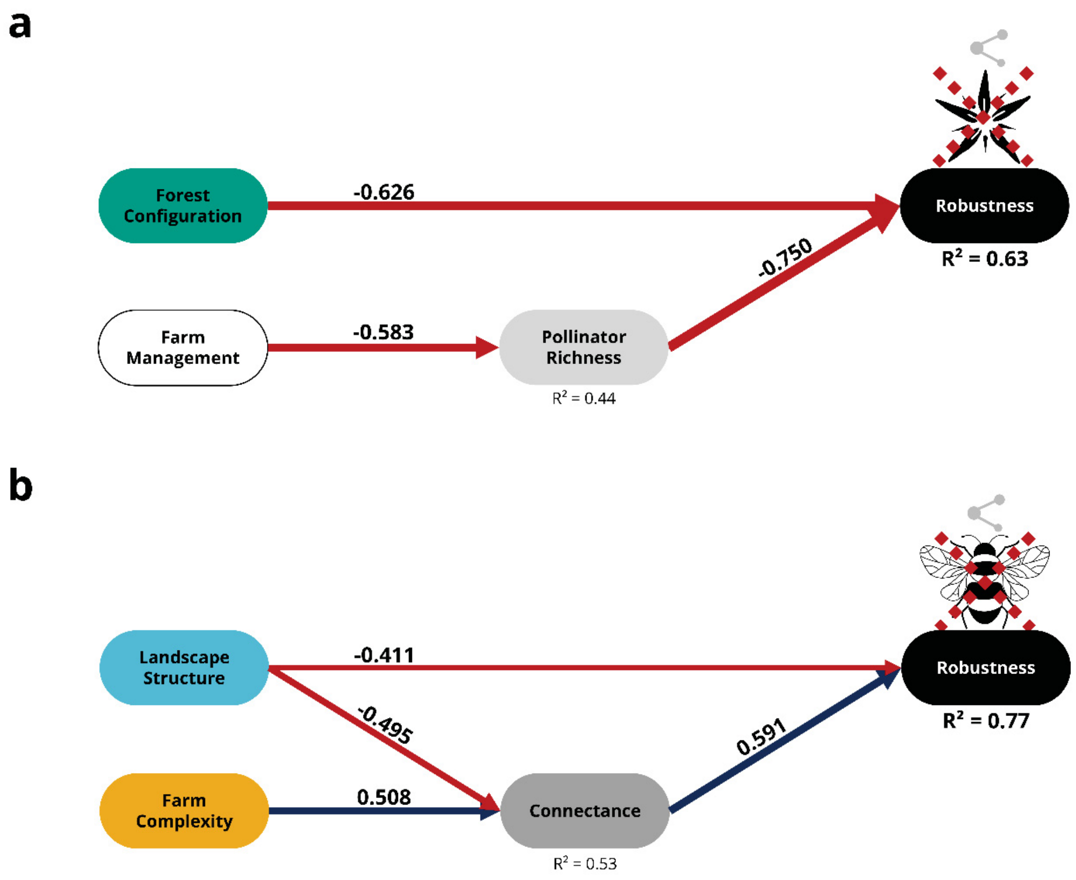

Figure S2a Graph of the paths observed for the robustness scenario considering the removal of crops by their interaction degree. S2b Graph of the paths observed for the robustness scenario considering the removal of pollinators by their interaction degree. In both cases more connected species being removed first. Arrows indicate relationships between variables in the predictor-response direction. Blue arrows represent positive relationships, while red arrows represent negative relationships. The values on the arrows indicate the standardized β values of the relationships between the variables. The R^2 values indicate the coefficient of determination for the variables used as responses at some point in the SEM flow. The colored boxes represent landscape and management variables obtained by *Capítulo I* and the white box the Farm Management variable. The grayscale boxes represent network topology metrics and pollinator richness. Black boxes represent robustness.

5. CONCLUSÃO GERAL

Nos estudos que compõem esta tese, observamos que as redes cultura-polinizador de pequenos estabelecimentos de policultura de hortaliças são afetadas tanto por fatores emergentes do entorno dos estabelecimentos quanto por fatores internos. Todos os aspectos das redes avaliadas neste estudo – composição, estrutura e robustez – mostraram-se sensíveis a pelo menos um fator regional e um fator local. Isso demonstra a complexidade das dinâmicas das interações de polinização em agrossistemas e o impacto que a agricultura exerce, em diferentes escalas, sobre a biodiversidade e os serviços que dela dependem. Concluímos, portanto, que essas redes são afetadas por mecanismos emergentes tanto da paisagem agrícola quanto do manejo agrícola. Isso destaca que a conservação das interações cultura-polinizador depende de medidas em diferentes níveis.

Ao observar a composição e a estrutura das redes, identificamos que os efeitos da agricultura sobre as redes cultura-polinizador emergem principalmente em escala local, em função do manejo dos estabelecimentos. Nesse sentido, os estabelecimentos atuam como moduladores da comunidade de polinizadores, eventualmente transbordando seus impactos para a paisagem ao redor. Quando analisamos a robustez, percebemos maior influência da paisagem, que canaliza seus efeitos sobre a comunidade de polinizadores no nível dos estabelecimentos. Vistos em conjunto, esses resultados destacam a interdependência entre os mecanismos em escala local e regional na manutenção da diversidade de polinizadores e na mediação dos efeitos da agricultura, seja em nível de paisagem ou de manejo dos estabelecimentos, sobre a dinâmica das interações cultura-polinizador.

Por um lado, o manejo agrícola sustentável coloca os produtores rurais como peças-chave na conservação da biodiversidade, dos serviços ecossistêmicos e da segurança alimentar. As decisões de manejo tomadas por eles, seja a intensificação ecológica ou agrícola do estabelecimento, afetam diretamente a dinâmica das redes em seus sistemas produtivos, com reflexos na produtividade e na economia. Por outro lado, a importância do contexto da paisagem agrícola, que cerca os estabelecimentos, evidencia a necessidade de medidas regionais integradas e de políticas públicas que devem ser adotadas por gestores públicos e privados. A sustentabilidade local dos estabelecimentos precisa ser sustentada por um entorno saudável e ecologicamente intensificado, capaz de prover polinizadores diversos e abundantes, mantendo assim um serviço estável e garantindo a segurança alimentar. Para que a agricultura seja resiliente, ela precisa ser sustentável.

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So long, and thanks for all the fish!