MINISTÉRIO DA EDUCAÇÃO

UNIVERSIDADE FEDERAL RURAL DE PERNAMBUCO

UNIVERSIDADE FEDERAL DE PERNAMBUCO

UNIVERSIDADE ESTADUAL DA PARAÍBA

UNIVERSIDADE DE PERNAMBUCO

PROGRAMA DE PÓS-GRADUAÇÃO EM ETNOBIOLOGIA E CONSERVAÇÃO DA NATUREZA – PPGETNO

DIEGO CENTENO ALVARADO

THE DIVERSITY OF PLANT-INSECT INTERACTIONS AND ASSOCIATED POLLINATION SERVICES IN AGROFORESTRY SYSTEMS IN A TROPICAL REGION IN NORTHEASTERN BRAZIL

RECIFE – PE

2024

DIEGO CENTENO ALVARADO

THE DIVERSITY OF PLANT-INSECT INTERACTIONS AND ASSOCIATED POLLINATION SERVICES IN AGROFORESTRY SYSTEMS IN A TROPICAL REGION IN NORTHEASTERN BRAZIL

Tese apresentada ao Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza (UFRPE, UFPE, UEPB e UPE) como parte dos requisitos para obtenção do título de doutor.

Linha de pesquisa: Síntese ecológica, conservação e manejo da biodiversidade

Orientador: Xavier Arnan

RECIFE – PE

2024

Dados Internacionais de Catalogação na Publicação
Sistema Integrado de Bibliotecas da UFRPE
Bibliotecário(a): Ana Catarina Macêdo – CRB-4 1781

A473t Alvarado, Diego Centeno.

The diversity of plant-insect interactions and associated pollination services in agroforestry systems in a tropical region in Northeastern Brazil / Diego Centeno Alvarado. – Recife, 2024.

274 f.; il.

Orientador(a): Xavier Arnan Viadiu.

Tese (Doutorado) – Universidade Federal Rural de Pernambuco, Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Recife, BR-PE, 2024.

Inclui referências, apêndice(s) e anexo(s).

1. Relação inseto-planta. 2. Polinização por insetos . 3. Manejo. 4. Agrobiodiversidade - Brasil 5. Polinizadores . I. Viadiu, Xavier Arnan, orient. II. Título

CDD 304.2

DIEGO CENTENO ALVARADO

THE DIVERSITY OF PLANT-INSECT INTERACTIONS AND ASSOCIATED POLLINATION SERVICES IN AGROFORESTRY SYSTEMS IN A TROPICAL REGION IN NORTHEASTERN BRAZIL

Tese apresentada ao Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza (UFRPE, UEPB, UPE e UFPE) como parte dos requisitos para obtenção do título de Doutor em Etnobiologia e Conservação da Natureza

Defendida e aprovada em: Recife (PE), 27 de junho de 2024

BANCA EXAMINADORA

Presidente

Prof. Dr. Xavier Arnan Viadiu

Universidade de Pernambuco (UPE, Garanhuns – PE)

Examinadores

Prof. Dr. Bruno Karol Cordeiro Filgueiras

Universidade de Pernambuco (UPE, Nazaré da Mata – PE)

Prof. Dr. Pedro Joaquim Bergamo

Universidade Estadual Paulista (UNESP, Rio Claro – SP)

Prof. Dr. Arthur Domingo de Melo

Universidade Federal de Sergipe (UFS, Itabaiana – SE)

Prof. Dr. Liedson Tavares de Sousa Carneiro

East Tennessee State University (ETSU, Tennessee – USA)

AGRADECIMENTOS

A conclusão desta tese é o resultado do apoio e dos esforços, diretos ou indiretos, de muitas pessoas. Gostaria de expressar minha mais profunda gratidão a todos que tornaram isso possível.

Ao meu orientador, Xavier Arnan, por sua confiança e apoio em cada uma das minhas ideias. Sou grato por me tratar como um igual, me incentivar a melhorar e me guiar.

À Ariadna V. Lopes, por seus ensinamentos e valiosas contribuições para a tese.

À Caroline Souza, por sua colaboração ativa no capítulo 3 da tese.

À FACEPE (Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco), pela concessão da bolsa, permitindo-me dedicar exclusivamente aos meus estudos de doutorado.

À minha família, pelo amor e apoio infinitos.

Ao Marcelo, por seu amor e apoio.

A todos os meus amigos do LIPA (Laboratório de Interação Planta-Animal) - UFPE, que, de certa forma, também se tornou um laboratório para mim, repleto de afeto e oportunidades de colaboração.

SUMÁRIO

LISTA DE TABELAS

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

LISTA DE FIGURAS

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

LISTA DE ANEXOS

RESUMO

Ao longo do tempo, os sistemas agrícolas passaram por intensificação para aumentar a produção e a segurança alimentar. No entanto, essas mudanças no uso da terra resultaram em declínios na biodiversidade e nos serviços ecossistêmicos, como a polinização, impactando negativamente a produção e a segurança alimentar. A diversidade de polinizadores é crucial para aumentar a resiliência dos serviços de polinização, e as perdas nessa diversidade podem ser mitigadas ou até revertidas por sistemas agroflorestais, que oferecem maior complexidade estrutural em comparação com sistemas agrícolas intensivos. Embora numerosos estudos tenham explorado a dinâmica da polinização em sistemas agroflorestais nos últimos anos, seus resultados permanecem dispersos. Além disso, os efeitos das práticas agroflorestais na polinização têm sido avaliados principalmente de forma teórica, em vez de experimental. Dessa forma, esta tese teve três objetivos principais, que estruturam o trabalho em três capítulos: (1) revisar a literatura existente sobre polinização em sistemas agroflorestais de maneira global, identificando tendências gerais, lacunas de conhecimento e oportunidades de pesquisa futura; (2) conduzir uma síntese de evidências globais avaliando como as práticas de manejo agroflorestal de café afetam a diversidade de polinizadores; (3) determinar os efeitos de fatores de manejo agroflorestal locais e regionais na diversidade funcional de abelhas polinizadoras e seus impactos no rendimento e na qualidade dos frutos da acerola (*Malpighia emarginata* DC.) em Pernambuco, nordeste do Brasil. Para atingir esses objetivos: (1) caracterizamos e quantificamos sistematicamente a literatura publicada globalmente com base em seus aspectos biogeográficos, econômicos e ecológicos, e sintetizamos as descobertas sobre como as práticas agroflorestais influenciam os polinizadores e os serviços de polinização; (2) conduzimos uma meta-análise global utilizando estudos que avaliaram os efeitos da quantidade de recursos florais locais e da cobertura de árvores de sombra, bem como a distância para florestas naturais sobre a abundância e a riqueza de polinizadores em sistemas agroflorestais de café, considerando fatores moderadores chave como o clima; (3) empregamos uma abordagem de resposta-efeito para investigar os impactos da cobertura floral e da intensidade luminosa (representando o manejo local), bem como da cobertura florestal (representando o manejo regional) na diversidade funcional dos polinizadores de acerola e na qualidade e rendimento dos frutos. Nossos principais resultados são os seguintes: (1) os níveis de serviços de polinização podem ser semelhantes ou até mesmo mais elevados em sistemas agroflorestais do que em sistemas agrícolas convencionais; (2) há uma forte correlação entre o aumento de recursos florais locais e uma maior diversidade de polinizadores de café. Além disso, a relação entre a cobertura de árvores de sombra e a distância para florestas naturais com a diversidade de polinizadores de café é amplamente influenciada pelas condições climáticas. O aumento dos níveis de precipitação é o principal fator, embora não seja o único, que afeta negativamente essa relação, impactando assim a diversidade de polinizadores de forma independente; (3) a abordagem de resposta-efeito sugere que as práticas de manejo agroflorestal exercem uma influência indireta na qualidade dos frutos. Embora os recursos florais não afetem a diversidade funcional dos polinizadores, é imperativo manter níveis reduzidos de intensidade luminosa e preservar diferentes graus de cobertura de floresta natural ao redor das áreas agroflorestais que promovem uma comunidade diversificada de polinizadores para otimizar a qualidade dos frutos. Nosso estudo enfatiza a importância das práticas sustentáveis de manejo agroflorestal na promoção dos serviços de polinização e na maximização do rendimento e qualidade dos frutos.

Palavras-chave: Agroecossistemas; diversidade de polinizadores; manejo agrícola; produção de culturas; serviços ecossistêmicos.

ABSTRACT

Over time, agricultural systems have undergone intensification to enhance food production and security. However, these changes in land use have resulted in declines in biodiversity and ecosystem services, such as pollination, negatively impacting food production and security. Pollinator diversity is crucial for enhancing the resilience of pollination services, and losses in this diversity could be mitigated or even reversed by agroforestry systems, which offer greater structural complexity compared to intensive agricultural systems. While numerous studies have explored pollination dynamics in agroforestry systems in recent years, their findings remain scattered. Additionally, the effects of agroforestry practices on pollination have primarily been examined theoretically rather than experimentally. Thus, this thesis had three primary objectives that structure the thesis into three chapters: (1) to review the existing literature on pollination in agroforestry systems worldwide, identifying general trends, knowledge gaps, and future research opportunities; (2) to conduct a global evidence synthesis evaluating how coffee agroforestry management practices affect pollinator diversity; (3) to determine the effects of local and regional agroforestry management factors on pollinating bee functional diversity and their impacts on fruit yield and quality of acerola (*Malpighia emarginata* DC.) in Pernambuco, northeastern Brazil. To achieve these objectives: (1) we systematically characterized and quantified global published research based on its biogeographical, economic, and ecological facets, and synthesized findings regarding how agroforestry practices influence pollinators and pollination services; (2) we conducted a global meta-analysis using studies that evaluated the effects of the amount of local floral resources and shade-tree cover, as well as the distance to natural forests on pollinator abundance and richness in coffee agroforestry systems, considering key moderating factors such as climate; (3) we employed a response-effect framework to investigate the impacts of floral cover and light intensity (representing local management) as well as forest land cover (representing regional management) on the functional diversity of acerola pollinators and fruit quality and yield. Our main findings are as follows: (1) levels of pollination services may be similar or even higher in agroforestry systems than in conventional agricultural systems; (2) strong correlation between increased local floral resources and enhanced diversity of bee pollinators. Additionally, the relationship between shade-tree cover and distance to natural forest largely hinges on climatic conditions, with increased levels of precipitation being the main factor, albeit not the sole one, negatively affecting the relationship between shade-tree cover and distance to natural forests, consequently impacting pollinator diversity separately; (3) the response-effect framework suggest that management practices exert an indirect influence on fruit quality Although floral resources did not directly affect pollinator functional diversity, it is imperative to maintain reduced light intensity levels and preserve varying degrees of natural forest cover around agroforestry areas that foster a diverse community of pollinators to optimize fruit quality. Our study underscores the importance of sustainable agroforestry management practices in fostering pollination services and maximizing fruit yield and quality.

Keywords: Agricultural management; agroecosystems; ecosystem services; pollinator diversity; Crop production.

1. INTRODUÇÃO GERAL

1.1. Objetivos e questionamentos

Nas últimas décadas, as pesquisas sobre polinização em sistemas agroflorestais têm gerado resultados significativos (e.g., REED et al., 2017; BARRIOS et al., 2017; KUYAH; ÖBORN; JONSSON, M., 2018). No entanto, essas descobertas estão dispersas, dificultando uma avaliação abrangente sobre se os sistemas agroflorestais poderiam servir como uma alternativa sustentável e viável aos sistemas agrícolas convencionais (CENTENO-ALVARADO; LOPES; ARNAN, 2023). Essa avaliação é crucial para determinar se os sistemas agroflorestais poderiam aprimorar ou ao menos manter os serviços de polinização em comparação com os sistemas agrícolas convencionais, garantindo assim a segurança alimentar. Além disso, o tema tem sido predominantemente abordado teoricamente em vez de explorado experimentalmente (por exemplo, KAY et al., 2018). Dentro desse contexto, realizamos uma revisão detalhada da literatura publicada até o momento sobre polinização em sistemas agroflorestais em todo o mundo. Caracterizamos e quantificamos sistematicamente os estudos com base na biogeografia, economia e aspectos ecológicos. Embora tenhamos sido capazes de estabelecer alguns padrões gerais, esse trabalho inicial também destaca a falta de atenção dada à eficácia das práticas de manejo agroflorestal, que permanece pouco avaliada (CENTENO-ALVARADO; LOPES; ARNAN, 2023). Diante dessa lacuna, realizamos uma meta-análise global para investigar como as práticas de manejo em sistemas agroflorestais de café (i.e., os sistemas agroflorestais mais predominantes em regiões tropicais; FAO, 2022) influenciam a diversidade de polinizadores. Nosso estudo visou testar se o aumento de recursos florais locais, maior cobertura de árvores de sombra e distâncias mais curtas para florestas naturais incrementam a diversidade de polinizadores, fornecendo mais oportunidades de forrageamento, abrigo e locais de nidificação, e melhorando a conectividade do habitat. Além disso, apesar de os sistemas agroflorestais serem mais comuns em regiões tropicais do que em regiões temperadas devido a desafios sociais e culturais, sua implementação no Brasil tem sido relativamente recente e moderada (MARTINELLI et al., 2019). No entanto, a adoção de agroflorestas no país é dificultada pela falta de recomendações e técnicas (MARTINELLI et al., 2019). Daí também surge o interesse em determinar os efeitos dos fatores de manejo agroflorestal locais e regionais sobre a diversidade funcional das abelhas polinizadoras e seu impacto no rendimento e qualidade dos frutos da acerola (*Malpighia emarginata* DC.), uma frutífera cultural e economicamente significativa dependente da polinização por insetos (EMBRAPA, 2012; SILVA et al., 2012; DIAS et al., 2018; BPBES; REBIPP, 2019) em Pernambuco, nordeste do Brasil. Especificamente, priorizamos a diversidade funcional, enfatizando os traços dos polinizadores que respondem às mudanças ambientais (traços de resposta) e que influenciam o funcionamento do ecossistema (traços de efeito), em vez da diversidade taxonômica. Ao perseguir esse objetivo, os três capítulos de nosso estudo contribuem de maneira sinérgica para elucidar as intricadas dinâmicas das interações planta-polinizador dentro de sistemas agroflorestais. Essa abordagem abrangente não apenas avança nossa compreensão dessas relações complexas, mas também oferece orientações práticas para a implementação de práticas de manejo agrícola sustentáveis.

1.2. Estratégias de pesquisa

Na tese utilizou-se uma combinação de revisão bibliográfica, meta-análise, trabalho de campo, construção da diversidade funcional e outras análises estatísticas. As estratégias de pesquisa foram as seguintes:

1.2.1. Revisão bibliográfica: Principais Itens para Relatar Revisões Sistemáticas e Meta-Análises (Declaração PRISMA)

Para conduzir um procedimento sistemático de busca e seleção de artigos, viabilizando a revisão sistemática no capítulo 1 e a meta-análise no capítulo 2, foi utilizada a declaração PRISMA. Essa declaração inclui uma lista de verificação e um fluxograma de quatro fases projetados para aprimorar a apresentação de revisões sistemáticas e meta-análises (MOHER et al., 2009). Esse processo de quatro fases envolve a identificação de artigos publicados, triagem de duplicatas, avaliação de elegibilidade com base em critérios específicos, exclusão de artigos que não atendem aos critérios de elegibilidade e, finalmente, seleção de artigos para síntese quantitativa e qualitativa (MOHER et al., 2009). Isso foi utilizado para realizar um procedimento sistemático de busca e seleção de artigos, possibilitando a revisão sistemática no capítulo 1, bem como a meta-análise no capítulo 2.

1.2.2. Meta-análise

No capítulo 2, utilizamos uma abordagem meta-analítica para avaliar a associação geral entre diversas práticas de manejo agroflorestal de café e a diversidade de polinizadores, abrangendo métricas como riqueza ou abundância. Meta-análises, também conhecidas como síntese de evidências, empregam modelos estatísticos para integrar e identificar resultados gerais a partir de uma coleção de estudos individuais (KORICHEVA; GUREVITCH, 2013).

Elas têm se tornado cada vez mais prevalentes na ecologia e evolução devido à sua natureza poderosa, informativa e imparcial, permitindo a identificação de tendências e sumarização de descobertas em múltiplos estudos sobre o mesmo tema (HEDGES; TIPTON; JOHNSON, 2010; KORICHEVA; GUREVITCH, 2013). Isso foi feito por meio de técnicas de estimativa de variância robusta (RVE) (FISHER; TIPTION; ZHIPENG, 2017) e métodos de aprendizado de máquina (árvores de regressão impulsionadas; BRT) (SHARMA; DURAND; GUR-ARIE, 1981; ELITH; LEATHWICK; HASTIE, 2008; KING, 2013; NAQA; MURPHY, 2015).

1.2.3. Trabalho de campo

No capítulo 3, para o trabalho de campo conduzimos coletas de polinizadores e frutos de acerola, além de medir fatores ambientais locais e regionais em 10 áreas situadas na região costeira úmida dominada pela Floresta Atlântica no estado de Pernambuco, nordeste do Brasil. As coletas de polinizadores foram realizadas ativamente, capturando-se os insetos que visitaram as flores, especificamente aqueles que pousaram nas flores e entraram em contato com suas partes reprodutivas. A coleta de frutos foi efetuada manualmente, marcando-se previamente as flores e, subsequentemente, coletando os frutos formados. Para a avaliação dos fatores locais, medimos a luminosidade como um proxy para a cobertura de árvores de sombra e a cobertura floral. Em relação aos fatores regionais, medimos a cobertura florestal. Para mais detalhes, consultar o capítulo 3.

1.2.4. Diversidade funcional

No capítulo 3, adotamos uma abordagem de diversidade funcional resposta-efeito para avaliar o impacto das práticas de manejo agroflorestal na diversidade funcional dos polinizadores de acerola, focando na diversidade derivada dos traços de resposta. Além disso, examinamos os efeitos da diversidade funcional dos polinizadores, derivados dos traços de efeito, na produção e qualidade dos frutos de acerola. A diversidade funcional foca nas funções dos organismos dentro dos ecossistemas, ao invés de apenas sua origem evolutiva (PETCHEY & GASTON, 2006). Pesquisas sobre distúrbios antropogênicos e polinização geralmente utilizam uma abordagem taxonômica (e.g., BIESMEIJER et al., 2006; ZATTARA; AIZEN, 2021). No entanto, uma perspectiva funcional pode oferecer uma visão mais completa, analisando como os traços das espécies respondem às mudanças ambientais e influenciam o funcionamento dos ecossistemas (HOOPER et al., 2000; TILMAN, 2001; STAVERT et al., 2016; WOODCOCK et al., 2019; COUTINHO et al., 2021; ROQUER-BENI et al., 2021).

Nesta abordagem, caracterizamos os traços de resposta e de efeito dos polinizadores, com base na literatura e em nossas próprias medições.

1.2.5. Análises estatísticas

No capítulo 1, os dados foram compilados descritivamente a partir de fontes existentes, não sendo analisados quantitativamente. Assim, a análise cienciométrica auxiliou na identificação de padrões ao quantificar avaliações, fenômenos, entre outros, utilizando a citação como um indicador semelhante a um "voto" ou "contagem" (JHA et al., 2015).

No capítulo 3, utilizamos uma série de modelos lineares generalizados (GLMs) e modelos lineares generalizados mistos (GLMMs) para responder à abordagem de diversidade funcional resposta-efeito. Os GLMs e GLMMs são técnicas estatísticas que funcionam de maneira semelhante à regressão linear padrão, com um preditor linear, distribuição de erro (variação não explicada pelo preditor) e função de ligação (tipo de relação entre o preditor linear e a variável resposta) (BUCKLEY, 2015; RICHARDS, 2015). No caso dos GLMMs, também incluem um fator aleatório, devido à correlação nos dados gerada pelo desenho do estudo (subconjuntos) (BUCKLEY, 2015; RICHARDS, 2015).

1.3. Estrutura da tese

Esta tese está organizada em uma revisão bibliográfica, três capítulos e uma seção de considerações. A revisão bibliográfica apresenta um referencial teórico, introduzindo conceitos-chave, abordagens e as principais implicações para o campo da ecologia, incluindo interações planta-polinizador, segurança alimentar e sustentabilidade. O Capítulo 1 consiste em um artigo de revisão publicado na revista *Agriculture, Ecosystems & Environment* (Qualis CAPES A1), que explora a literatura publicada até o momento sobre polinização em sistemas agroflorestais em todo o mundo com o objetivo de identificar tendências gerais, lacunas de conhecimento e oportunidades de pesquisas futuras. O Capítulo 2 consiste em um artigo publicado na revista *Insect Conservation and Diversity* (Qualis CAPES A2), que conduziu uma meta-análise global para explorar como as práticas de manejo de agroflorestas de café afetam a diversidade de polinizadores. O Capítulo 3 consiste em um artigo submetido à revista *Agriculture, Ecosystems & Environment,* que aplicou uma abordagem de resposta-efeito para avaliar como as características de manejo agroflorestal local e regional influenciam a diversidade funcional de abelhas polinizadoras e o rendimento e qualidade dos frutos de acerola (*Malpighia emarginata* DC.) no nordeste do Brasil. Por fim, as considerações finais apresentam as principais conclusões, contribuições teóricas e metodológicas da tese, principais limitações do estudo e propostas para pesquisas futuras.

2. FUNDAMENTAÇÃO TEÓRICA

2.1. Fome mundial e segurança alimentar

Nos últimos anos, tem sido documentada uma grave escassez de alimentos nutritivos, decorrente de políticas agrícolas, problemas de escassez de água, mudanças climáticas e conflitos sociais (BEHERA et al., 2022). Como resultado, a fome tornou-se uma preocupação crônica em escala global, especialmente em áreas rurais com condições climáticas adversas e localidades de difícil acesso (BEHERA et al., 2022). Projeções recentes indicam que aproximadamente 10% da população mundial, ou cerca de 750 milhões de pessoas, enfrentaram desnutrição e fome em 2019 (FAO, 2020). Atingir níveis aceitáveis de segurança alimentar (i.e., condições físicas e econômicas que garantem acesso a alimentos suficientes, seguros e de qualidade para atender às necessidades dietéticas para uma vida ativa e saudável) tem sido um desafio em todas as regiões do mundo, com exceção da América do Norte e da Europa (Porter et al., 2014; FAO, 2020). Isso se deve ao fato de que a produção de alimentos não tem sido suficiente para atender ao consumo diário recomendado pela FAO para toda a população, e a maioria das pessoas de baixa renda não possui poder aquisitivo econômico para obtê-los (Porter et al., 2014; FAO, 2020). O custo de uma dieta saudável ultrapassa o valor total da linha de pobreza, estabelecida em aproximadamente USD 1,90 por dia (Porter et al., 2014).

A produção de alimentos é um serviço ecossistêmico (i.e., benefícios ou vantagens que as pessoas obtêm dos ecossistemas; BENNETT; PETERSON; GORDON, 2009; PALMER; FILOSO, 2009) que engloba todos os processos e infraestrutura necessários para garantir a segurança alimentar, desde o cultivo do alimento até a distribuição (PORTER et al., 2014; HOLT et al., 2016). Uma das formas mais importantes de produção de alimentos ocorre por meio da polinização (VAN DER SLUIJS; VAAGE, 2016). Esse processo é um serviço ecossistêmico crucial, com funções de regulação, suporte e cultural, que estabelece conexões entre a vegetação terrestre, a vida selvagem e o bem-estar humano (KEVAN; MENZEL, 2012; CHAGNON et al., 2015).

2.2. Polinização

Nas plantas, a falta de mobilidade cria uma limitação na dispersão de seus genes (PELLMYR, 2009). No entanto, a maioria das plantas tem superado essa limitação por meio de vetores abióticos ou através da formação de mutualismos com animais (PELLMYR, 2009). Os mutualismos são interações que geralmente beneficiam tanto o animal quanto a planta (PELLMYR, 2009). Alguns desses mutualismos incluem a polinização e a dispersão de sementes (PELLMYR, 2009). A polinização é o processo pelo qual o pólen é transferido dos órgãos reprodutivos masculinos para os órgãos reprodutivos femininos das plantas, permitindo a fertilização e a produção de sementes e frutos (PELLMYR, 2009; NEUSCHULZ et al., 2016). Esse processo ocorre através de animais que coletam o pólen e o depositam nos estigmas coespecíficos de outras plantas (PELLMYR, 2009). Isso é feito pelos animais em troca de uma recompensa, geralmente alimento, como néctar (PELLMYR, 2009). A importância da polinização surge de sua influência na reprodução das plantas e na estabilização e funcionamento das teias alimentares, fornecendo recursos alimentares-chave (IPBES, 2016; KLEIN et al., 2006; OLLERTON; WINFREE; TARRANT, 2011). A polinização biótica também é considerada um dos principais fatores para a diversificação de vários grupos de plantas e animais (IPBES, 2016). Os principais animais que participam da polinização são insetos, especialmente as abelhas, junto com outros como moscas, borboletas, vespas, besouros e formigas (IPBES, 2016). Outros grupos de polinizadores incluem animais vertebrados, como morcegos, pássaros, répteis, roedores, marsupiais e primatas (IPBES, 2016). Além disso, aproximadamente 87,5% das plantas com flores dependem de animais para a polinização, algumas das quais são culturas importantes (KLEIN et al., 2006; OLLERTON; WINFREE; TARRANT, 2011; IPBES, 2016).

Adicionalmente, a produção de alimentos depende da polinização animal, pois aproximadamente 75% das principais culturas aumentam a produção com a visitação de polinizadores (KLEIN et al., 2006; OLLERTON; WINFREE; TARRANT, 2011). Estima-se que a produção de 70% das principais culturas comerciais nas regiões tropicais seja aprimorada pela polinização animal (ROUBIK, 1995; KLEIN et al., 2006). Nas áreas temperadas, 84% da produção das principais culturas comerciais depende da polinização animal (WILLIAMS, 1994; KLEIN et al., 2006). A polinização animal também é um dos fatores que influenciam a segurança alimentar global, pois a qualidade das culturas pode ser melhorada pela polinização biótica, proporcionando macro e micronutrientes essenciais para uma dieta saudável (SUNDRIVAL; SUNDRIVAL, 2004; GARIBALDI et al., 2013; BRITTAIN et al., 2014; RAMOS-JILIBERTO; ESPAÑÉS; VÁSQUEZ, 2020). Apesar de as plantas serem flexíveis em suas interações com animais, tem havido declínios nos polinizadores nas últimas décadas, o que pode levar a um ponto de redundância ecológica e à perda de interações essenciais (STEFFAN-DEWENTER et al., 2005; IPBES, 2016; KLEIN et al., 2006; OLLERTON; WINFREE; TARRANT, 2011). A perda de polinizadores pode reduzir uma parte substancial da flora global e, assim, empobrecer a dieta humana, tanto nutricional quanto culturalmente (STEFFAN-DEWENTER et al., 2005; IPBES, 2016; KLEIN et al., 2006; OLLERTON; WINFREE; TARRANT, 2011).

As abelhas são os principais visitantes florais para mais de 90% das principais culturas globais, seguidas por moscas e outros táxons (IPBES, 2016). Nos trópicos, abelhas, borboletas, mariposas, pássaros e morcegos são polinizadores importantes, enquanto em áreas temperadas, a maioria da polinização é realizada por abelhas melíferas (*Apis mellifera*), abelhas solitárias, vespas e moscas-das-flores (GARIBALDI et al., 2011; GARIBALDI et al., 2013; HANLEY et al., 2015). Embora as abelhas manejadas sejam comumente usadas para melhorar a polinização de culturas, há evidências de que abelhas nativas e outros insetos são mais eficientes para o sucesso da polinização (GARIBALDI et al., 2011; GARIBALDI et al., 2013; HANLEY et al., 2015).

2.2.1. Diversidade funcional dos polinizadores

Animais e plantas interagem em um sistema trófico diverso e complexo que influencia a manutenção e o funcionamento dos ecossistemas (BALLANTYNE; BALDOCK; WILLMER, 2015; NOVELLA-FERNANDEZ et al., 2019; LUNA & DÁTTILO, 2021). Diversidade funcional se refere aos aspectos da biodiversidade que determinam o funcionamento de um ecossistema (TILMAN, 2001). É um componente específico da biodiversidade geral, avaliado pelos traços ou características dos organismos que respondem (i.e., traços de resposta) ou influenciam (i.e., traços de efeito) diferentes processos do ecossistema (TILMAN, 2001). Esta diversidade é crucial porque afeta a dinâmica, a estabilidade, a produtividade e várias outras funções dos ecossistemas (TILMAN, 2001).

Na ecologia da polinização, a maioria dos estudos tem dado maior importância aos traços florais e como esses traços constituem síndromes de polinização (MURÚA, 2020). No entanto, a influência dos traços funcionais na polinização tem sido negligenciada (MURÚA, 2020). Especificamente, os traços ou características devem ser estudados para entender os serviços de polinização nos ecossistemas (WOODCOCK et al., 2019; MURÚA, 2020). A diversidade funcional das espécies pode aumentar a polinização e a produção agrícola, apoiando a hipótese da complementaridade (WOODCOCK et al., 2019), que afirma que o aumento no uso de recursos é impulsionado pela partição de recursos ou interações positivas entre plantas e polinizadores (LOREAU & HECTOR, 2001; LOSAPIO et al., 2021). Na polinização, aumentos no sucesso reprodutivo das plantas podem ocorrer com aumentos na distribuição de traços não sobrepostos (WOODCOCK et al., 2019).

Adicionalmente, pesquisas anteriores sobre a interação entre polinizadores e atividades humanas focavam principalmente na classificação e no estudo demográfico dos polinizadores (e.g., BIESMEIJER et al., 2006; BRITTAIN et al., 2010; CARVALHEIRO et al., 2013; ZATTARA; AIZEN, 2021). Contudo, a intensificação agrícola necessária para manter ou aumentar a produção e, assim, garantir a segurança alimentar tem levado a declínios na biodiversidade. Em resposta, as pesquisas estão cada vez mais focadas na diversidade funcional para entender a complexidade dos efeitos das mudanças antropogênicas nos serviços ecossistêmicos (GAGIC et al., 2015). Isso envolve analisar como os traços fenológicos, fisiológicos e comportamentais dos polinizadores reagem às mudanças ambientais (i.e., traços de resposta) e/ou como influenciam o funcionamento dos ecossistemas (i.e., traços de efeito) (HOOPER et al., 2000; TILMAN, 2001; MCGILL et al., 2006).

2.3. Intensificação agrícola para garantir a segurança alimentar

A intensificação agrícola resultou do aumento populacional, especialmente em regiões com densidades populacionais mais altas, com o objetivo de garantir a segurança alimentar (RICKERGILBERT; JUMBE; CHAMBERLIN, 2014; FAO, 2017). Tanto o aumento no número de pessoas quanto as mudanças na dinâmica populacional são importantes impulsionadores da demanda por alimentos e produtos agrícolas (FAO, 2017). A transformação de ecossistemas naturais tem sido exacerbada pela conversão do uso da terra para cultivos agrícolas e criação de gado (FAO, 2017). Essas transformações causam desmatamento, aumento no uso de pesticidas para aumentar a produção, emissões elevadas de metano dos ruminantes e uso insustentável de água e energia (FAO, 2017). Essas ações são prejudiciais para a conservação de espécies e para a manutenção e funcionamento dos serviços ecossistêmicos, como a polinização, o que, por sua vez, pode reduzir a produção de alimentos (KLEIN et al., 2006).

Adicionalmente, uma das principais causas da perda de biodiversidade é a transformação de ecossistemas naturais em sistemas agrícolas, principalmente durante o desmatamento (FIRBANK et al., 2008). As atividades agrícolas, junto com outras atividades humanas, estão impactando negativamente os ecossistemas, levando à eliminação de genes, espécies e características ecológicas em taxas alarmantes (CARDINALE et al., 2012). Ao longo dos últimos séculos, as atividades humanas têm causado extinções e reduções nas populações locais, comparáveis à magnitude de extinções em massa anteriores na história da Terra (DIRZO et al., 2014). A perda de biodiversidade reduz a eficiência de alguns processos ecológicos, gerando efeitos em cascata na produção e manutenção de serviços e recursos (CARDINALE et al., 2012).

Em relação à fauna, estima-se que entre 11.000 e 58.000 espécies sejam perdidas anualmente (SCHEFFERS et al., 2012; MORA; ROLLO; TITTENSOR, 2013; DIRZO et al., 2014). Nas últimas cinco décadas, houve uma queda estimada de 28% na abundância de espécies de vertebrados (COLLEN et al., 2009; BUTCHART et al., 2010; DIRZO et al., 2014). Apesar disso, acredita-se que as extinções de espécies de invertebrados, as quedas na abundância e as contrações de alcance sejam tão graves quanto para as espécies de vertebrados (COLLEN & BAILLIE, 2010; BAILLIE et al., 2012; DIRZO et al., 2014). Isso pode ter consequências graves para alguns serviços ecossistêmicos importantes, como a polinização (POTTS et al., 2010; DIRZO et al., 2014).

Nas últimas décadas, tem sido registrada uma crescente evidência de declínios de polinizadores, tanto em abundância quanto em diversidade globalmente, com evidências mais substanciais surgindo na América do Norte e Europa (BIESMEIJER et al., 2006; POTTS et al., 2009; POTTS et al., 2010; ANDERSON et al., 2011). Também foi demonstrado que os declínios de polinizadores podem afetar as espécies vegetais (BIESMEIJER et al., 2006; ANDERSON et al., 2011). Isso pode reduzir o sucesso reprodutivo das plantas, especialmente culturas agrícolas, devido a sua dependência da polinização animal (BIESMEIJER et al., 2006). A limitação de polinizadores pode aumentar a demanda por terra agrícola, pois áreas de intensificação agrícola precisarão se expandir para compensar os déficits de polinização (AIZEN et al., 2009; CARVALHEIRO et al., 2011; GARIBALDI et al., 2011; VIANA et al., 2012). Esse aumento será mais significativo em áreas com maior pressão humana, incluindo as mudanças climáticas antropogênicas, causando a perda de espécies e, consequentemente, deteriorando as redes planta-polinizador e empobrecendo os serviços de polinização (CARVALHEIRO et al., 2011; GARIBALDI et al., 2011; VIANA et al., 2012).

2.4. Mudanças climáticas antropogênicas como impulsionadoras dos efeitos negativos da intensificação agrícola nos serviços de polinização

As mudanças climáticas antropogênicas referem-se às alterações aceleradas nos padrões de temperatura e precipitação, resultantes das emissões de gases de efeito estufa decorrentes das atividades humanas (HANSEN; STONE, 2016). A destruição de áreas naturais para o cultivo de lavouras tem aumentado rapidamente, apesar de alguns esforços para desacelerá-la (HANSEN; STONE, 2016; RAVEN; WAGNER, 2020). Grande parte dessas terras são dedicadas principalmente a monoculturas, que têm um impacto significativo nas mudanças climáticas (RAVEN; WAGNER, 2020). As monoculturas são sistemas agrícolas que cultivam uma única espécie de planta em grande escala, o que reduz a diversidade de plantas na área (DRURY et al., 2008). Essa falta de diversidade diminui a resiliência do ecossistema agrícola, tornando-o mais suscetível a doenças, pragas e mudanças climáticas (DRURY et al., 2008). Além disso, as monoculturas muitas vezes requerem o uso intensivo de fertilizantes sintéticos e pesticidas, que contribuem para a emissão de gases de efeito estufa (DRURY et al., 2008). Por outro lado, as mudanças climáticas também representam um desafio para a agricultura, pois os habitats adequados para as culturas estão mudando e muitas terras aráveis estão se tornando inadequadas para o cultivo devido às condições cada vez mais secas (RAVEN; WAGNER, 2020).

Adicionalmente as mudanças climáticas antropogênicas exacerbam os impactos adversos da intensificação agrícola nos serviços de polinização de várias maneiras. Isso abrange a dessincronização entre os períodos de floração das plantas e a atividade dos polinizadores devido a mudanças na fenologia, a migração forçada de polinizadores para áreas climaticamente mais adequadas, a crescente frequência de eventos climáticos extremos prejudiciais às plantas e aos polinizadores, além da diminuição da disponibilidade de recursos alimentares para os polinizadores (GÓMEZ-RUIZ; LACHER JR., 2019; GÉRARD et al., 2020; DEVOT et al., 2023). Esses efeitos combinados comprometem a eficiência da polinização natural, aumentando a necessidade de métodos artificiais de polinização e colocando em risco a produção agrícola e a segurança alimentar (BROUSSARD; COATES; MARTINSEN, 2023). Diante das consequências da intensificação da agricultura e das mudanças climáticas antropogênicas sobre a biodiversidade e serviços ecossistêmicos, a implementação de métodos agrícolas alternativos é urgente (GODFRAY & GARNETT, 2014; FAO, 2017).

2.5. Sistemas agroecológicos como estratégia para mitigar as causas e consequências da intensificação agrícola e das mudanças climáticas antropogênicas

Devido à crescente demanda por produtos agrícolas e a alarmante perda de biodiversidade, sistemas agrícolas alternativos têm sido propostos para mitigar os efeitos negativos da intensificação agrícola (VALENZUELA, 2016). Os sistemas agroecológicos promovem práticas agrícolas que consideram as condições socioeconômicas locais e a proteção dos processos ecológicos naturais (VALENZUELA, 2016). Esses sistemas baseiam-se em processos sustentáveis de ciclagem de nutrientes, controle populacional e trocas de energia. Essas características refletem as encontradas nos ecossistemas naturais e, ainda que modificadas, também estão presentes nos ecossistemas humanos ou agrícolas (WEZER et al., 2014). A adoção de sistemas agroecológicos promove o controle de pragas, uso eficiente da água, melhoria da qualidade do solo e teor de matéria orgânica, mineralização de nitrogênio mais eficiente e uniforme, além de melhorar a biodiversidade, os serviços ecossistêmicos e a resiliência em nível de fazenda e paisagem (VALENZUELA, 2016). Tipos de sistemas agroecológicos incluem: (1) adubo verde, que consiste no cultivo de plantas que são posteriormente aradas ou incorporadas ao solo para melhorar sua fertilidade e teor orgânico; (2) agroflorestas, um sistema de manejo de terra no qual árvores ou arbustos são cultivados ao redor ou entre cultivos ou pastagens; (3) consorciação e rotação de culturas, que envolvem o cultivo simultâneo de duas ou mais culturas no mesmo campo, ou a alternância temporal entre cultivos; (4) culturas de cobertura, plantações destinadas principalmente a controlar a erosão do solo, fertilidade, qualidade do solo, entre outros fatores; e (5) integração pecuária, que consiste na incorporação de animais, como gado, ovelhas, cabras ou aves, nos sistemas agrícolas de forma a maximizar a produtividade e melhorar o ciclo de nutrientes (WEZER et al., 2014).

Dentro das práticas de agroecologia, a agrofloresta se destaca, promovendo o manejo sustentável dos recursos naturais (PRABHU et al., 2014). De maneira específica, a agrofloresta é definida como a prática de incorporar árvores (perenes lenhosas) em sistemas de cultivo (incluindo pastagens) e/ou criação de animais, ou vice-versa, seja em arranjo espacial ou em sequência temporal (NAIR, 1985; LIPPER et al., 2014; BLASER et al., 2018). É considerada uma forma de agricultura inteligente para o clima porque utiliza os serviços ecossistêmicos para manter a produção enquanto se adapta e mitiga os efeitos das mudanças climáticas (LIPPER et al., 2014; BLASER et al., 2018). Os sistemas agroflorestais podem aumentar o sequestro de carbono, manter a biomassa acima do solo, fornecer sombra para melhorar o microclima e diversificar a renda dos agricultores, reduzindo os riscos econômicos para eles (HARVEY et al., 2013). Da mesma forma, esses sistemas podem melhorar a fertilidade do solo e regular pragas e patógenos por meio de controles biológicos (BLASER et al., 2018).

2.6. Fatores de manejo local e regional que afetam a diversidade e as interações entre plantas e polinizadores em sistemas agroflorestais

Mesmo que a diversificação de plantas e a complexidade do habitat em sistemas agroflorestais possam melhorar os serviços ecossistêmicos, como a polinização (e.g., GRAHAM & NASSAUER, 2017; STATON et al., 2019; TOLEDO-HERNÁNDEZ et al., 2021), pouco se sabe sobre quais práticas de manejo locais e regionais em sistemas agroflorestais maximizam as interações entre plantas e polinizadores e os serviços associados de polinização e segurança alimentar.

2.6.1. Práticas de manejo local

Alguns dos fatores locais que têm sido avaliados como potenciais influências na polinização em sistemas agroflorestais são a densidade ou cobertura de sombra de árvores, a diversidade floral e o uso de insumos agrícolas. No primeiro caso, uma maior densidade de árvores pode proporcionar uma área de nidificação maior e melhor para alguns insetos polinizadores (HILL & WEBSTER, 1995; FIERRO et al., 2012; GRAHAM & NASSAUER, 2017; PAVAGEAU et al., 2017; BENTRUP et al., 2019), aumentando assim a chance de sucesso na polinização sob condições microclimáticas ideais. Em sistemas agroflorestais de cacau no México, foi observada uma densidade maior de ninhos de abelhas sem ferrão em áreas com condições microclimáticas melhoradas e maior disponibilidade de habitat (FIERRO et al., 2012). Da mesma forma, em outros tipos de sistemas agroflorestais no sul da Índia, a presença e densidade de ninhos de abelhas estavam correlacionadas com uma cobertura arbórea mais densa (PAVAGEAU et al., 2018). No segundo caso, uma maior diversidade de plantas e recursos florais diversificados poderiam atrair mais polinizadores do que em áreas homogêneas (GRAHAM & NASSAUER, 2019; BARRERA; BROSAS; SACIL, 2020; TOLEDO-HERNÁNDEZ et al., 2021). De fato, uma síntese mostrou que sistemas agrícolas diversificados aumentam a abundância de artrópodes, com as respostas mais fortes em polinizadores e predadores, facilitando serviços ecossistêmicos (LICHTENBERG et al., 2017). No terceiro caso, os insumos agrícolas (i.e., pesticidas) são uma das principais causas do declínio de polinizadores, e as práticas em sistemas agroflorestais geralmente previnem ou reduzem o uso de pesticidas (BENTRUP et al., 2019).

Além disso, fatores climáticos podem modificar a maneira como as práticas de manejo afetam as comunidades de plantas e polinizadores, e consequentemente, os serviços de polinização. Temperatura e precipitação têm impactos significativos na fisiologia e fenologia das plantas, alterando assim as interações entre plantas e polinizadores (DESCAMPS et al., 2018; LAWSON & RANDS, 2019). Por exemplo, no caso dos recursos florais, mudanças mediadas pelo clima no volume de néctar e na concentração de açúcar podem resultar em alterações na atratividade dos recursos, modificando a abundância e a atividade dos polinizadores (DESCAMPS et al., 2018; LAWSON & RANDS, 2019; DESCAMPS et al., 2021).

2.6.2. Práticas de manejo regional

Alguns dos fatores regionais que têm sido avaliados como potenciais influências na polinização em sistemas agroflorestais são a configuração da paisagem (i.e., tamanho e conectividade dos fragmentos), a composição da paisagem (i.e., diversidade da paisagem) e o tipo de ecorregião. No primeiro caso, uma maior conectividade em sistemas agroflorestais pode facilitar o movimento dos polinizadores entre diferentes áreas, melhorando assim os serviços de polinização (BENTRUP et al., 2019). Evidências disso têm sido registradas para insetos polinizadores, incluindo abelhas, borboletas, mariposas e moscas (DOVER & FLY, 2001; OUIN & BUREL, 2002; MEIER et al., 2005; CRANMER; MCCOLLIN; OLLERTON, 2012; HAENKE et al., 2014; KLAUS et al., 2015; COULTHARD; MCCOLLIN; LITTLEMORE, 2016). No segundo caso, a composição da paisagem também pode afetar a polinização. Por exemplo, uma proporção maior de cercas vivas e habitats naturais pode mitigar os efeitos negativos das altas temperaturas na riqueza e abundância de abelhas nativas, apoiando uma maior diversidade funcional e riqueza de abelhas nativas, o que, por sua vez, influencia a manutenção da população (DOVER & FLY, 2001; PONISIO et al., 2016; BENTRUP et al., 2019). No terceiro caso, as ecorregiões fornecem variabilidade natural em chuvas e temperaturas que impactam a produção agrícola e a segurança alimentar. Portanto, o manejo, escolha de árvores e culturas devem ser ajustados de acordo (MOLUA, 2002).

Além disso, eventos climáticos extremos podem impor limitações mecânicas e energéticas aos polinizadores durante suas atividades de forrageamento e nidificação (LAWSON; RANDS, 2019). Como consequência, à medida que a distância das florestas naturais aumenta, os polinizadores podem encontrar disparidades mais significativas nos recursos e enfrentar obstáculos maiores. Em última análise, tais circunstâncias poderiam reduzir a probabilidade de os polinizadores percorrerem a distância entre as florestas naturais e os sistemas agroflorestais, possivelmente resultando em uma diminuição da diversidade de polinizadores.

2.7. Sistemas agroflorestais no Brasil: O caso da Região da Mata Atlântica em Pernambuco, Nordeste do Brasil

Embora os sistemas agroflorestais sejam encontrados com maior frequência em áreas tropicais em comparação com regiões temperadas, devido a obstáculos sociais e culturais, sua adoção no Brasil é relativamente nova e está ocorrendo em um ritmo moderado (MARTINELLI et al., 2019). Contudo, a implementação de sistemas agroflorestais no país enfrenta desafios devido à escassez de orientações e métodos específicos (MARTINELLI et al., 2019). Dessa maneira, o governo brasileiro está cada vez mais promovendo a implementação de sistemas agroflorestais, como pode ser visto no Plano Setorial de Adaptação às Mudanças Climáticas e Emissões de Baixo Carbono na Agricultura (Plano ABC+) 2020–2030 (MINISTÉRIO DE AGRICULTURA, PECUÁRIA E ABASTECIMENTO, 2021). Este plano descreve uma estratégia nacional para impulsionar adaptações às mudanças climáticas e controlar as emissões de gases de efeito estufa nos sistemas agrícolas brasileiros (MINISTÉRIO DE AGRICULTURA, PECUÁRIA E ABASTECIMENTO, 2021). Um dos principais objetivos é incentivar a implementação de sistemas agroflorestais (MINISTÉRIO DE AGRICULTURA, PECUÁRIA E ABASTECIMENTO, 2021), que poderiam ajudar a proteger a lucratividade média da agricultura ao mitigar os efeitos negativos das mudanças climáticas (SCHEMBERGUE et al., 2017). Na região Nordeste do Brasil, especificamente em Pernambuco, a região de Mata Atlântica úmida e tropical é particularmente fragmentada devido ao extenso cultivo de cana-de-açúcar (RANTA et al., 1998; SIQUEIRA FILHO et al., 2007). Além disso, a maior parte da produção agrícola no estado de Pernambuco (90%) provém de agricultura familiar. No entanto, uma disparidade evidente surge, uma vez que apenas 3% dessas famílias produtoras atualmente incorporam práticas agroflorestais (IBGE, 2017). Essa marcante incongruência não apenas sublinha a necessidade premente de se afastar de paradigmas monoculturais, exemplificados pela predominância do cultivo de cana-de-açúcar, mas também apresenta uma oportunidade para explorar e promover a adoção de sistemas agroflorestais.

3. CAPÍTULO 1: Fostering pollination through agroforestry: A global review

Diego Centeno-Alvarado, Ariadna Valentina Lopes, Xavier Arnan

https://doi.org/10.1016/j.agee.2023.10478

Agriculture, Ecosystems & Environment:

- Qualis CAPES (Classificações de periódicos quadriênio 2017-2020: Biodiversidade): A1
- Impact Factor: 6.6
- Percentile SCOPUS: 98%

Agriculture, Ecosystems and Environment 351 (2023) 108478

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Fostering pollination through agroforestry: A global review

Diego Centeno-Alvarado [a,*,1], Ariadna Valentina Lopes [b,2], Xavier Arnan [a,c,3]

[a] Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil
[b] Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil
[c] Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

ARTICLE INFO

Keywords:
Agricultural management
Agroecosystems
Ecosystem services
Pollinator diversity
Crop production

ABSTRACT

Over time, agricultural systems have undergone intensification with a view to increasing food production and security. However, the resulting land use conversions have led to declines in biodiversity and ecosystem services, such as pollination, and have thus negatively affected food production and security. It may be that the harmful impacts of conventional agriculture could be somewhat mitigated by diversifying current farming systems. Notably, the incorporation of agroforestry can provide suitable habitat for native pollinators and thus maintain pollination services. In recent years, several studies have examined pollination dynamics in agroforestry systems. However, their findings remain scattered, and the effects of agroforestry practices on pollination have generally been approached from a theoretical rather than an experimental point of view. Here, we reviewed the literature published to date on pollination in agroforestry systems across the world with a view to identifying general trends, gaps in knowledge, and future opportunities. To this end, we systematically characterized and quantified the research based on its biogeographical, economic, and ecological facets, and we synthesized discoveries about how agroforestry practices influence pollinators and pollination services. Our results highlight that, compared to conventional agriculture, agroforestry generally promotes or maintains pollination services. Therefore, this review supports the perspective that agroforestry systems represent a sustainable alternative to conventional agricultural systems. Future research should focus on improving understanding of how crop management intensity, irrigation, and organic inputs affect pollination services. We need more studies looking at a broader range of crop species and pollinator guilds as well as research examining the effects of crop management intensity on plant-pollinator interaction networks.

1. Introduction

Over the course of decades, agricultural systems have undergone intensification: increasing quantities of inputs have been used to boost yields per unit of farmland, thus increasing food production (Porter et al., 2014; Ricker-Gilbert et al., 2014; Struik and Kuyper, 2017; Food and Agriculture Organization of the United Nations, 2017). The inevitable result has been the loss of natural ecosystems, which has reduced the ecosystem services supplied by biodiversity (Food and Agriculture Organization of the United Nations, 2017; Convention on Biological Diversity, 2018; Ramos-Jiliberto et al., 2020). Pollination has been particularly impacted because simpler agricultural environments reduce the diversity and availability of pollinator habitat (Tscharntke et al., 2005; Potts et al., 2010; Cardinale et al., 2012). Furthermore, since global crop production significantly depends on animal pollination, food security may also be at risk (Klein et al., 2007).

Over recent decades, we have witnessed major declines in pollinator richness, abundance, and biogeographical distributions and, in some cases, pollinator extinctions (e.g., bees and wild butterflies; see Convention on Biological Diversity, 2018; Ramos-Jiliberto et al., 2020). These trends may negatively affect important ecosystem services, such as global food production and food security, given that many crop species improve in nutritional value and yield thanks to animal-mediated pollination (e.g., Bartomeus et al., 2014; Bailes et al.,

---

* Correspondence to: Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife, PE 52171-900, Brazil.

E-mail address: diego.centenoalvarado@ufrpe.br (D. Centeno-Alvarado).

[1] http://orcid.org/0000-0003-0273-8538
[2] http://orcid.org/0000-0001-5750-5913
[3] http://orcid.org/0000-0002-9904-274X

https://doi.org/10.1016/j.agee.2023.108478
Received 1 July 2022; Received in revised form 10 March 2023; Accepted 13 March 2023

2015; IPBES, 2016; Ramos-Jiliberto et al., 2020). The forces responsible include climate change, introduced species, land use change, and agricultural intensification (e.g., Lichtenberg et al., 2017; Ramos-Jiliberto et al., 2020). During agricultural intensification, natural ecosystems are transformed and/or input levels are increased, which can detrimentally affect pollinators (Ramos-Jiliberto et al., 2020). Furthermore, climate change can exacerbate the impacts of conventional agricultural practices, reducing the resilience and sustainability of natural and socio-ecological systems (Lichtenberg et al., 2017).

Conventional agricultural practices reduce pollinator abundance, richness, and community composition because they rely on agrochemical inputs, destroy sources of food and shelter, and simplify the landscape (Epule and Bryant, 2016; Shennan et al., 2017). Furthermore, agricultural intensification can reduce pollinator trait diversity because the landscape changes can filter species based on characteristics related to dispersal, feeding, nesting, and physiological tolerance (Forrest et al., 2015). These traits are correlated with the ability of pollinators to cope with environmental shifts (Violle et al., 2007, Roquer-Beni et al., 2021). A reduction in trait diversity could negatively affect pollination success since some traits are directly associated with pollen uptake and transport (Roquer-Beni et al., 2020, 2021).

A solution to the above problem could be more diverse farming approaches (Lichtenberg et al., 2017). Agroecological systems combine traditional, local, and scientific practices to increase species richness and make optimal use of genetic resources (Food and Agriculture Organization of the United Nations, 2017; Lichtenberg et al., 2017). Agroecological systems utilize natural nutrient cycling techniques and rarely employ synthetic substances or agrochemicals (Epule and Bryant, 2016; Shennan et al., 2017). One such system is agroforestry, in which food production is combined with the conservation of natural forest habitat (Nair, 1985). Agroforestry can take the form of alley cropping, where agricultural crops are grown between spaced tree rows; silvopastoral management, where grasses are grown under trees to feed livestock; windbreaks or shelterbelts, where trees are arranged to protect crops from the wind; and forest farming, where shade-tolerant crops are grown within natural forest stands, to name a few examples (Garrett and Buck, 1997; Nair, 2005, 2007).

By creating more diverse agricultural landscapes, agroforestry can increase sources of food and shelter for pollinators, thus improving habitat quality, pollination services, and crop quality and yields (e.g., Maccagnani et al., 2020). The presence of plant diversity can increase the taxonomic range and functional diversity of both plants and pollinators, contributing to greater plant reproductive success (e.g., Girão et al., 2007; Weiner et al., 2014). Furthermore, plant-pollinator interactions are affected by the diversification of agricultural systems, namely by modifications to vegetation composition, flower availability, and environmental conditions (Weiner et al., 2014).

Mutualistic interactions, such as those underlying pollination, play a major role in maintaining ecosystems, community dynamics, and ecological services (e.g., Xiao et al., 2019). Agroecological systems can promote the stability and quality of ecological services (e.g., Bohan et al., 2013) as well as the quality and connectivity of the agricultural matrix, thus enhancing plant-animal interactions (Klein et al., 2003c). Considering that agricultural production relies heavily on animal-mediated pollination (e.g., Ollerton et al., 2011; IPBES, 2016) and that agroforestry may represent a more sustainable alternative to conventional agriculture, there is an urgent need to assess pollinator status and pollination services in agroforestry systems.

Over recent decades, several studies have been published on the topic of pollination in agroforestry systems. However, their findings remain scattered, and the topic has generally been approached from a theoretical rather than an experimental perspective (e.g., Kay et al., 2018). There have also been attempts to review this body of work, but they have been focused on particular crops (e.g., Perfecto et al., 2007; Toledo-Hernández et al., 2017), specific pollinators (e.g., Ya, 2000; Chain-Guadarrama et al., 2019), or certain geographical regions (e.g., Bentrup et al., 2019). Another important facet that has received little attention is the socioeconomic context associated with agroforestry systems, given that the latter's ecosystem services are shaped by natural, anthropogenic, and economic forces that are rooted in local realities and priorities (Munyuli, 2014b; Food and Agriculture Organization of the United Nations, 2016). Here, we have reviewed the global research published to date on pollination in agroforestry systems with a view to identifying general trends, gaps in knowledge, and future opportunities. The broader goal is to furnish information that can inform agricultural practices by considering the balance between biodiversity conservation and food production. This review sought to accomplish the following: (1) characterize and quantify studies on pollination in agroforests based on biogeographical, socioeconomic, and ecological elements; (2) identify the mechanistic factors in agroforestry systems that affect pollinator type, diversity, and traits as well as pollination services (e.g., pollen dynamics and crop production; (3) determine how pollinator diversity and pollination services differ in agroforestry systems versus conventional agroecosystems.

2. Methodology

2.1. Systematic bibliographic search and eligibility criteria

A systematic bibliographic search was carried out using a Boolean approach in ISI Web of Science (www.webofknowledge.com) and Scopus (www.scopus.com). The following search arguments were used: (1) agroforest* AND pollinat* ; (2) silvopast* AND pollinat* ; (3) windbreak* AND pollinat* ; (4) "alley cropping" AND pollinat* ; and (5) "forest farming" AND pollinat* . The search terms appeared in the title, keywords, and/or abstract. We chose the arguments silvopast* (derived from the terms silvopasture and silvopastoral), windbreak* , alley cropping, and forest farming because they refer to different types of agroforestry practices (Mosquera-Losada et al., 2009; Atangana et al., 2014; Cardinael et al., 2015; Jose and Dollinger, 2019), and we could thus broaden the scope of the literature search. Our review covered a timespan from the earliest available digital records through July 2021 and included work from peer-reviewed, English-language scientific journals. We then filtered the articles to retain only those that directly discussed or addressed at least one type of pollinator or pollination service in agroforestry systems. We excluded articles that exclusively dealt with the topic in an indirect way, such as those that evaluated ecosystem services as a whole or dealt with pollination as one metric among many. In addition, we combed through the literature cited in review papers and meta-analyses and incorporated any articles that met our criteria. In our literature search and screening workflow, we adopted the PRISMA approach (Preferred Reporting Items for Systematic Reviews and Meta-Analysis; *sensu* Moher et al., 2009, www.prisma-statement.org/PRISMAStatement/FlowDiagram; Fig. S1).

2.2. Data analysis

After filtering our results, we classified information from the remaining articles based on 12 items (Table 1). The goal was to conduct a scientometric analysis to characterize the overall scientific exploration of patterns and mechanisms related to the topic (Jha et al., 2016). We then generated a final database containing the following categories of information (Tables S1–S9): (1) article year, to analyze publication patterns over time; (2) country of the corresponding author and study site(s), to determine which countries are conducting research on the topic and where this work is occurring; this information also helps clarify whether the country is a major producer, importer, or exporter of agricultural commodities (according to Food and Agriculture Organization of the United Nations, 2022), which is knowledge of interest in this research; (3) climatic zone of the study site(s), to determine which regions are subject to the greatest research focus and to characterize their levels of agroforestry use; (4) economic situation of the

Table 1
Structure of scientometric analysis exploring the subject of pollination in agroforestry systems (adapted from Viana et al., 2012).

Point of analysis	Categories
1. Article year	-
2. Country of corresponding author and study site(s)	-
3. Climatic zone of study site(s)	1. tropical, 2. subtropical, 3, temperate, 4. global
4. Economic situation of corresponding author's country and study site(s) according to UN	1. developed, 2. developing
5. Type of methodology	1. review, 2. observational (sampling), 3. experimental, 4. meta-analysis, 5. modeling
6. Crop(s) studied	-
7. Pollinator dependence on crop(s) studied[1]	1. essential, 2. high, 3. modest, 4. little, 5. none, 6. unknown
8. Focal pollinators	1. bees, 2. other insects, 3. bats, 4. birds, 5. abiotic factor, 6. not specified
9. Main pollinator(s) observed by authors	-
10. Management practices	1. organic, 2. non-organic, 3. not specified
11. Research question or objective	-
12. Effects on pollinator diversity and pollination services by: • Management practices within agroforestry systems • Agroforestry systems versus conventional agroecosystems	1. positive, 2. negative, 3. neutral

[1] According to the classification system by Klein et al. (2007)

corresponding author's country and study site(s) according to the United Nations (UN), to infer the economic interests underlying the relationship between the countries conducting the research and the countries where agroforestry use is more concentrated; (5) type of methodology, to determine the primary approaches used to study the topic; (6) crop(s) studied, to characterize the species most commonly used in agroforestry systems and their relative importance as global agricultural commodities; (7) pollinator dependence on the study crop(s), to determine the relative role of pollinators in agroforestry systems; dependence was established based on Klein et al. (2007), which described a classification system with categories defined by the relative impact of animal-mediated pollination on crop production and quality; (8) main pollinators, to determine which pollinators (e.g., bees, other insects, birds, abiotic vectors) have been the focus of research efforts; (9) main pollinators observed, to determine which pollinator species are commonly seen in agroforestry systems, including whether they are specialists or generalists and whether their occurrence is natural or the result of management practices; (10) management practices, to determine agroforestry's relative usage of agricultural inputs; (11) research question or objective, to determine the main approaches used in research on this topic; (12) effects of agroforestry versus conventional agriculture on pollinator diversity and crop production, to determine the potential advantages and disadvantages of using agroforestry systems to boost pollination services.

Meta-analysis is an ineffective tool for examining studies on agroforestry management and pollination services. The variability in study design and small sample sizes render statistical approaches problematic (Borenstein et al., 2009). Therefore, we performed a comprehensive analysis using vote counting (i.e., treating each citation as one "vote") (Pullin and Stewart, 2006; Jha et al., 2016), and, when possible, statistical analysis was utilized. We employed a modified version of the method described by Pardo and Borges (2020): a multinomial logistic regression model was used to compare pollination services in agroforestry systems versus conventional agroecosystems. We included data from studies that reported differences in pollinator diversity and pollination services (i.e., pollinator behavior, crop traits, pollen dynamics, or crop production) ($n = 18$). Directionality was the predictor variable (agroforestry systems > conventional agroecosystems, conventional agroecosystem > agroforestry systems, or no difference between the two) and pollination service frequency was the response variables. This analysis was carried out with the package *nnet* (v. 7.3–18; Ripley and Venables, 2022) in R (v. 4.1.3; R Core Team, 2022).

2.3. Scientometric results

2.3.1. Publication patterns over time

Our initial bibliographic search found 442 articles across the Web of Science and Scopus. They had been published between February 1984 and July 2021. After removing duplicates, 323 articles remained. After applying our filter, we were left with 89 articles, which included the literature and meta-analyses (18 articles) and the studies they cited that met our criteria (2 articles) (Fig. S1, Appendix S1). The first article on this study topic was seen in 1984; publications then appeared in 22 of the 37 subsequent years. The second article on this topic was published in 1988, and the third in 2000. It was in 2000 that publications began to occur more frequently, with a peak in 2018 ($n = 11$ articles). These results show that interest in this topic is relatively recent and parallels increasing levels of global crop production (358,649,274 tons in 1984–865,875,138 tons in 2018; Food and Agriculture Organization of the United Nations, 2022). Interestingly, researchers only shifted their attention to agroforestry practices in the 1970 s, even though this farming approach has a much longer history; substantial scientific progress has since been made in this domain (Nair, 2005). The first paper on agroforestry systems in general was published in 1979 (Borough, 1979), five years before the first paper dealing specifically with pollination in agroforestry systems (McAneney et al., 1984).

2.3.2. Socioeconomic context

The above articles were produced by corresponding authors in 22 countries, of which 11 are developed countries and 11 are developing countries, based on UN terminology (Table S1). The most prolific publishers were Germany (20 articles), the United States (20 articles), the United Kingdom (9 articles), and Switzerland (8 articles). This list does not overlap with the countries with the greatest volumes of common agroforestry commodities, which are Brazil, Côte d'Ivoire, Ghana, and Indonesia (Food and Agriculture Organization of the United Nations, 2022). That said, the United States and the United Kingdom are among the top 20 importers of such commodities (Food and Agriculture Organization of the United Nations, 2022), which could help explain their countries' research involvement. The study sites in the articles represented a total of 27 countries, of which 21 are developing countries and 6 are developed countries (Table S2). Indonesia showed up the most often (16 articles). It is one of the world's largest producers of agroforestry commodities, including coffee, and one of the top 20 global exporters of such commodities (Food and Agriculture Organization of the United Nations, 2022). Indonesia is a lower-middle-income economy and is grappling with increased demand for food production (Waldron et al., 2017). In Indonesia, many local communities have been practicing agroforestry for centuries, a subject of intensive research (Rohadi et al., 2013). This pronounced pattern of higher-income countries carrying out research in lower-income countries is unsurprising: in recent years, environmental concerns and green policies have been shaped by post-colonial frameworks, where the world is divided into "rich" (or "developed") countries and "poor" (or "developing") countries. Higher-income countries seek to control land and knowledge, a phenomenon known as "green colonialism" (Torgerson, 2007; Kumar, 2010).

2.3.3. Biogeographical context

This research has mostly been carried out in 19 countries in the tropics (64 articles), 5 countries in the temperate zone (5 articles), and 2 countries in the subtropics (3 articles) (Fig. 1, Table S2). This finding fits with the fact that, worldwide, most of the land covered by agroforests

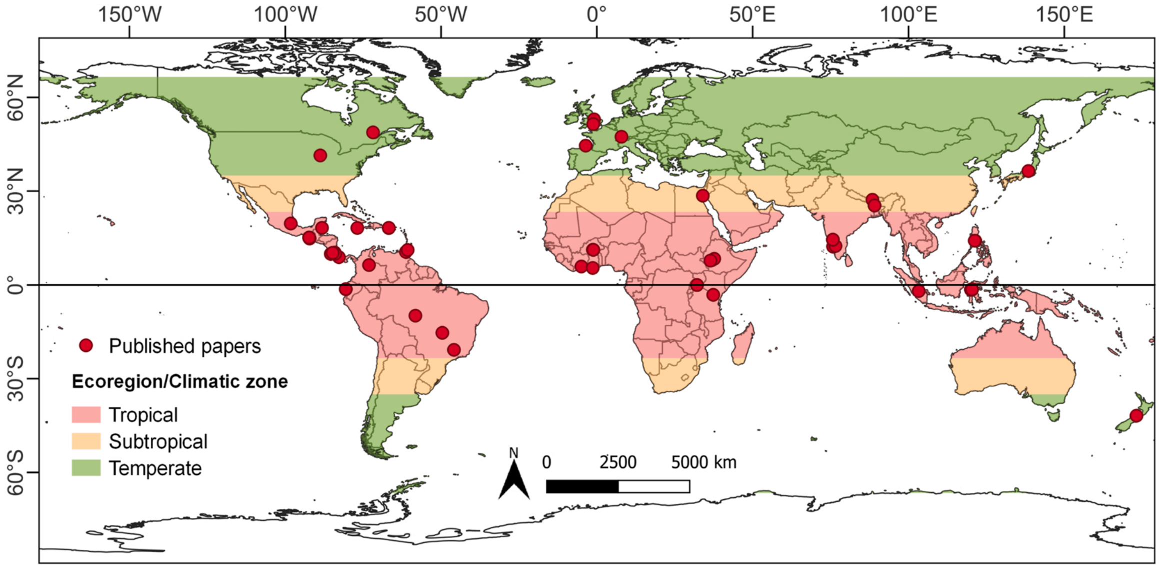


Fig. 1. Map showing the global biogeographical distribution of studies that have been conducted on pollination dynamics in agroforestry systems ($N = 71$).

occurs in Western and Central Africa as well as in South and Southeast Asia (41.9 million ha, 92.3% of all land dedicated to agroforestry) (Food and Agriculture Organization of the United Nations, 2020), which are tropical regions of the world. Agroforestry is more common in the tropics because the environmental conditions are better suited to its implementation (Raj et al., 2019; Udawatta et al., 2019; Mahmud et al., 2020). There are greater quantities of biological resources (e.g., greater species diversity), better soil characteristics (e.g., higher rate of soil carbon sequestration), and a more suitable climate (Raj et al., 2019; Udawatta et al., 2019; Mahmud et al., 2020).

2.3.4. Methodology

Most of this research is observational in nature (45% of articles), although some are experimental (26% of articles). There are also some literature reviews (19% of articles) (Table S3). Modeling work (9% of articles) and meta-analyses (1% of articles) (Table S3 - Supplementary Material) were less common. The observational studies were mostly carried out at local or regional scales, which means lower costs but also lower complexity compared to the experimental studies conducted at larger spatial scales. The reviews addressed a variety of topics: a summary of the ecosystem services provided by agroforestry systems (Dubeux et al., 2017; Reed et al., 2017; Barrios et al., 2018; Kuyah et al., 2018; Roy et al., 2018; Sollen-Norrlin et al., 2020); the ecosystem services (including pollination) provided by coffee and/or cocoa agroforestry systems (Perfecto et al., 2007; Klein et al., 2008; Tscharntke et al., 2011; Chain-Guadarrama et al., 2019); the benefits of increasing plant diversity in agroforestry systems (Isbell et al., 2017); landscape constraints on the functional diversity of birds and insects in agroforestry systems (Tscharntke et al., 2008); the benefits provided by windbreaks (Norton, 1988); pollinator-mediated increases in cocoa yield (Toledo-Hernández et al., 2017); the arthropod communities associated with agroforestry systems (Sridhar and Vinesh, 2016); beekeeping in agroforestry systems (Ya, 2000); and the influence of agroforestry practices on insect pollinators and pollination services in the temperate zone (Bentrup et al., 2019).

2.3.5. Crops studied

Most of the studies focused on coffee and cocoa (Arabica coffee = 18 articles; Robusta coffee = 10 articles; *Coffea* spp. = 9 articles; and cocoa = 13 articles; Table S4), which makes sense because they are the most common agroforestry crops (Clough et al., 2009). They are attractive agricultural products because they display greater resilience to climate change and less price volatility (Vaast et al., 2015). They are also highly profitable (Somarriba and Lopez-Sampson, 2018; Food and Agriculture Organization of the United Nations, 2022). Globally, coffee crops are found on 11 million hectares across agroforestry and non-agroforestry systems alike; are produced by the labor by 10 million farmers; and generate US$17 billion per year (Somarriba and Lopez-Sampson, 2018; Food and Agriculture Organization of the United Nations, 2022). Cocoa covers 10.2 million hectares globally, again across both agroforestry and non-agroforestry systems; is produced by 10 million farmers; and generates US$7 billion per year (Somarriba and Lopez-Sampson, 2018; Food and Agriculture Organization of the United Nations, 2022). Reliance on pollinators is modest for Arabica coffee (i.e., production declines 10–40% without animal-mediated pollination); high for Robusta coffee (i.e., production declines 40–90% without animal-mediated pollination); and essential for cocoa (i.e., production declines 90% without animal-mediated pollination) (Table S4) (*sensu* Klein et al., 2007). Thus, most studies focused on crops that rely on animal pollination, which suggests it is important to understand how agroforestry systems affect pollinator communities to bolster food security.

2.3.6. Main pollinators

Most studies (98% of articles) have looked at animal-mediated pollination. Just 2% examine abiotic vectors, which underscores the importance of living pollinators in agroforestry systems. Bees have been the main pollinators of interest (72% of articles), where they were either the direct object of research or studied as part of pollinator-plant interactions. Other insects, mainly dipterans, wasps, and butterflies, came in second (28% of articles), followed by unspecified animal vectors (11% of articles) and, finally, birds (1% of articles) (Table S5). None of the studies addressed pollination by bats, even though some species are major pollinators of economically important fruit crops (e.g., durian in Southeast Asia) (Stewart and Dudash, 2016). However, one research challenge is distinguishing between when bats are simply visiting versus pollinating plants. Bees are among the world's most important pollinators worldwide, and honey bees in particular frequently pollinate and visit crops (e.g., Greeenleaf and Kremen, 2006; Rader et al., 2016; Stein et al., 2017; Hung et al., 2018). Our review confirms the central role played by bees. Indeed, many studies named honey bees as the main pollinators seen within agroforestry systems (*Apis mellifera* = 23 articles; *Apis dorsata* = 7 articles; *Apis cerana* = 6 articles; *Apis* spp. = 2 articles; *Apis florea* = 1 article; and *Apis nigrocinta* = 1 article; Table S6).

2.3.7. *Agroforestry management practices*

Most studies provided no information about input use (49 articles). In a few cases, the authors indicated that the agroforestry systems were being managed using organic practices (11 articles) or more conventional practices (i.e., usage of one or more agrochemical inputs) (10 articles) (Table S7). This lack of information is a limitation in this domain, since a key objective in agroforestry is to improve system sustainability through the reduction or elimination of chemical inputs (Oelbermann et al., 2004; Silva et al., 2015; Caron et al., 2019). For example, agroforestry management practices can improve soil dynamics via organic inputs, such as crop residues or tree litter (Oelbermann et al., 2004; Silva et al., 2015; Caron et al., 2019). In addition, an equal proportion of study areas appears to be under organic versus conventional management, which puts into question the assumption that agroforestry systems help limit the use of agricultural inputs (Wilson and Lovell, 2016).

2.3.8. *Research questions or objectives*

Most studies have examined factors associated with agroforestry management that could impact any stage of pollination, from pollinator diversity, behavior, and traits to pollen flow or dynamics, and finally, to fruit production. They include (1) shade-tree cover, (2) floral resources, (3) crop management intensity, (4) distance between agroforestry fragments and nearby natural forest, (5) irrigation and rainfall, (6) pollinator management, (7) organic inputs, and (8) windbreak type (Fig. 2A, Table S8). Some of these factors act locally, while some act regionally. Other studies have compared agroforestry systems to conventional agroecosystems, with a focus on pollinator diversity (7 articles), pollinator behavior (4 articles), plant traits (2 articles), pollen dynamics (1 article), and crop production (4 articles) (Table S9). The main results found in response to these questions/objectives are detailed in the next two sections.

2.4. *Factors affecting pollinators and pollination services in agroforestry systems*

2.4.1. *Shade-tree cover*

In general, in agroforestry systems, there is a positive relationship between shade-tree cover and pollination services because higher levels of cover foster greater pollinator diversity and/or floral visitation (8 articles), increase foraging time (1 article), and boost crop production (1 article) (Fig. 2B, Table S8). However, in some cases, pollinator diversity may be negatively associated with the degree of cover (3 articles) or even unrelated (1 article); in rare instances, pollinator traits could be modified to the detriment of pollination dynamics (1 article) (Fig. 2B, Table S8).

For instance, in tropical coffee agroforestry systems, higher levels of shade-tree cover have been associated with greater pollinator diversity and visitation rates (particularly by bees), probably because of better microclimatic conditions, such as lower light intensity and more nesting resources (Jha and Vandermeer, 2009a,b; Samnegård et al., 2014; Bravo-Monroy et al., 2015). Similarly, in tropical cocoa agroforestry systems, shade-tree cover has been correlated with the diversity of insect pollinators, namely dipterans, bees, wasps, and beetles (Bos et al., 2007a; Toledo-Hernández et al., 2021). In tropical shea tree agroforestry systems, greater shade-tree cover increases bee visitation rates, thus reducing pollen limitation (Delaney et al., 2020). To date, research remains rare on how shade-tree cover affects pollinator behavior (1 article). The one study available found that *Heriades fulvescens*, a bee that carries out pollination in tropical coffee agroforestry systems, spent less time foraging as light intensity increased (Klein et al., 2004). This finding suggests that shade-tree cover moderates temperatures, thus improving microclimatic conditions and allowing pollinators to forage longer (Klein et al., 2004). Finally, in a subtropical mango agroforestry system, shade-tree cover enhanced fruit set by improving microclimatic conditions, namely by stabilizing relative humidity, limiting solar radiation, and more optimally distributing precipitation, wind, carbon dioxide, and water vapor; the result was increased habitat for pollinators and predators alike, leading to fewer attacks by pests (Amin et al., 2015).

However, other types of relationships have also been seen. The diversity of ground-nesting bees was negatively associated with shade-tree cover in tropical coffee agroforestry systems (Klein et al., 2003b, 2003c; Krishnan et al., 2018), and temperature was positively correlated with insect abundance in subtropical mango agroforestry systems (Amin et al., 2018). In coffee agroforestry systems in Costa Rica, the degree of cover did not influence pollinator diversity or activity; instead, coffee flower number explained bee abundance and flower visitation frequency (Caudill et al., 2017). In general, higher levels of shade-tree cover may help sustain pollinator diversity, except in the case of those few pollinator species that benefit from light intensity. Indeed, in tropical coffee agroforestry systems, nest brood cell number was positively correlated with light intensity, since more shade leads to greater levels of humidity, which can interfere with larval development and survival (Klein et al., 2004).

2.4.2. *Floral resources*

In general, when more floral resources are available—meaning flower abundance and diversity is higher—pollination services are improved because pollinator diversity and/or floral visitation rates receive a boost (13 articles); no research to date has observed a negative or uncorrelated relationship (Fig. 2B, Table S8). The same positive association has been seen with crop production (3 articles), although,

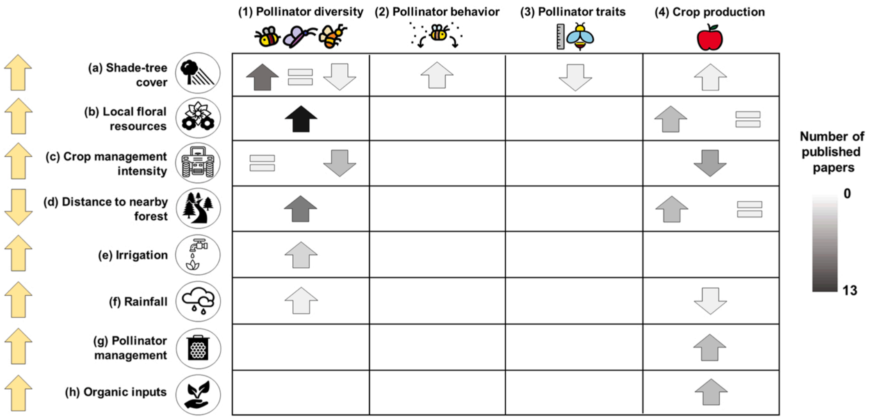


Fig. 2. Effects of agroforestry management practices on pollinator diversity and pollination services. The yellow upward and downward arrows indicate an increase or decrease in a factor, respectively. The grayscale upward and downward arrows indicate the direction of a variable's response to changes in a factor. The grayscale equal signs indicate the variable does not respond to changes in the factor. The blanks indicate that studies are lacking with respect to a given topic.

infrequently, no link has emerged (1 article; Fig. 2B, Table S8).

For instance, higher levels of floral resources have been associated with greater pollinator diversity and floral visitation in tropical coffee agroforestry systems (Klein et al., 2003c; Veddeler et al., 2006; Tylianakis et al., 2008; Jha and Vandermeer, 2009a, 2010; Peters et al., 2013; Samnegård et al., 2014; Caudill et al., 2017). In the same vein, higher levels of pollinators have been tied to higher levels of floral resources in tropical cocoa agroforestry systems. Cocoa flower abundance was positively correlated with the abundance of dipterans, which are key cocoa pollinators (Toledo-Hernández et al., 2021). Furthermore, numbers of cocoa midges (Diptera: Ceratopogonidae) were found to peak during periods of intensive cocoa flowering (Arnold et al., 2018). Floral resource abundance and/or diversity were also found to promote pollinator diversity, pollinator visitation rates, and, thus, fruit production in a range of agroforestry systems (cardamom in the tropics: Gaira et al., 2016; almonds in the subtropics: Norfolk et al., 2016; and apples in the temperate zone: Staton et al., 2021). This pattern may be rooted in niche complementarity: as resource diversity increases, different pollinators are more likely to coexist, since competition decreases (Ashton et al., 2010). In contrast, one study has shown that, when apple agroforestry systems were compared with mown plantations in the temperate zone, increased local floral resources did not bolster the number of seeds per fruit (Staton et al., 2021). Indeed, in apple orchards, production appears to be strongly related to ground-nesting bees rather than understory floral resources (Staton et al., 2021).

2.4.3. *Crop management intensity*

Research examining crop management intensity in agroforestry systems remains sparse. The work done to date has found that more intense management leads to declines in pollinator diversity and pollination services (3 articles) and, as a consequence, crop production (4 papers) (Fig. 2B, Table S8). Such practices may include the removal of shrubs other than the main crop, excessive canopy thinning, filling gaps with crop seedlings, and utilizing agrochemical inputs (Rice, 2008). A single study found that pollinator diversity was unaffected by management intensity (Fig. 2B, Table S8). No research has suggested that higher levels of crop management intensity could positively affect pollination dynamics.

In tropical coffee agroforestry systems, studies have demonstrated that pollinator diversity decreases when there is an increase in coffee shrub density, understory shrub removal, and upper canopy thinning (Klein et al., 2002; Berecha et al., 2015; Geeraert et al., 2019). Similarly, crop production declined when larger quantities of agrochemicals were deployed during flowering in tropical cocoa systems (Munyuli, 2014a) and when the plant community underwent homogenization in tropical coffee systems (Bos et al., 2007b; Priess et al., 2007). That said, pollinator diversity was unaffected by the use of tractors and pesticides in tropical agroforestry systems containing grain crops (Cuevas et al., 2021). However, the researchers highlighted that tractor use was constrained by physical limitations and agrochemical usage was minimal, so the fact that management intensity was low could explain the lack of effects on pollinator diversity (Cuevas et al., 2021).

Intense crop management can negatively affect pollination services because it reduces functional redundancy and complementarity (Geeraert et al., 2019). Functional redundancy occurs when two or more species serve similar ecological functions, which means one species could act as a substitute for the other (Blüthgen and Klein, 2011). When pollinator taxonomic diversity decreases, the number of species occupying the same functional niche might shrink, which could threaten pollination dynamics (Geeraert et al., 2019). Functional complementarity exists when two or more species make a combined contribution to an ecological function (Blüthgen and Klein, 2011). If pollinator taxonomic diversity falls, functional complementarity may decline as well because more functional niches might be left unoccupied, negatively affecting pollination services (Geeraert et al., 2019).

2.4.4. *Distance between agroforestry fragments and nearby natural forest*

In general, when agroforestry fragments occur closer to nearby natural forests, pollinator diversity and/or floral visitation rates climb (5 articles), as does crop production (3 articles); that said, two studies found no influence on pollinator diversity or fruit production, respectively (Fig. 2B, Table S8). For instance, closer proximity between fragments and forest led to increased pollinator diversity in tropical coffee agroforestry systems (Klein et al., 2003b, c; Boreux et al., 2013a; Bravo-Monroy et al., 2015) and temperate blueberry agroforestry systems (Moisan-DeSerres et al., 2015), seemingly because the greater availability of nutritional and nesting resources promotes pollinator stability and resilience (Klein et al., 2003c; Boreux et al., 2013a; Bravo-Monroy et al., 2015). Thus, pollination efficiency climbs, as does the coffee fruit set (Klein et al., 2003c; Boreux et al., 2013a; Bravo-Monroy et al., 2015). A study of a tropical cocoa agroforestry system discovered that there was no influence of farm distance to the forest on ceratopogonid midge abundance or cocoa pod set (Frimpong et al., 2011). In contrast, Krishnan et al. (2018) found no relationship between farm distance to the forest and coffee yield in a tropical coffee agroforestry system. The authors suggested that the results did not necessarily imply an absence of pollination services and proposed that research scale could have had an effect.

2.4.5. *Irrigation and rainfall*

Some research has shown that irrigation promotes pollination services, increasing pollinator diversity and/or floral visitation (2 articles) (Fig. 2B, Table S8). For example, in tropical coffee agroforestry systems, irrigation increased pollinator diversity as it induced flowering and thus augmented the availability of floral resources (Boreux et al., 2013b; Krishnan et al., 2018). Rainfall may have contrasting effects on pollination services (2 articles; Fig. 2B, Table S8). On the one hand, precipitation can prompt flowering and thus cause higher pollinator visitation rates, as was the case in subtropical mango agroforestry systems (Amin et al., 2018). On the other hand, rainfall can also interfere with pollinator foraging and destroy flowers, thereby reducing fruit production, as seen in Costa Rican coffee agroforestry systems (Peters and Carroll, 2012).

2.4.6. *Pollinator management*

The limited research to date suggests that, regardless of crop type, fostering pollinator levels in agroforestry systems significantly enhances pollination services, namely crop production (3 articles; Fig. 2B, Table S8). Introducing and maintaining honey bee colonies has been found to increase fruit production in tropical coffee, cocoa, and shea tree agroforestry systems (Klein et al., 2003a, Groeneveld et al., 2010, Lassen et al., 2018, respectively). Pollinator management strategies can help ensure production levels by reducing the pollination deficit (Klein et al., 2003a, Groeneveld et al., 2010; Lassen et al., 2018). However, it is important to evaluate the repercussions of introducing honey bees because non-native bee species may negatively affect native bee diversity, which could detrimentally impact fruit quality (Mallinger et al., 2017).

2.4.7. *Organic inputs*

Utilizing organic inputs in agroforestry systems fosters pollination services, such as crop production, based on the few studies that have been carried out (3 articles; Fig. 2B, Table S8). In tropical cocoa agroforestry systems, it is a common practice to exploit rotting plant matter, such as banana pseudostems, for this purpose (Sousa et al., 2014). Banana pseudostems are the “trunk” of the banana tree, which is actually a tightly packed overlapping leaf sheath that rises from the ground to fruit; they serve as breeding substrate for cocoa’s main pollinators, cocoa midges (Diptera: Ceratopogonidae; Vanhove et al., 2020). When banana pseudostems were placed near cocoa shrubs, significant increases in cocoa yield and pod production were observed (Vanhove et al., 2020; Morel et al., 2019; Young and Hunter, 2018).

2.4.8. *Windbreak type*

The type of windbreak used could potentially change pollen dispersal dynamics and thus affect fruit production. Theoretical work has shown that windbreak configuration and height influence levels of maize outcrossing (3 articles; Fig. 2A, Table S8). When artificial windbreaks are employed, optimal outcrossing can be ensured by utilizing a 3-m-high mesh with 1-mm openings (Du et al., 2019), an idea that has received further support from Ushiyami et al. (2019). In the field, windbreak type was found to affect fruit yield in temperate kiwifruit agroforestry systems. While artificial porous cloth provided only limited protection, vines grown on a Tatura trellis (i.e., in a close-planting system that forms a V-shaped canopy) led to very low fruit losses to wind damage (1% of total biomass; McAneney et al., 1984).

2.5. *Agroforestry versus conventional agriculture*

2.5.1. *Pollinator diversity*

Based on theoretical work, agroforestry systems are largely thought to increase or maintain pollinator diversity (e.g., Bentrup et al., 2019). However, just a few studies (7 articles; Table S9) have experimentally tested this idea. Here, we summarize the results of all these studies to explore the effects of agroforestry systems versus conventional agroecosystems on pollinator diversity and floral visitation. It appears that, compared to nearby conventional agroecosystems, agroforestry systems had higher levels of pollinator diversity and floral visitation (4 articles; Fig. 3, Table S9). Research on agroforestry systems in the tropics (i.e., cocoa and coffee) and in the temperate zone (i.e., the California poppy) found that pollinator abundance and richness were higher in agroforestry systems than in conventional agroecosystems because the former offered more nutritional and nesting resources to pollinators (Hoehn et al., 2010; Munyuli, 2012; Varah et al., 2020; Neto et al., 2021). However, some studies have found agroecosystem type to have no influence on pollinator diversity (2 articles; Fig. 3, Table S9). For instance, in palm oil agroforestry systems (Tarigan et al., 2021), diversity may remain unchanged because oil palms have a detrimental impact on biodiversity (Knowlton et al., 2019). In other tropical agroforestry systems, pollinator diversity was more strongly correlated with environmental variables outside of agroecosystem type (Matos et al., 2016). Finally, a single study has found that pollinator abundance was lower in agroforestry systems than in conventional agroecosystems (Fig. 3, Table S9). More specifically, bee abundance was greater in low-elevation pastures than in coffee agroforestry systems because traditionally managed pastures can support a broad range of pollinators adapted to open habitats (Galbraith et al., 2020).

2.5.2. *Pollinator behavior*

Research has found that, compared to nearby conventional agroecosystems, agroforestry systems modified pollinator behavior in such a way as to enhance pollination efficiency or quality (4 articles; Fig. 3, Table S9). For instance, a modeling study showed that, in a temperate region, agroforestry systems would allow pollinators to forage significantly greater distances (i.e., within a radius of 100 m) and access more potential nesting sites (Kay et al., 2018, 2020). Furthermore, pollinator nest density was found to be greater in tropical cocoa and coffee agroforestry systems (Fierro et al., 2012; Pavageau et al., 2018, respectively) than in conventional agroecosystems. Greater foraging distances and nesting opportunities could translate into higher floral visitation levels and, in turn, increased crop production. Such dynamics also increase the probability that outcrossing will occur among plants found further afield, which can lower inbreeding levels as these plants are likely more genetically differentiated (Ksiazek-Mikenas et al., 2019).

2.5.3. *Crop traits and pollen dynamics*

A few studies have shown that, compared to conventional agroecosystems, agroforestry systems help foster or maintain crop traits that enhance pollination efficiency (2 articles; Fig. 3, Table S9). Coffee flowers were found to have larger floral displays and higher nitrogen content in tropical coffee agroforestry systems versus coffee monocultures (Prado et al., 2019). Furthermore, in the temperate zone, there were higher levels of flowering resources in cherry agroforestry systems than in non-agroforestry systems (Kay et al., 2020). Floral resources of greater size and quantity may attract more pollinators, generating higher visitation rates and boosting the likelihood of pollination. Such dynamics could maintain pollinator diversity while also increasing crop yield. Thus, in this respect, agroforestry systems represent a sustainable alternative to conventional agricultural systems. Only one study analyzing pollen dynamics failed to find that the implementation or maintenance of agroforestry systems had a significant effect (Barrera et al., 2021) (Fig. 3, Table S9). Bees (*Tetragonula biroi;* Hymenoptera: Apidae, Meliponini) preferred pollen from the few crops in conventional agroecosystems over the more diverse pool of pollen in agroforestry systems (Barrera et al., 2021).

2.5.4. *Crop production*

At present, it is unclear as to whether crop production is different in agroforestry systems versus conventional agroecosystems (Fig. 3, Table S9). In temperate California poppy agroforestry systems, seed set was up to 4.5 times than in monocultures, which was attributed to the higher number of pollinators (including solitary bees, bumble bees, and hover flies) (Varah et al., 2020). In coffee production systems, fruits were heavier in a tropical agroforestry system than in coffee monocultures, which could result from ant-mediated pollination or the interaction of flying pollinators and ants (Philpott et al., 2006). However, in tropical pumpkin agroforestry systems, seed set was correlated not with agroecosystem type but rather with pollinator functional diversity (Hoehn et al., 2008). Finally, in the tropics, conventional coffee production systems generate more revenue than coffee agroforestry systems, which creates an incentive to transform natural ecosystems

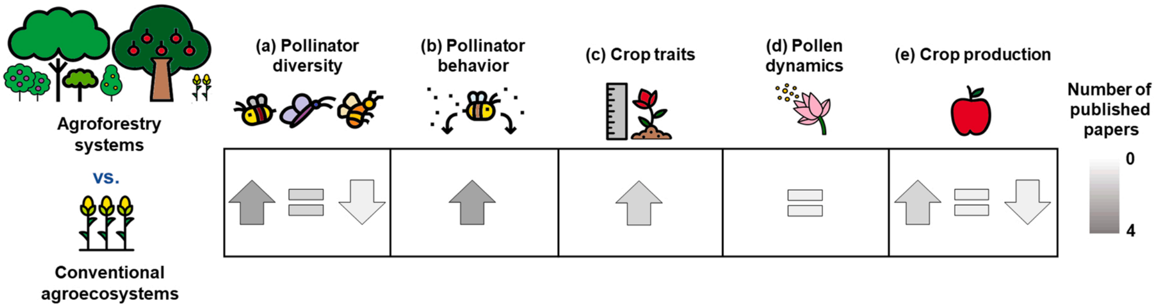


Fig. 3. Effects of agroforestry systems versus conventional agroecosystems on pollinator diversity and pollination services. The upward and downward arrows indicate the direction of a variable's response in agroforestry systems versus conventional agroecosystems. The equal signs indicate the variable did not differ between the two system types. The grayscale shading of the arrows indicates the relative research effort, from darker (i.e., more publications) to lighter (i.e., fewer publications).

(Olschewski et al., 2006).

2.5.5. Synthesis

We first tabulated the votes for pollinator diversity and the pollination services (i.e., pollinator behavior, crop traits, pollen dynamics, and crop production) to assess the most common patterns. We then conducted the multinomial logistic regression, which indicated that pollinator diversity and pollination services did not show any significant pattern of directionality in agroforestry systems versus conventional agroecosystems ($x^2 = 10.1$, p-value = 0.25). Thus, the existing literature suggests that pollinator diversity and pollination services are similar in agroforestry systems and conventional agroecosystems. Consequently, agroforestry systems at least maintain pollination services, making them a sustainable alternative to conventional agriculture.

3. Conclusions, gaps in knowledge, and future perspectives

Our review shows that scientific interest in pollination in agroforestry systems has grown since 1984, which is when tropical deforestation, fuel-wood shortages, and soil degradation became issues of concern (Nair, 2007). Most of the research on this topic has been carried out by higher-income countries in lower-income countries, which suggests green colonialism is occurring. Research interest may be rooted in a desire to impose Western environmentalism and conservation values on non-Western environments (Domínguez and Luoma, 2020). Furthermore, this work has largely taken place in the tropics, the climatic zone with the highest concentration of agroforestry systems. It is necessary to apply greater research efforts to temperate and subtropical zones, so as to determine whether the patterns and processes are the same. Indeed, major agricultural commodities are produced in these climatic zones as well, and it is important to more broadly understand how agroforestry systems function. To date, the most commonly studied crops are coffee and cocoa, which is likely due to their higher economic value and level of dependence on pollinators. However, this fact means that there is an urgent need to study other crop species, since agroforestry systems could represent a sustainable alternative for growing crops of economic importance that are generally cultivated via intensive agriculture. Not surprisingly, most studies have focused on bees, which highlights the importance of this taxon for agroforestry systems. However, we must discover more about other pollinators, especially birds and bats (also see Lopes et al., 2021) since we know next to nothing about their contributions even though they may play an essential role in pollinating economically important crops, such as durian. In general, we know little about the use of agricultural inputs within agroforestry systems since most of the studies did not provide any related information. From the limited data available, it would seem that the use of organic inputs is more common than that of non-organic inputs or agrochemicals. Going forward, researchers should seek to determine the agricultural inputs being deployed, and they must mention what they know. Such knowledge is especially important since one of the guiding principles behind agroforestry is to reduce or eschew agrochemicals in favor of sustainable crop management practices. Furthermore, having access to this information could help resolve questions around how agroforestry systems are currently defined. Indeed, it is possible that some of the work we cited here was carried out in other types of agroecosystems that were not strictly agroforestry systems.

Our review highlights that, in general, levels of pollination services may be higher in agroforestry systems than in conventional agricultural systems; at the very least, they are equivalent in the two system types. However, it remains rare to encounter studies that conduct direct comparisons. We call for more research that tackles this question experimentally, which should provide solid scientific evidence that agroforestry systems are a much more sustainable alternative. Having access to this information can help encourage a positive view of agroforestry systems in the media and society at large, which could render their usage more popular. It is equally interesting to note that agroforestry systems can be managed to boost productivity. Our review has underscored that pollination services can be maximized by increasing shade-tree cover, increasing local floral resources, and decreasing the distance between agroforestry fragments and nearby natural forests. Future research should explore the utility of other management practices, including irrigation, pollinator management, crop management intensity, and environmental factors because they have been scarcely studied, and their effectiveness remains poorly characterized. Finally, we wish to highlight that nothing is known about how pollinators affect fruit quality within agroforestry systems. Because animal-mediated pollination has been shown to enhance fruit nutritional composition, which has human health benefits, we also call for research focused on this topic.

Agroforestry systems can represent a better approach to agriculture because they allow for the production of food resources, income, and medicinal compounds while simultaneously preserving biodiversity (Place et al., 2012). Consequently, it is important to establish incentives and public policies that encourage their broader use. While the basic principle of agroforestry is to combine crops with trees, there are nonetheless major technical and economic hurdles that must be considered because they could make it difficult for farmers to implement and/or maintain agroforestry systems (Buttoud, 2013). Furthermore, historically, agricultural policies have penalized agroforestry practices. For example, the European Union's Common Agricultural Policy prior to 2001 granted farming subsidies based exclusively on the surface area covered by crops, excluding intercropping. These same policies simultaneously promoted intensive conventional agricultural practices that delivered large volumes of food and fuel products (Buttoud, 2013). It is essential that public policies not create bureaucratic hurdles for farmers and investors that impede the implementation of agroforestry systems, as the latter can help promote biodiversity.

Funding

This study was supported by a grant (IBPG-0068-2.05/21) awarded to DC-A and XA by *Fundaç ão de Amparo à Ciência e Tecnologia do Estado de Pernambuco* (FACEPE) and research productivity grants awarded to AVL (PQ-1D: 309505/2018-6) and XA (PQ-2: 307385/2020-5) by the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq).

CRediT authorship contribution statement

Concepts and design: DC-A; Data curation, Formal analysis, and research: DC-A; methodology and writing: DC-A, AVL, and XA; Funding acquisition, Project administration, Project supervision, and scientific validation: AVL and XA.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

Acknowledgments

We thank the FACEPE and CNPq for their essential financial support and Jessica Pearce-Duvet for the English editing.

Code availability

Not applicable.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108478.

References

Amin, M.R., Mia, M.R., Rahman, H., Miah, M.G., Ge, F., 2018. Insect Community in agroforestry: role of weather parameters on population dynamics. Indian J. Ecol. 45 (1), 88–92.

Amin, M.R., Namni, S., Miah, M.R.U., Miah, M.G., Zakaria, M., Suh, S.J., Kwon, Y.J., 2015. Insect inventories in a mango-based agroforestry area in Bangladesh: foraging behavior and performance of pollinators on fruit set. Entomol. Res. 45 (4), 217–224. https://doi.org/10.1111/1748-5967.12112.

Arnold, S.E.J., Bridgemohan, P., Perry, G.B., Spinelli, G.R., Pierre, B., Murray, F., Haughton, C., Dockery, O., Grey, L., Murphy, S.T., Belmain, S.R., Stevenson, P.C., 2018. The significance of climate in the pollinator dynamics of a tropical agroforestry system. Agric. Ecosyst. Environ. 254, 1–9. https://doi.org/10.1016/j.agee.2017.11.013.

Asthon, I.W., Miller, A.E., Bowman, W.D., Suding, K.N., 2010. Niche complementarity due to plasticity in resource use: Plant partitioning of chemical N forms. Ecology 9 (11), 3252–3260. https://doi.org/10.1890/09-1849.1.

Atangana, A., Khasa, D., Chang, S., Degrande, A., 2014. Agroforestry for soil conservation. In: Atangana, A., Khasa, D., Chang, S., Degrande, A. (Eds.), Tropical Agroforestry. Springer, Dordrecht, pp. 203–216.

Bailes, E.J., Ollerton, J., Pattrick, J.G., Glover, B.J., 2015. How can an understanding of plant-pollinator interactions contribute to global food security? Curr. Opin. Plant Biol. 26, 72–79. https://doi.org/10.1016/j.pbi.2015.06.002.

Barrera Jr, W.B., Brosas, J.V., Sacil, M.D., 2021. Pollen sources of *Tetragonula biroi* (Friese, 1898) (Hymenoptera: Apidae, Meliponini) in two agroecosystems in Nagcarlan, Laguna, Philippines. Palynology 45 (2), 215–223. https://doi.org/10.1080/01916122.2020.1789773.

Barrios, E., Valencia, V., Jonsson, M., Brauman, A., Hairiah, K., Mortimer, P.E., Okubo, S., 2018. Contribution of trees to the conservation of biodiversity and ecosystem services in agricultural landscapes. Int. J. Biodivers. Sci., Ecosyst. Serv. Manag. 14 (1), 1–16. https://doi.org/10.1080/21513732.2017.1399167.

Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, T., Roberts, S.P.M., Szentgyörgyi, H., Westphal, C., Bommarco, R., 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ 2, e328. https://doi.org/10.7717/peerj.328.

Bentrup, G., Hopwood, J., Adamson, N.L., Vaughan, M., 2019. Temperate agroforestry systems and insect pollinators: a review. Forests 10 (11), 981. https://doi.org/10.3390/f10110981.

Berecha, G., Aerts, R., Muys, B., Honnay, O., 2015. Fragmentation and management of Ethiopian moist evergreen forest drive compositional shifts of insect communities visiting wild Arabica coffee flowers. Environ. Manag. 55 (2), 373–382. https://doi.org/10.1007/s00267-014-0393-9.

Blüthgen, N., Klein, A.M., 2011. Functional complementarity and specialisation: the role of biodiversity in plant-pollinator interactions. Basic Appl. Ecol. 12 (4), 282–291. https://doi.org/10.1016/j.baae.2010.11.001.

Bohan, D.A., Raybould, A., Mulder, C., Woodward, G., Tamaddoni-Nezhad, A., Blüthgen, N., Pocock, M.J.O., Muggleton, S., Evans, D.M., Astegiano, J., Massol, F., Loeuille, N., Petit, S., Macfadyen, S., 2013. Networking agroecology: integrating the diversity of agroecosystem interactions. In: Woodward, G., Bohan, D.A. (Eds.), Ecological Networks in an Agricultural World: Advances in Ecological Research. Academic Press, pp. 1–67.

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R., 2009. When does it make sense to perform a meta-analysis? In: Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R. (Eds.), Introduction to Meta-analysis. John Wiley and Sons, pp. 357–364.

Boreux, V., Krishnan, S., Cheppudira, K.G., Ghazoul, J., 2013a. Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agroforests. Agric. Ecosyst. Environ. 172, 42–48. https://doi.org/10.1016/j.agee.2012.05.003.

Boreux, V., Kushalappa, C.G., Vaast, P., Ghazoul, J., 2013b. Interactive effects among ecosystem services and management practices on crop production: Pollination in coffee agroforestry systems. Proceedings of the National Academy of Sciences of the United States of America. 110(21), 8387–8392. https://doi.org/10.1073/pnas.1210590110.

Borough, C.J., 1979. Agroforestry in New Zealand – The current situation. Aust. For. 42, 23–29. https://doi.org/10.1080/00049158.1979.10674203.

Bos, M.M., Steffan-Dewenter, I., Tscharntke, T., 2007b. Shade tree management affects fruit abortion, insect pests and pathogens of cacao. Agric. Ecosyst. Environ. 120 (2–4), 201–205. https://doi.org/10.1016/j.agee.2006.09.004.

Bos, M.M., Höhn, P., Saleh, S., Büche, B., Buchori, D., Steffan-Dewenter, I., Tscharntke, T., 2007a. Insect diversity responses to forest conversion and agroforestry management. In: Tscharntke, T., Leuschner, C., Zeller, M., Guhardja, E., Bidin, A. (Eds.), Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation. Springer, Berlin, pp. 225–261.

Bravo-Monroy, L., Tzanopoulos, J., Potts, S.G., 2015. Ecological and social drivers of coffee pollination in Santander, Colombia. Agric. Ecosyst. Environ. 211, 145–154. https://doi.org/10.1016/j.agee.2015.06.007.

Buttoud, G., 2013. Advancing Agroforestry on the Policy Agenda: A guide for decision-makers. Food and Agriculture Organizations of the United Nations, Rome.

Cardinael, R., Mao, Z., Prieto, I., Stokes, A., Dupraz, C., Kim, J.H., Jourdan, C., 2015. Competition with winter crops induces deeper rooting of walnut trees in a Mediterranean alley cropping agroforestry system. Plant Soil 391, 219–235. https://doi.org/10.1007/s11104-015-2422-8.

Cardinale, B.J., Duffy, E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148.

Caron, B.O., Pinheiro, M.V.M., Korcelski, C., Schwerz, F., Elli, E.F., Sgarbossa, J., Tibolla, L.B., 2019. Agroforestry systems and understory harvest management: The impact on growth and productivity of dual-purpose wheat. An. da Acad. Bras. De. Ciências 91 (4), e20180667. https://doi.org/10.1590/0001-3765201920180667.

Caudill, S., Brokaw, J., Doublet, D., Rice, R., 2017. Forest and trees: Shade management, forest proximity and pollinator communities in southern Costa Rica coffee agriculture. Renew. Agric. Food Syst. https://doi.org/10.1017/S1742170516000351.

Chain-Guadarrama, A., Martínez-Salinas, A., Aristizábal, N., Ricketts, T.H., 2019. Ecosystem services by birds and bees to coffee in a changing climate: a review of coffee berry borer control and pollination. Agric. Ecosyst. Environ. 280, 53–67. https://doi.org/10.1016/j.agee.2019.04.011.

Clough, Y., Faust, H., Tscharntke, T., 2009. Cacao boom and bust: Sustainability of agroforests and opportunities for biodiversity conservation. Conserv. Lett. 2, 197–205. https://doi.org/10.1111/j.1755-263X.2009.00072.x.

Convention on Biological Diversity, 2018. Decision adopted by the Conference of the Parties to the Convention on Biological Diversity. Convention on Biological Diversity, Sharm El-Sheikh.

Cuevas, E., Blancas, J., Caballero, J., Hinojosa-Díaz, I.A., Martínez-Ballesté, A., 2021. Agricultural management and local knowledge: key factors for the conservation of socio-ecosystems in the face of the pollinator world crisis. Bot. Sci. 99 (2), 305–320. https://doi.org/10.17129/botsci.2659.

Food and Agriculture Organization of the United Nations, 2020a. Global Forest Resources Assessment 2020: Main report. Food and Agriculture Organization of the United Nations,, Rome.

Delaney, A., Dembele, A., Nombré, I., Lirasse, F.G., Marshall, E., Nana, A., Vickery, J., Tayleur, C., Stout, J.C., 2020. Local-scale tree and shrub diversity improves pollination services to shea trees in tropical West African parklands. J. Appl. Ecol. 57 (8), 1504–1513. https://doi.org/10.1111/1365-2664.13640.

Domínguez, L., Luoma, C., 2020. Decolonising conservation policy: how colonial land and conservation ideologies persist and perpetuate indigenous injustices at the expense of the environment. Land 9 (65). https://doi.org/10.3390/land9030065.

Du, M., Ushiyama, T., Yonemura, S., Shibaike, H., 2019. Three-dimensional numerical simulations of windbreak effects of pollen dispersal and cross-pollination. IOP Conference Series: Earth and Environmental Science. 227(5), 052002. https://doi.org/10.1088/1755–1315/227/5/05002.

Dubeux Jr, J.C.B., Muir, J.P., Apolinário, V.X.O., Nair, P.K.R., Lira, M.A., Sollenberger, L.E., 2017. Tree legumes: and underexploited resource in warm-climate silvopastures. Rev. Bras. De. Zootec. 46 (8), 689–703. https://doi.org/10.1590/S1806-92902017000800010.

Epule, E.T., Bryant, C.R., 2016. Assessing the effects of agroecology and conventional farming techniques on small-scale peasant farmers' crop yields in the Fako and Meme divisions of Cameroon. Afr. J. Agric. Res. 11 (10), 849–866. https://doi.org/10.5897/AJAR2015.10498.

Fierro, M.M., Cruz-López, L., Sánchez, D., Villanueva-Gutiérrez, R., Vandame, R., 2012. Effect of biotic factors on the spatial distribution of stingless bees (Hymenoptera: Apidae, Meliponini) in fragmented neotropical habitats. Neotrop. Entomol. 41 (2), 95–104. https://doi.org/10.1007/s13744-011-0009-5.

Food and Agriculture Organization of the United Nations, 2016. A quantitative approach to the socio-economic valuation of pollinator-friendly practices: A protocol for its use. Food and Agriculture Organization of the United Nations, Rome, In Press.

Food and Agriculture Organization of the United Nations, 2017. The future of food and agriculture – Trends and Challenges. Food and Agriculture Organization of the United Nations, Rome, In Press.

Food and Agriculture Organization of the United Nations, 2022. FAOSTAT Online database. Food and Agriculture Organization of the United Nations, Rome. www.faostat.org (consulted in January 2022).

Forrest, J.R.K., Thorp, R.W., Kremen, C., Williams, N.M., 2015. Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. Journal of Applied Ecology 52 (3), 706–715. https://doi.org/10.1111/1365-2664.12433.

Frimpong, E.A., Gemill-Herren, B., Gordon, I., Kwapong, P.K., 2011. Dynamics of insect pollinators as influenced by cocoa production systems in Ghana. J. Pollinat. Ecol. 5 (10), 74–80. https://doi.org/10.26786/1920-7603(2011)12.

Gaira, K.S., Rawal, R.S., Singh, K.K., 2016. Variations in pollinator density and impacts on large cardamom (*Amomum subulatum* Roxb.) crop yield in Sikkim Himalaya, India. J. Asia-Pac. Biodivers. 9 (1), 17–21. https://doi.org/10.1016/j.japb.2015.12.010.

Galbraith, S.M., Griswold, T., Price, W.J., Bosque-Pérez, N.A., 2020. Biodiversity and community composition of native bee populations vary among human-dominated land uses within the seasonally dry tropics. J. Insect Conserv. 24 (6), 1045–1059. https://doi.org/10.1007/s10841-020-00274-8.

Garrett, H.E.G., Buck, L., 1997. Agroforestry practice and policy in the United States of America. For. Ecol. Manag. 91, 5–15. https://doi.org/10.1016/s0378-1127(96)03884-4.

Geeraert, L., Aerts, R., Jordaens, K., Dox, I., Wellens, S., Couri, M., Berecha, G., Hoonay, O., 2019. Intensification of Ethiopian coffee agroforestry drives impoverishment of the Arabica coffee flower visiting bee and fly communities. Agrofor. Syst. 93, 1729–1739. https://doi.org/10.1007/s10457-018-0280-0.

Girão, L.C., Lopes, A.V., Tabarelli, M., Bruna, E.M., 2007. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic Forest landscape. PLoS One 2, e908 https://doi.org/10.1371/journal. pone.0000908.

Greeenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. Proc. Natl. Acad. Sci. USA 103 (37), 13890–13895. https://doi.org/10.1073/pnas.0600929103.

Groeneveld, J.H., Tscharntke, T., Moser, G., Clough, Y., 2010. Experimental evidence for stronger cacao yield limitation by pollination than by plant resources. Perspect. Plant Ecol. Evol. Syst. 12 (3), 183–191. https://doi.org/10.1016/j.ppees.2010.02.005.

Hoehn, P., Steffan-Dewenter, I., Tscharntke, T., 2010. Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity. Biodivers. Conserv. 19, 2189–2200. https://doi.org/10.1007/s10531-010-9831-z.

Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. Proceedings of the Royal Society B. 275, 2283–2291. https://doi.org/10.1098/rspb.2008.0405.

Hung, K.L.J., Kingston, J.M., Albrecht, M., Holway, D.A., Kohn, J.R., 2018. The worldwide importance of honey bees as pollinator in natural habitats. Proceedings of the Royal Society B. 285, 20172140. https://doi.org/10.1098/rspb.2017.2140.

IPBES, 2016. The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn.

Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau, D. K., Liebman, M., Polley, H.W., Quijas, S., Scherer-Lorenzen, M., 2017. Benefits of increasing plant diversity in sustainable agroecosystems. J. Ecol. 105 (4), 871–879. https://doi.org/10.1111/1365-2745.12789.

Jha, R., Jbara, A.A., Qazvinian, V., Radev, D.R., 2016. NLP-driven citation analysis for scientometrics. Nat. Lang. Eng. 23 (1), 93–130. https://doi.org/10.1017/S1351324915000443.

Jha, S., Vandermeer, J.H., 2009a. Contrasting bee foraging in response to resource scale and local habitat management. Oikos 118 (8), 1174–1180. https://doi.org/10.1111/j.1600-0706.2009.17523.x.

Jha, S., Vandermeer, J.H., 2009b. Contrasting foraging patterns for Africanized honeybees, native bees and native wasps in a tropical agroforestry landscape. J. Trop. Ecol. 25 (1), 13–22. https://doi.org/10.1017/S026646740800566X.

Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. Biol. Conserv. 143 (6), 1423–1431. https://doi.org/10.1016/j.biocon.2010.03.017.

Jose, S., Dollinger, J., 2019. Silvopasture: a sustainable livestock production systems. Agrofor. Syst. 93, 1–9. https://doi.org/10.1007/s10457-019-00366-8.

Kay, S., Kühn, E., Albrecht, M., Sutter, L., Szerencsits, E., Herzog, F., 2020. Agroforestry can enhance foraging and nesting resources for pollinators with focus on solitary bees at the landscape scale. Agrofor. Syst. 94, 379–387. https://doi.org/10.1007/s10457-019-00400-9.

Kay, S., Crous-Duran, J., Ferreiro-Domínguez, N., Jalón, S.G., Graves, A., Moreno, G., Mosquera-Losada, M.R., Palma, J.H.N., Roces-Díaz, J.V., Santiago-Freijanes, J.J., Szerencsits, E., Weibel, R., Herzog, F., 2018. Spatial similarities between European agroforestry systems and ecosystem services at the landscape scale. Agrofor. Syst. 92, 1075–1089. https://doi.org/10.1007/s10457-017-0132-3.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003a. Bee pollination and fruit set of *Coffea arabica* and *C. canephora* (Rubiaceae). Am. J. Bot. 90 (1), 153–157. https://doi.org/10.3732/ajb.90.1.153.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003b. Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society B. 270, 955–961. https://doi.org/10.1098/rspb.2002.2306.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003c. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. J. Appl. Ecol. 40 (5), 837–845. https://doi.org/10.1046/j.1365-2664.2003.00847.x.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2004. Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. J. Anim. Ecol. 73 (3), 517–525. https://doi.org/10.1111/j.0021-8790.2004.00826.x.

Klein, A.M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conserv. Biol. 16 (4), 1003–1014. https://doi.org/10.1046/j.1523-1739.2002.00499.x.

Klein, A.M., Cunningham, A.S., Bos, M., Steffan-Dewenter, I., 2008. Advances in pollination ecology from tropical plantation crops. Ecology 89 (4), 935–943. https://doi.org/10.1890/07-0088-1.

Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinator in changing landscapes for world crops. Proceeding of the Royal Society B. 274, 303–313. https://doi.org/10.1098/rspb/2006.3721.

Knowlton, J.L., Zayas, E.E.M., Ripley, A.J., Valenzuela-Cordova, B., Collado-Torres, R., 2019. Mammal diversity in oil palm plantations and forest fragments in a highly modified landscape in Southern Mexico. Front. For. Glob. Change 2. https://doi.org/10.3389/ffgc.2019.00067.

Krishnan, S., Cheppudira, K.G., Ghazoul, J., 2018. Pollinator services in coffee agroforests of the Western Ghats. In: Dagar, J.C., Tewari, V.P. (Eds.), Agroforestry: Anecdotal to Modern Science. Springer, Cham, pp. 771–795.

Ksiazek-Mikenas, K., Fant, J.B., Skogen, K.A., 2019. Green roof populations across the urban matrix: a paternity analysis of the self-compativle forb *Penstemon hirsutus*. Front. Ecol. Evol. 7, 299. https://doi.org/10.3389/fevo.2019.00299.

Kumar, V.M.R., 2010. Green colonialism and forest policies in South India, 1800-1900. Glob. Environ. 3 (5), 101–125. https://doi.org/10.3197/ge.2010.030505.

Kuyah, S., Öborn, I., Jonsson, M., 2018. Regulating ecosystem services delivered in agroforestry systems. In: Dagar, J.C., Tewari, V.P. (Eds.), Agroforestry: Anecdotal to Modern Science. Springer, Cham, pp. 797–815.

Lassen, K.M., Nielsen, L.R., Lompo, D., Dupont, Y.L., Kjær, E.D., 2018. Honey bees are essential for pollination of *Vitellaria paradoxa* subsp. *paradoxa* (Sapotaceae) in Burkina Faso. Agrofor. Syst. 92, 23–34. https://doi.org/10.1007/s10457-016-007-z.

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalheiro, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Aström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzchuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pocock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardiñas, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tscharntke, T., Veselý, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Glob. Change Biol. 23, 4946–4957. https://doi.org/10.1111/gcb.13714.

Lopes, A.V., Porto, R.G., Cruz-Neto, O., Peres, C., Viana, B.F., Giannini, T.C., Tabarelli, M., 2021. Neglected diversity of crop pollinators: Lessons from the world's largest tropical country. Perspect. Ecol. Conserv. 19, 500–504 https://doi.org/10.1016.j.pecon.2021.06.004.

Maccagnani, B., Veromann, E., Ferrari, R., Boriani, L., Boecking, O., 2020. Agroecosystem design supports the activity of pollinator networks. In: Smagghe, G., Boecking, O., Maccagnani, B., Mänd, M., Kevan, P.G. (Eds.), Entomovectoring for Precision Biocontrol and Enhanced Pollination of Crops. Springer, Cham, pp. 1–17.

Mahmud, A.A., Raj, A., Jhariya, M.K., 2020. Agroforestry systems in the tropics: a critical review. Agric. Biol. Res. 37 (1), 83–87.

Mallinger, R.E., Gaines-Day, H.R., Gratton, C., 2017. Do managed bees have negative effects on wild bees?: A systematic review of the literature. PLoS One 12 (12), e0189268. https://doi.org/10.1371/journal.pone.0189268.

Matos, M.C.B., Silva, S.S., Teodoro, A.V., 2016. Seasonal population abundance of the assembly of solitary wasps and bees (Hymenoptera) according to land-use in Maranhão state, Brazil. Rev. Bras. De. Èntomol. 60, 171–176. https://doi.org/10.1016/j.rbe.2016.02.001.

McAneney, K.J., Judd, M.J., Trought, M.C.T., 1984. Wind damage to kiwifruit (*Actinidia chinensis* Planch.) in relation to windbreak performance. N. Z. J. Agric. Res. 27, 255–263. https://doi.org/10.1080/00288233.1984.10430427.

Moher, D., Liberati, A., Tetzlaff, J., 2009. Preferred reporting items for systematic reviews and meta- analyses: the PRISMA statement (The PRISMA Group). PLoS Med. 6 (7), e1000097. https://doi.org/10.1371/journal.pmed.1000097.

Moisan-DeSerres, J., Chagnon, M., Fournier, V., 2015. Influence of windbreaks and forest borders on abundance and species richness of native pollinators in lowbush blueberry fields in Québec, Canada. Can. Èntomol. 147 (4), 432–442. https://doi.org/10.4039/tce.2014.55.

Morel, A.C., Hirons, M., Sasu, M.A., Quaye, M., Asare, A., Mason, J., Adu-Bredu, S., Boyd, E., McDermott, C.L., Robinson, E.J.Z., Straser, R., Malhi, Y., Norris, K., 2019. The ecological limits of poverty alleviation in an African Forest-Agriculture Landscape. Front. Sustain. Food Syst. 3, 57. https://doi.org/10.3389/fsufs.2019.00057.

Mosquera-Losada, M.R., McAdam, J.H., Romero-Franco, R., Santiago-Freijanes, J.J., Rigueiro-Rodríguez, A., 2009. Definitions and components of agroforestry practices in Europe, In: Rigueiro-Rodríguez, A., McAdam, J., Mosquera-Losada, M.R. (Eds.), Agroforestry in Europe, vol. 6. Springer, Dordrecht, pp. 3–19.

Munyuli, T., 2012. Butterfly diversity from farmlands of central Uganda. Psyche.: J. Entomol. 2012, 481509 https://doi.org/10.1155/2012/481509.

Munyuli, T., 2014a. Influence of functional traits on foraging behaviour and pollination efficiency of wild social and solitary bees visiting coffee (*Coffea canephora*) flowers in Uganda. Grana 53 (1), 69–89. https://doi.org/10.1080/00173134.2013.853831.

Munyuli, T., 2014b. Social and ecological drivers of the economic value of pollination services delivered to coffee in Central Uganda. J. Ecosyst. 2014. https://doi.org/10.1155/2014/298141.

Nair, P.K.R., 1985. Classification of agroforestry systems. Agrofor. Syst. 3, 97–128. https://doi.org/10.1007/BF00122638.

Nair, P.K.R., 2005. Agroforestry. In: Hillel, D. (Ed.), Encyclopedia of Soils in the Environment. Elsevier Academic Press, Amsterdam, pp. 35–44.

Nair, P.K.R., 2007. The coming of age of agroforestry. J. Sci. Food Agric. 87 (9), 1613–1619. https://doi.org/10.1002/jsfa.2897.

Neto, C.M.S., Santos, L.A.C., Souza, W.G., Martins, T.O., Silva, T.C., Lima, A.A., Calil, F. N., Souza, M.M.O., 2021. Bees in agroforestry systems in the Cerrado. J. Apic. Res. https:/doi.org/10.1080/00218839.2021.1907977.

Norfolk, O., Eichhorn, M.P., Gilbert, F., 2016. Flowering ground vegetation benefits wild pollinators and fruit set of almond within arid smallholder orchards. Insect Conserv. Divers. 9 (3), 236–243 https:/doi.org/10.1111/icad.12162.

Norton, R.L., 1988. Windbreaks: benefits to orchard and vineyard crops. Agric. Ecosyst. Environ. 22–23, 205–213. https://doi.org/10.1016/0167-8809(88)90019-9.

Oelbermann, M., Voroney, R.P., Gordon, A.M., 2004. Carbon sequestration in tropical and temperate agroforestry systems: a review with examples from Costa Rica and southern Canada. Agric. Ecosyst. Environ. 104, 359–377. https://doi.org/10.1016/jagee.2004.04.001.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals. Oikos 120 (3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x.

Olschewski, R., Tscharntke, T., Benítez, P.C., Schwarze, S., Klein, A.M., 2006. Economic evaluation of pollination services comparing coffee landscapes in Ecuador and Indonesia. Ecol. Soc. 11 (1), 7.

Pardo, A., Borges, P.A.V., 2020. Worldwide importance of insect pollination in apple orchards: A review. Agriculture, Ecosystems and Environment 293, 106839. https://doi.org/10.1016/j.agee.2020.106839.

Pavageau, C., Gaucherel, C., Garcia, C., Ghazoul, J., 2018. Nesting sites of giant honeybees modulated by landscape patterns. J. Appl. Ecol. 55 (3), 1230–1240. https://doi.org/10.1111/1365-2664.13069.

Perfecto, I., Armbrecht, I., Philpott, S.M., Soto-Pinto, L., Dietsch, T.V., 2007. Shaded coffee and the stability of rainforest margins in northern Latin America. In: Tscharntke, T., Leuschner, C., Zeller, M., Guhardja, E., Bidin, A. (Eds.), Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation. Springer, Berlin, pp. 225–261.

Peters, V.E., Carroll, C.R., 2012. Temporal variation in coffee flowering may influence the effects of bee species richness and abundance on coffee production. Agrofor. Syst. 85, 95–103. https://doi.org/10.1007/s10457-011-9476-2.

Peters, V.E., Carroll, C.R., Cooper, R.J., Greenberg, R., Solis, M., 2013. The contribution of plant species with a steady-state flowering phenology to native bee conservation and bee pollination services. Insect Conserv. Divers. 6 (1), 45–56. https://doi.org/10.1111/j.1752-4598.2012.00189.x.

Philpott, S.M., Uno, S., Maldonado, J., 2006. The importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. Biodivers. Conserv. 15, 487–501. https://doi.org/10.1007/s10531-005-0602-1.

Place, F., Ajayi, O.C., Torquebiau, E., Detlefsen, G., Gauthier, M., Buttoud, G., 2012. Improved policies for facilitating the adoption of agroforestry, in: Kaonga, M.L., (Ed.), Agroforestry for biodiversity and ecosystem services: Science and Practice. IntechOpen, London, pp. 113–128.

Porter, J.R., Xie, L., Challinor, A.J., Cochrane, K., Howden, S.M., Iqbal, M.M., Lobel, D.B., Travasso, M.I., 2014. Food security and food production systems, In: Intergovernmental Panel on Climate Change, (Ed.), Climate Change 2014: Impacts. Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects – Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp. 485–533.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25 (6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007.

Prado, S.G., Collazo, J.Á., Stevenson, P.C., Irwin, R.E., 2019. A comparison of coffee floral traits under two different agricultural practices. Sci. Rep. 9, 7331. https://doi.org/10.1038/s41598-019-43753-y.

Priess, J.A., Mimler, M., Klein, A.M., Schwarze, S., Tscharntke, T., Steffan-Dewenter, I., 2007. Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. Ecol. Appl. 17 (2), 407–417. https://doi.org/10.1890/05-1795.

Pullin, A.S., Stewart, G.B., 2006. Guidelines for systematic review in conservation and environmental management. Conserv. Biol. 20 (6), 1647–1656. https://doi.org/10.1111/j.1523-1739.2006.00485.x.

R Core Team, 2022. The R Project for Statistical Computing. www.r-project.org/ (consulted in February 2022).

Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein, A.M., Kleijn, D., Krishnan, S., Lemos, C. Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N.O., Pisanty, G., Potts, S.G., Reemer, M., Runlöff, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. Proceedings of the National Academy of Sciences of the United States of America. 113(1), 146–151. https://doi.org/10.1073/pnas.1517092112.

Raj, A., Jhariya, M.K., Yadav, D.K., Banerjee, A., Meena, R.S., 2019. Agroforestry: a holistic approach for agricultural sustainability. In: Jhariya, M.K., Banerjee, A., Meena, R.S., Yadav, D.K. (Eds.), Sustainable Agriculture, Forest and Environmental Management. Springer, Singapore, pp. 101–131.

Ramos-Jiliberto, R., Espanés, P.M., Vázquez, D.P., 2020. Pollinator declines and the stability of plant-pollinator networks. Ecosphere 11 (4), e03069. https://doi.org/10.1002/ecs2.3069.

Reed, J., Vianen, J.V., Foli, S., Clendenning, J., Yang, K., MacDonald, M., Petrokofsky, G., Padoch, C., Sunderland, T., 2017. Trees for life: the ecosystem service contribution of trees to food production and livelihoods in the tropics. For. Policy Econ. 84, 62–71. https://doi.org/10.1016/j.forpol.2017.01.012.

Rice, R.A., 2008. Agricultural intensification within agroforestry: the case of coffee and wood products. Agric. Ecosyst. Environ. 128 (4), 212–218. https://doi.org/10.1016/j.agee.2008.06.007.

Ricker-Gilbert, J., Jumbe, C., Chamberlin, J., 2014. How does population density influence agricultural intensification and productivity? Evidence from Malawi. Food Policy 48, 114–128. https://doi.org/10.1016/j.foodpol.2014.02.006.

Ripley, B., Venables, W., 2022. Package "nnet": Feed-Forward Neural Networks and Multinomial Log-Linear Models. CRAN R Project. www.cran.r-project.org/web/packages/nnet/ (consulted in February 2022).

Rohadi, D., Herawati, T., Firdaus, N., Maryani, R., Permadi, P., 2013. National Strategy for Agroforestry Research in Indonesia 2013-2030. FORDA Press, Jawa Barat.

Roquer-Beni, L., Rodrigo, A., Arnan, X., Klein, A.M., Fornoff, F., Boreux, V., Bosch, J., 2020. A novel method to measure hairiness in bees and other insect pollinators. Ecol. Evol. 10 (6), 2979–2990. https://doi.org/10.1002/ece3.6112.

Roquer-Beni, L., Alins, G., Arnan, X., Boreux, V., García, D., Hambäck, P.A., Happe, A.K., Klein, A.M., Miñarro, M., Mody, K., Porcel, M., Rodrigo, A., Samnegård, U., Tasin, M., Bosch, J., 2021. Management-dependent effects of pollinator functional diversity on apple pollination services: a response-effect traits approach. J. Appl. Ecol. 58 (12), 2843–2853. https://doi.org/10.1111/1365-2664.14022.

Roy, S., Roy, M.M., Saxena, P., Bano, R., 2018. Role of entomology in sustaining agroforestry productivity. In: Dagar, J.C., Tewari, V.P. (Eds.), Agroforestry: Anecdotal to Modern Science. Springer, Cham, pp. 691–704.

Samnegård, U., Hambäck, P.A., Nemomissa, S., Hylander, K., 2014. Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia. J. Trop. Ecol. 30 (5), 401–408. https://doi.org/10.1017/S0266567414000327.

Shennan, C., Krupnik, T.J., Baird, G., Cohen, H., Forbush, K., Lovell, R.J., Olimpi, E.M., 2017. Organic and conventional agriculture: a useful framing. Annu. Rev. Environ. Resour. 42, 317–346. https://doi.org/10.1146/annurev-environ-110615-085750.

Silva, A.R., Collier, L.S., Flores, R.A., Santos, V.M., Barbosa, J.M., 2015. Soil fertility in agroforestry system with introduction of green manure. American-Eurasian J. Agric. Environ. Sci. 15 (1), 29–35. https://doi.org/10.5829/idosi.aejaes.2015.15.1.12477.

Sollen-Norrlin, M., Ghaley, B.B., Rintoul, N.L.J., 2020. Agroforestry benefits and challenges for adoption in Europe and beyond. Sustainability 12 (17), 7001. https://doi.org/10.3390/su12177001.

Somarriba, E., Lopez-Sampson, A., 2018. Coffee and Cocoa Agroforestry Systems: Pathways to Deforestation, Reforestation, and Tree Cover Change. CATIE, Turrialba.

Sousa, A.E.A., Gomes, E.C.C., Melo, D.Q., Diógenes, I.C.N., Becker, H., Longhinotti, E., 2014. Adsorption of safranin on pseudostem banana fibers. Sep. Sci. Technol. 49 (17), 2681–2688. https://doi.org/10.1080/01496395.2014.937496.

Sridhar, V., Vinesh, L.S., 2016. Arthropod diversity and management in legume-based cropping systems in the tropics. In: Chakravarthy, A.K., Sridhara, S. (Eds.), Economic and Ecological Significance of Arthropods in Diversified Ecosystems. Springer, Cham, pp. 223–242.

Staton, T., Walters, R., Smith, J., Breeze, T., Girling, R., 2021. Management to promote flowering understoreys benefits natural enemy diversity, Aphid suppression and income in an agroforestry system. Agronomy 11 (4), 651. https://doi.org/10.3390/agronomy11040651.

Stein, K., Coulibaly, D., Stenchly, K., Goetze, D., Porembski, S., Lindner, A., Konaté, S., Linsenmair, E.K., 2017. Bee pollination increases yield quantity and quality of cash crop in Burkina Faso, West Africa. Sci. Rep. 7, 17691. https://doi.org/10.1038/s41598-017-17970-2.

Stewart, A.B., Dudash, M.R., 2016. Flower-visiting bat species contribute unequally toward agricultural pollination ecosystem services in southern Thailand. Biotropica 49 (2), 239–248. https://doi.org/10.1111/btp.12401.

Struik, P.C., Kuyper, T.W., 2017. Sustainable intensification in agriculture: the richer shade of green. A review. Agron. Sustain. Dev. 37, 39. https://doi.org/10.1007/s13593-017-0445-7.

Tarigan, S., Buchori, D., Siregar, I.Z., Azhar, A., Ullyta, A., Tjoa, A., Edy, N., 2021. Agroforestry inside oil palm plantation for enhancing biodiversity-based ecosystem functions. IOP Conference Series: Earth and Environmental Science. 694(1), 012058. https://doi.org/10.1088/1755–1315/694/1/012058.

Toledo-Hernández, M., Wanger, T.C., Tscharntke, T., 2017. Neglected pollinators: can enhanced pollination services improve cocoa yields? A review. Agric. Ecosyst. Environ. 247, 137–148. https://doi.org/10.1016/j.agee.2017.05.021.

Toledo-Hernández, M., Tscharntke, T., Tjoa, A., Anshary, A., Cyio, B., Wanger, C., 2021. Landscape and farm-level management for conservation of potential pollinators in Indonesian cocoa agroforests. Biol. Conserv. 257, 109106 https://doi.org/10.1016/j.biocon.2021.109106.

Torgerson, D., 2007. Expanding the green public sphere: Post-colonial connections. Environ. Polit. 15 (5), 713–730. https://doi.org/10.1080/09644010600937157.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol. Lett. 8, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x.

Tscharntke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P., Tylianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89 (4), 944–951. https://doi.org/10.1890/07-0455.1.

Tscharntke, T., Clough, Y., Bhagwat, A.S., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., Wanger, T.C., 2011. Multifunctional shade-tree management in tropical agroforestry landscapes – a review. J. Appl. Ecol. 48 (3), 619–629. https://doi.org/10.1111/j.1365-2664.2010.01939.x.

Tylianakis, J.M., Rand, T.A., Kahmen, A., Klein, A.M., Buchmann, N., Perner, J., Tscharntke, T., 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. PLoS Biol. 6 (5), e122 https://doi.org/10.1371/journal.pbio.0060122.

Udawatta, R.P., Rankoth, L.M., Jose, S., 2019. Agroforestry and biodiversity. Sustainability 11, 2879. https://doi.org/10.3390/su11102879.

Vaast, P., Harmand, J.M., Rapidel, B., Jagoret, P., Deheuvels, O., 2015. Coffee and cocoa production in agroforestry – a climate-smart agriculture model. In: Torquebiau, E. (Ed.), Climate Change and Agriculture Worldwide. Springer, Cham, 209-204.

Vanhove, W., Yao, R.K., N'Zi, J.C., Toussaint, L.A.N., Kaminski, A., Smagghe, G., Damme, P.V., 2020. Impact of insecticide and pollinator-enhancing substrate applications on cocoa (*Theobroma cacao*) cherelle and pod production in Côte d’Ivoire. Agric. Ecosyst. Environ. 293, 106855 https://doi.org/10.1016/j.agee.2020.106855.

Varah, A., Jones, H., Smith, J., Potts, S.G., 2020. Temperate agroforestry systems provide greater pollination service than monoculture. Agric. Ecosyst. Environ. 301, 107031 https://doi.org/10.1016/j.agee.2020.107031.

Veddeler, D., Klein, A.M., Tscharntke, T., 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. Oikos 112 (3), 594–601. https://doi.org/10.1111/j.0030-1299.2006.14111.x.

Viana, B.F., Boscolo, D.N., Lopes, E.M., Lopes, A.V., Ferreira, P.A., Pigozzo, C.M., Primo, L.M., 2012. How well do we understand landscape effects on pollinators and pollination services. J. Pollinat. Ecol. 7, 31–41. https://doi.org/10.26786/1920-7603(2012)2.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional. Oikos 116 (5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Waldron, A., Garrity, D., Malhi, Y., Girardin, C., Miller, D.C., Seddon, N., 2017. Agroforestry can enhance food security while meeting other sustainable development goals. Trop. Conserv. Sci. 10. https://doi.org/10.1177/1940082917720667.

Weiner, C.N., Werner, M., Lisenmair, K.E., Blüthgen, N., 2014. Land-use impacts on plant-pollinator networks: interaction strength and specialization predict pollinator declines. Ecology 95 (2), 466–474. https://doi.org/10.1890/13-0436.1.

Wilson, M.H., Lovell, S.T., 2016. Agroforestry – The next step in sustainable and resilient agriculture. Sustainability 8 (6), 574. https://doi.org/10.3390/su8060574.

Xiao, H., McDonald-Madden, E., Sabbadin, R., Peyrard, N., Dee, L.E., Chadès, I., 2019. The value of understanding feedbacks from ecosystem functions to species for managing ecosystems. Nat. Commun. 10, 3901. https://doi.org/10.1038/s41467-019-11890-7.

Ya, T., 2000. Agroforestry: Its Role in Crop Pollination and Beekeeping, in: Matsuka, M., Verma, L.R., Wongsiri, S., Shrestha, K.K., Partap, U. (Eds.), Asian Bees and Beekeeping: Progress of Research and Development. International Centre for Integrated Mountain Development, Kathmandu, pp. 209–212.

Young, A.M., Hunter, J.R., 2018. A technique to increase cocoa pod production by enhancing insect pollination: Implications for different environments. In: Espinal, B. Z. (Ed.), The Diversified Benefits of Cocoa and Chocolate. Nova Science Publishers, New York.

Appendix S1. References included in the review.

Amin, M.R., Mia, M.R., Rahman, H., Miah, M.G., Ge, F., 2018. Insect Community in agroforestry: Role of weather parameters on population dynamics. Indian Journal of Ecology. 45(1), 88-92.

Amin, M.R., Namni, S., Miah, M.R.U., Miah, M.G., Zakaria, M., Suh, S.J., Kwon, Y.J., 2015. Insect inventories in a mango-based agroforestry area in Bangladesh: foraging behavior and performance of pollinators on fruit set. Entomological Research. 45(4), 217-224. https://doi.org/10.1111/1748-5967.12112.

Arnold, S.E.J., Bridgemohan, P., Perry, G.B., Spinelli, G.R., Pierre, B., Murray, F., Haughton, C., Dockery, O., Grey, L., Murphy, S.T., Belmain, S.R., Stevenson, P.C., 2018. The significance of climate in the pollinator dynamics of a tropical agroforestry system. Agriculture, Ecosystems & Environment. 254, 1-9. https://doi.org/10.1016/j.agee.2017.11.013.

Barrera Jr, W.B., Brosas, J.V., Sacil, M.D., 2021. Pollen sources of *Tetragonula biroi* (Friese, 1898) (Hymenoptera: Apidae, Meliponini) in two agroecosystems in Nagcarlan, Laguna, Philippines. Palynology. 45(2), 215-223. https://doi.org/10.1080/01916122.2020.1789773.

Barrios, E., Valencia, V., Jonsson, M., Brauman, A., Hairiah, K., Mortimer, P.E., Okubo, S. 2018. Contribution of trees to the conservation of biodiversity and ecosystem services in agricultural landscapes. International Journal of Biodiversity Science, Ecosystem Services & Management. 14(1), 1-16. https://doi.org/10.1080/21513732.2017.1399167.

Bentrup, G., Hopwood, J., Adamson, N.L., Vaughan, M., 2019. Temperate agroforestry systems and insect pollinators: A review. Forests. 10(11), 981. https://doi.org/10.3390/f10110981.

Berecha, G., Aerts, R., Muys, B., Honnay, O., 2015. Fragmentation and management of Ethiopian moist evergreen forest drive compositional shifts of insect communities visiting wild Arabica coffee flowers. Environmental Management. 55(2), 373-382. https://doi.org/10.1007/s00267-014-0393-9.

Boreux, V., Krishnan, S., Cheppudira, K.G., Ghazoul, J., 2013a. Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agroforests. Agriculture, Ecosystems & Environment. 172, 42-48. https://doi.org/10.1016/j.agee.2012.05.003.

Boreux, V., Kushalappa, C.G., Vaast, P., Ghazoul, J., 2013b. Interactive effects among ecosystem services and management practices on crop production: Pollination in coffee agroforestry systems. Proceedings of the National Academy of Sciences of the United States of America. 110(21), 8387-8392. https://doi.org/10.1073/pnas.1210590110

Bos, M.M., Höhn, P., Saleh, S., Büche, B., Buchori, D., Steffan-Dewenter, I., Tscharntke, T., 2007a. Insect diversity responses to forest conversion and agroforestry management in: Tscharntke, T., Leuschner, C., Zeller, M., Guhardja, E., Bidin, A. (Eds.), Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation. Springer, Berlin, pp. 225-261.

Bos, M.M., Steffan-Dewenter, I., Tscharntke, T., 2007b. Shade tree management affects fruit abortion, insect pests and pathogens of cacao. Agriculture, Ecosystems & Environment, 120(2-4), 201-205. https://doi.org/10.1016/j.agee.2006.09.004.

Bravo-Monroy, L., Tzanopoulos, J., Potts, S.G., 2015. Ecological and social drivers of coffee pollination in Santander, Colombia. Agriculture, Ecosystems & Environment. 211, 145-154. https://doi.org/10.1016/j.agee.2015.06.007.

Caudill, S., Brokaw, J., Doublet, D., Rice, R., 2017. Forest and trees: Shade management, forest proximity and pollinator communities in southern Costa Rica coffee agriculture. Renewable Agriculture and Food Systems. 32(5), 417-427. https://doi.org10.1017/S1742170516000351.

Chain-Guadarrama, A., Martínez-Salinas, A., Aristizábal, N., Ricketts, T.H., 2019. Ecosystem services by birds and bees to coffee in a changing climate: A review of coffee berry borer control and pollination. Agriculture, Ecosystems & Environment. 280, 53-67. https://doi.org/10.1016/j.agee.2019.04.011.

Classen, A., Peters, M.K., Ferger, S.W., Helbig-Bonitz, M., Schmack, J.M., Maassen, G., Schleuning, M., Kalko, E.K.V., Böhning-Gaese, K., Steffan-Dewenter, I., 2014. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. Proceeding of the Royal Society B. 281, 20133148. https://doi.org/10.1098/rspb.2013.3148.

Cuevas, E., Blancas, J., Caballero, J., Hinojosa-Díaz, I.A., Martínez-Ballesté, A., 2021. Agricultural management and local knowledge: key factors for the conservation of socio-ecosystems in the face of the pollinator world crisis. Botanical Sciences. 99(2), 305-320. https://doi.org/10.17129/botsci.2659.

Dáttilo, W., Martins, R.L., Uhde, V., Noronha, J.C., Florêncio, F.P., Izzo, T.J., 2012. Floral resource partitioning by ants and bees in a jambolan *Syzygium jambolanum* (Myrtaceae) agroforestry system in Brazilian Meridional Amazon. Agroforestry Systems. 85, 105-111. https://doi.org/10.1007/s10457-012-9489-5.

Delaney, A., Dembele, A., Nombré, I., Lirasse, F.G., Marshall, E., Nana, A., Vickery, J., Tayleur, C., Stout, J.C., 2020. Local-scale tree and shrub diversity improves pollination services to shea trees in tropical West African parklands. Journal of Applied Ecology. 57(8), 1504-1513. https://doi.org/10.1111/1365-2664.13640.

Du, M., Ushiyama, T., Yonemura, S., Shibaike, H., 2019. Three-dimensional numerical simulations of windbreak effects of pollen dispersal and cross-pollination. IOP Conference Series: Earth and Environmental Science. 227(5), 052002. https://doi.org/10.1088/1755-1315/227/5/05002.

Dubeux Jr, J.C.B., Muir, J.P., Apolinário, V.X.O., Nair, P.K.R., Lira, M.A., Sollenberger, L.E., 2017. Tree legumes: and underexploited resource in warm-climate silvopastures. Revista Brasileira de Zootecnia. 46(8), 689-703. https://doi.org/10.1590/S1806-92902017000800010.

Fierro, M.M., Cruz-López, L., Sánchez, D., Villanueva-Gutiérrez, R., Vandame, R., 2012. Effect of biotic factors on the spatial distribution of stingless bees (Hymenoptera: Apidae, Meliponini) in fragmented neotropical habitats. Neotropical Entomology, 41(2), 95-104. https://doi.org/10.1007/s13744-011-0009-5.

Fisher, K., Gonthier, D.J., Ennis, K.K., Perfecto, I., 2017. Floral resource availability from groundcover promotes bee abundance in coffee agroecosystems. Ecological Applications. 27(6), 1815-1826. https://doi.org/10.1002/eap.1568.

Frimpong, E.A., Gemill-Herren, B., Gordon, I., Kwapong, P.K., 2011. Dynamics of insect pollinators as influenced by cocoa production systems in Ghana. Journal of Pollination Ecology. 5(10), 74-80. https://doi.org/10.26786/1920-7603(2011)12.

Gaira, K.S., Rawal, R.S., Singh, K.K., 2016. Variations in pollinator density and impacts on large cardamom (*Amomum subulatum* Roxb.) crop yield in Sikkim Himalaya, India. Journal of Asia-Pacific Biodiversity. 9(1), 17-21. https://doi.org/10.1016/j.japb.2015.12.010.

Galbraith, S.M., Griswold, T., Price, W.J., Bosque-Pérez, N.A., 2020. Biodiversity and community composition of native bee populations vary among human-dominated land uses within the seasonally dry tropics. Journal of Insect Conservation. 24(6), 1045-1059. https://doi.org/10.1007/s10841-020-00274-8.

Geeraert, L., Aerts, R., Jordaens, K., Dox, I., Wellens, S., Couri, M., Berecha, G., Hoonay, O., 2019. Intensification of Ethiopian coffee agroforestry drives impoverishment of the Arabica coffee flower visiting bee and fly communities. Agroforestry Systems. 93, 1729-1739. https://doi.org/10.1007/s10457-018-0280-0.

Graham, J.B., Nassauer, J.I., 2019. Wild bee abundance in temperate agroforestry landscapes: Assessing effects of alley crop composition, landscape configuration, and agroforestry area. Agroforestry Systems. 93, 837-850. https://doi.org/10.1007/s10457-017-0179-1.

Groeneveld, J.H., Tscharntke, T., Moser, G., Clough, Y., 2010. Experimental evidence for stronger cacao yield limitation by pollination than by plant resources. Perspectives in Plant Ecology, Evolution and Systematics. 12(3), 183-191. https://doi.org/10.1016/j.ppees.2010.02.005.

Hass, A.L., Liese, B., Heong, K.L., Settele, J., Tscharntke, T., Westphal, C., 2018. Plant-pollinator interactions and bee functional diversity are driven by agroforests in rice-dominated landscapes. Agriculture, Ecosystems & Environment. 253, 140-147. https://doi.org/10.1016/j.agee.2017.10.019.

Hoehn, P., Steffan-Dewenter, I., Tscharntke, T., 2010. Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity. Biodiversity and Conservation. 19, 2189-2200. https://doi.org/10.1007/s10531-010-9831-z.

Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. Proceedings of the Royal Society B. 275, 2283-2291. https://doi.org/10.1098/rspb.2008.0405.

Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau, D.K., Liebman, M., Polley, H.W., Quijas, S., Scherer-Lorenzen, M., 2017. Benefits of increasing plant diversity in sustainable agroecosystems. Journal of Ecology. 105(4), 871-879. https://doi.org/10.1111/1365-2745.12789.

Jha, S., Vandermeer, J.H. 2009a. Contrasting bee foraging in response to resource scale and local habitat management. Oikos. 118(8), 1174-1180. https://doi.org/10.1111/j.1600-0706.2009.17523.x.

Jha, S., Vandermeer, J.H., 2009b. Contrasting foraging patterns for Africanized honeybees, native bees and native wasps in a tropical agroforestry landscape. Journal of Tropical Ecology. 25(1), 13-22. https://doi.org/10.1017/S026646740800566X.

Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. Biological Conservation. 143(6), 1423-1431. https://doi.org/10.1016/j.biocon.2010.03.017.

Kay, S., Crous-Duran, J., Ferreiro-Domínguez, N., Jalón, S.G., Graves, A., Moreno, G., Mosquera-Losada, M.R., Palma, J.H.N., Roces-Díaz, J.V., Santiago-Freijanes, J.J., Szerencsits, E., Weibel, R., Herzog, F., 2018. Spatial similarities between European agroforestry systems and ecosystem services at the landscape scale. Agroforestry Systems. 92; 1075-1089. https://doi.org/10.1007/s10457-017-0132-3.

Kay, S., Kühn, E., Albrecht, M., Sutter, L., Szerencsits, E., Herzog, F., 2020. Agroforestry can enhance foraging and nesting resources for pollinators with focus on solitary bees at the landscape scale. Agroforestry Systems. 94, 379-387. https://doi.org/10.1007/s10457-019-00400-9.

Klein, A.M., Cunningham, A.S., Bos, M., Steffan-Dewenter, I., 2008. Advances in pollination ecology from tropical plantation crops. Ecology. 89(4), 935-943. https://doi.org/10.1890/07-0088-1.

Klein, A.M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conservation Biology. 16(4), 1003-1014. https://doi.org/10.1046/j.1523-1739.2002.00499.x.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003a. Bee pollination and fruit set of *Coffea arabica* and *C. canephora* (Rubiaceae). American Journal of Botany. 90(1), 153-157. https://doi.org/10.3732/ajb.90.1.153.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003b. Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society B. 270, 955-961. https://doi.org/10.1098/rspb.2002.2306.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003c. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. Journal of Applied Ecology. 40(5), 837-845. https://doi.org/10.1046/j.1365-2664.2003.00847.x.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2004. Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. Journal of Animal Ecology. 73(3), 517-525. https://doi.org/10.1111/j.0021-8790.2004.00826.x.

Krishnan, S., Cheppudira, K.G., Ghazoul, J., 2018. Pollinator services in coffee agroforests of the Western Ghats, in: Dagar, J.C., Tewari, V.P., (Eds.), Agroforestry: Anecdotal to Modern Science. Springer, Cham, pp. 771-795.

Kuyah, S., Öborn, I., Jonsson, M., 2018. Regulating ecosystem services delivered in agroforestry systems, in: Dagar, J.C., Tewari, V.P., (Eds.), Agroforestry: Anecdotal to Modern Science. Springer, Cham, pp. 797-815.

Lassen, K.M., Nielsen, L.R., Lompo, D., Dupont, Y.L., Kjær, E.D., 2018. Honey bees are essential for pollination of *Vitellaria paradoxa* subsp. *paradoxa* (Sapotaceae) in Burkina Faso. Agroforestry Systems. 92, 23-34. https://doi.org/10.1007/s10457-016-007-z.

Magrach, A., Champetier, A., Krishnan, S., Boreux, V., Ghazoul, J., 2019. Uncertainties in the value and opportunity costs of pollination services. Journal of Applied Ecology. 56(7), 1549-1559. https://doi.org/10.1111/1365-2664.13399.

Marco Jr, P., Coelho, F.M., 2004. Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. Biodiversity & Conservation, 13. 1245-1255. https://doi.org/10.1023/B:BIOC.0000019402.51193.e8.

Matos, M.C.B., Silva, S.S., Teodoro, A.V., 2016. Seasonal population abundance of the assembly of solitary wasps and bees (Hymenoptera) according to land-use in Maranhão state, Brazil. Revista Brasileira de Entomologia 60: 171-176. https://doi.org/10.1016/j.rbe.2016.02.001.

McAneney, K.J., Judd, M.J., Trought, M.C.T., 1984. Wind damage to kiwifruit (*Actinidia chinensis* Planch.) in relation to windbreak performance. New Zealand Journal of Agricultural Research. 27, 255-263. https://doi.org/10.1080/00288233.1984.10430427.

Moisan-DeSerres, J., Chagnon, M., Fournier, V., 2015. Influence of windbreaks and forest borders on abundance and species richness of native pollinators in lowbush blueberry fields in Québec, Canada. The Canadian Entomologist, 147(4), 432-442. https://doi.org/10.4039/tce.2014.55.

Morel, A.C., Hirons, M., Sasu, M.A., Quaye, M., Asare, A., Mason, J., Adu-Bredu, S., Boyd, E., McDermott, C.L., Robinson, E.J.Z., Straser, R., Malhi, Y., Norris, K., 2019. The ecological limits of poverty alleviation in an African Forest-Agriculture Landscape. Frontiers in Sustainable Food Systems. 3, 57. https://doi.org/10.3389/fsufs.2019.00057.

Munyuli, T., 2014a. Influence of functional traits on foraging behaviour and pollination efficiency of wild social and solitary bees visiting coffee (*Coffea canephora*) flowers in Uganda. Grana. 53(1), 69-89. https://doi.org/10.1080/00173134.2013.853831.

Munyuli, T., 2012a. Assessment of indicator species of butterfly assemblages in coffee-banana farming system in central Uganda. African Journal of Ecology. 50(1), 77-89. https://doi.org/10.1111/j.1365-2028.2011.01298.x.

Munyuli, T., 2012b. Butterfly diversity from farmlands of central Uganda. Psyche: A Journal of Entomology. 2012: 481509. https://doi.org/10.1155/2012/481509.

Neto, C.M.S., Santos, L.A.C., Souza, W.G., Martins, T.O., Silva, T.C., Lima, A.A., Calil, F.N., Souza, M.M.O., 2021. Bees in agroforestry systems in the Cerrado. Journal of Apicultural Research. https:/doi.org/10.1080/00218839.2021.1907977

Norfolk, O., Eichhorn, M.P., Gilbert, F., 2016. Flowering ground vegetation benefits wild pollinators and fruit set of almond within arid smallholder orchards. Insect Conservation and Diversity. 9(3), 236-243. https:/doi.org/10.1111/icad.12162.

Norton, R.L., 1988. Windbreaks: Benefits to orchard and vineyard crops. Agriculture, Ecosystems & Environment. 22-23, 205-213. https://doi.org/10.1016/0167-8809(88)90019-9.

Olschewski, R., Tscharntke, T., Benítez, P.C., Schwarze, S., Klein, A.M., 2006. Economic Evaluation of Pollination Services Comparing Coffee Landscapes in Ecuador and Indonesia. Ecology and Society. 11(1), 7.

Pavageau, C., Gaucherel, C., Garcia, C., Ghazoul, J., 2018. Nesting sites of giant honeybees modulated by landscape patterns. Journal of Applied Ecology. 55(3), 1230-1240. https://doi.org/10.1111/1365-2664.13069.

Perfecto, I., Armbrecht, I., Philpott, S.M., Soto-Pinto, L., Dietsch, T.V., 2007. Shaded coffee and the stability of rainforest margins in northern Latin America, in: Tscharntke, T., Leuschner, C., Zeller, M., Guhardja, E., Bidin, A., (Eds.), Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation. Springer, Berlin, pp. 225-261.

Peters, V.E., 2014. Intercropping with shrub species that display a 'Steady-state' flowering phenology as a strategy for biodiversity conservation in tropical agroecosystems. PLOS ONE. 9(3), e90510. https://doi.org/10.1371/jornal.pone.0090510.

Peters, V.E., Carroll, C.R., 2012. Temporal variation in coffee flowering may influence the effects of bee species richness and abundance on coffee production. Agroforestry Systems. 85, 95-103. https://doi.org/10.1007/s10457-011-9476-2.

Peters, V.E., Carroll, C.R., Cooper, R.J., Greenberg, R., Solis, M., 2013. The contribution of plant species with a steady-state flowering phenology to native bee conservation and bee pollination services. Insect Conservation and Diversity. 6(1), 45-56. https://doi.org/10.1111/j.1752-4598.2012.00189.x.

Philpott, S.M., Uno, S., Maldonado, J., 2006. The importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. Biodiversity & Conservation. 15, 487-501. https://doi.org/10.1007/s10531-005-0602-1.

Prado, S.G., Collazo, J.A., Marand, M.H., Irwin, R.E., 2021 The influence of floral resources and microclimate on pollinator visitation in an agro-ecosystem. Agriculture, Ecosystems & Environment. 307, 107196. https://doi.org/10.1016/j.agee.2020.107196.

Prado, S.G., Collazo, J.Á., Stevenson, P.C., Irwin, R.E., 2019. A comparison of coffee floral traits under two different agricultural practices. Scientific Reports. 9, 7331. https://doi.org/10.1038/s41598-019-43753-y.

Priess, J.A., Mimler, M., Klein, A.M., Schwarze, S., Tscharntke, T., Steffan-Dewenter, I., 2007. Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. Ecological Applications. 17(2), 407-417. https://doi.org/10.1890/05-1795.

Reed, J., Vianen, J.V., Foli, S., Clendenning, J., Yang, K., MacDonald, M., Petrokofsky, G., Padoch, C., Sunderland, T., 2017. Trees for life: The ecosystem service contribution of trees to food production and livelihoods in the tropics. Forest Policy and Economics. 84, 62-71. https://doi.org/10.1016/j.forpol.2017.01.012.

Roy, S., Roy, M.M., Saxena, P., Bano, R., 2018. Role of entomology in sustaining agroforestry productivity, in: Dagar, J.C., Tewari, V.P., (Eds.), Agroforestry: Anecdotal to Modern Science. Springer, Cham, pp. 691-704.

Samnegård, U., Hambäck, P.A., Nemomissa, S., Hylander, K., 2014. Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia. Journal of Tropical Ecology. 30(5), 401-408. https://doi.org/10.1017/S0266567414000327.

Schüepp, C., Rittiner, S., Entling, M.H., 2012. High bee and wasp diversity in heterogeneous tropical farming system compared to protected forest. PLOS ONE. 7(12), e52109. https://doi.org/10.1371/journal.pone.0052109.

Sollen-Norrlin, M., Ghaley, B.B., Rintoul, N.L.J., 2020. Agroforestry benefits and challenges for adoption in Europe and beyond. Sustainability. 12(17), 7001. https://doi.org/10.3390/su12177001.

Sporn, S.G., Bos, M.M., Gradstein, R., 2007. Is productivity of cacao impeded by epiphytes? An experimental approach. Agriculture, Ecosystems & Environment. 122(4), 490-493. https://doi.org/10.1016/j.agee.2007.02.009.

Sridhar, V., Vinesh, L.S., 2016 Arthropod diversity and management in legume-based cropping systems in the tropics, in: Chakravarthy, A.K., Sridhara, S., (Eds.), Economic and Ecological Significance of Arthropods in Diversified Ecosystems. Springer, Cham, pp. 223-242.

Staton, T., Walters, R., Smith, J., Breeze, T., Girling R., 2021. Management to promote flowering understoreys benefits natural enemy diversity, Aphid suppression and income in an agroforestry system. Agronomy. 11(4), 651. https://doi.org/10.3390/agronomy11040651.

Staton, T., Walters, R., Smith, J., Girling, R., 2019. Evaluating the effects of integrating trees into temperate arable systems on pest control and pollination. Agricultural Systems. 176, 102676. https://doi.org/10.1016/j.agsy.2019.102676.

Tarigan, S., Buchori, D., Siregar, I.Z., Azhar, A., Ullyta, A., Tjoa, A., Edy, N., 2021. Agroforestry inside oil palm plantation for enhancing biodiversity-based ecosystem functions. IOP Conference Series: Earth and Environmental Science. 694(1), 012058. https://doi.org/10.1088/1755-1315/694/1/012058.

Toledo-Hernández, M., Tscharntke, T., Tjoa, A., Anshary, A., Cyio, B., Wanger, C., 2021. Landscape and farm-level management for conservation of potential pollinators in Indonesian cocoa agroforests. Biological Conservation. 257, 109106. https://doi.org/10.1016/j.biocon.2021.109106.

Toledo-Hernández, M., Wanger, T.C., Tscharntke, T. 2017. Neglected pollinators: Can enhanced pollination services improve cocoa yields? A review. Agriculture, Ecosystems & Environment. 247, 137-148. https://doi.org/10.1016/j.agee.2017.05.021.

Tscharntke, T., Clough, Y., Bhagwat, A.S., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., Wanger, T.C., 2011. Multifunctional shade-tree management in tropical agroforestry landscapes – a review. Journal of Applied Ecology. 48(3), 619-629. https://doi.org/10.1111/j.1365-2664.2010.01939.x.

Tscharntke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P., Tylianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology. 89(4), 944-951. https://doi.org/10.1890/07-0455.1.

Tylianakis, J.M., Rand, T.A., Kahmen, A., Klein, A.M., Buchmann, N., Perner, J., Tscharntke, T., 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. PLOS Biology. 6(5), e122. https://doi.org/10.1371/journal.pbio.0060122.

Ushiyama, T., Du, M., Inoue, S., Shibaike, H., Yonemura, S., Kawashima, S., Amano, K., 2009. Three-dimensional prediction of maize pollen dispersal and cross-pollination, and the effects of windbreaks. Environmental Biosafety Research. 8(4), 183-202. https://doi.org/10.1051/ebr/2010002.

Vanhove, W., Yao, R.K., N’Zi, J.C., Toussaint, L.A.N., Kaminski, A., Smagghe, G., Damme, P.V., 2020. Impact of insecticide and pollinator-enhancing substrate applications on cocoa (*Theobroma cacao*) cherelle and pod production in Côte d’Ivoire. Agriculture, Ecosystems & Environment. 293, 106855. https://doi.org/10.1016/j.agee.2020.106855

Varah, A., Jones, H., Smith, J., Potts, S.G., 2020. Temperate agroforestry systems provide greater pollination service than monoculture. Agriculture, Ecosystems & Environment. 301, 107031. https://doi.org/10.1016/j.agee.2020.107031

Veddeler, D., Klein, A.M., Tscharntke. T., 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. Oikos. 112(3), 594-601. https://doi.org/10.1111/j.0030-1299.2006.14111.x.

Ya, T., 2000. Agroforestry: Its Role in Crop Pollination and Beekeeping, in: Matsuka, M., Verma, L.R., Wongsiri, S., Shrestha, K.K., Partap, U. (Eds.), Asian Bees and Beekeeping: Progress of Research and Development. International Centre for Integrated Mountain Development, Kathmandu, pp. 209-212.

Young, A.M., Hunter, J.R., 2018. A technique to increase cocoa pod production by enhancing insect pollination: Implications for different environments, in: Espinal, B.Z. (Ed.), The diversified benefits of cocoa and chocolate. Nova Science Publishers, New York.

Table S1. Economic situation of correspondence author's country according to the United Nations.

Country	Economic situation	References	Number of published papers
Germany	Developed	Klein et al., 2002; Klein et al., 2003a; Klein et al., 2003b; Klein et al., 2003c; Klein et al., 2004; Olschewski et al., 2006; Veddeler et al., 2006; Bos et al., 2007a; Bos et al., 2007b; Priess et al., 2007; Sporn et al., 2007; Hoehn et al., 2008; Tscharntke et al., 2008; Hoehn et al., 2010; Groeneveld et al., 2010; Tscharntke et al., 2011; Classen et al., 2014; Toledo-Hernández et al., 2017; Hass et al., 2018; Toledo-Hernández et al., 2021	20
United States of America	Developed	Norton, 1988; Philpott et al., 2006; Perfecto et al., 2007; Klein et al., 2008; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Jha & Vandermeer, 2010; Peters & Carroll, 2012; Peters et al., 2013; Peters, 2014; Caudill et al., 2017; Dubeux Jr et al., 2017; Fisher et al., 2017; Isbell et al., 2017; Young & Hunter, 2018; Bentrup et al., 2019; Graham & Nassauer, 2019; Prado et al., 2019; Galbraith et al., 2020; Prado et al., 2021	20
United Kingdom	Developed	Bravo-Monroy et al., 2015; Norfolk et al., 2016; Arnold et al., 2018; Morel et al., 2019; Staton et al., 2019; Delaney et al., 2020; Sollen-Norrlin et al., 2020; Varah et al., 2020; Staton et al., 2021	9
Switzerland	Developed	Schüepp et al., 2012; Boreux et al., 2013a; Boreux et al., 2013b; Kay et al., 2018; Krishnan et al., 2018; Pavageau et al., 2018; Magrach et al., 2019; Kay et al., 2020	8
Brazil	Developing	Marco Jr & Coelho, 2004; Dáttilo et al., 2012; Matos et al., 2016; Neto et al., 2021	4
Belgium	Developed	Berecha et al., 2015; Geeraert et al., 2019; Vanhove et al., 2020	3
Democratic Republic of Congo	Developing	Munyuli, 2012a; Munyuli, 2012b; Munyuli, 2014a	3
India	Developing	Gaira, 2016; Sridhar & Vinesh, 2016; Roy et al., 2018	3
Indonesia	Developing	Reed et al., 2017; Tarigan et al., 2021	2

Japan	Developed	Ushiyama et al., 2009; Du et al., 2019	2
Mexico	Developing	Fierro et al., 2012; Cuevas et al., 2021	2
New Zealand	Developed	McAneney et al., 1984; Tylianakis et al., 2008	2
Sweden	Developed	Samnegård et al., 2014; Kuyah et al., 2018	2
Bangladesh	Developing	Amin et al., 2018	1
Canada	Developed	Moisan-DeSerres et al., 2015	1
Costa Rica	Developing	Chain-Guadarrama et al., 2019	1
Denmark	Developed	Lassen et al., 2018	1
Ghana	Developing	Frimpong et al., 2011	1
Kenya	Developing	Barrios et al., 2018	1
Nepal	Developing	Ya, 2000	1
Philippines	Developing	Barrera Jr et al., 2021	1
South Korea	Developed	Amin et al., 2015	1

Table S2. Biogeographical distribution of studies on pollination dynamics in agroforestry systems. Note that studies may appear several times in this table since work may have been conducted in multiple countries.

Climatic zone	**Country**	**Economic situation**	**References**	**Number of published studies**
Tropical	Indonesia	Developing	Klein et al., 2002; Klein et al., 2003a; Klein et al., 2003b; Klein et al., 2003c; Klein et al., 2004; Olschewski et al., 2006; Bos et al., 2007a; Bos et al., 2007b; Priess et al., 2007; Sporn et al., 2007; Hoehn et al., 2008; Tylianakis et al., 2008; Hoehn et al., 2010; Groeneveld et al., 2010; Toledo-Hernández et al., 2021; Tarigan et al., 2021	16
	Mexico	Developing	Philpott et al., 2006; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Jha & Vandermeer, 2010; Fierro et al., 2012; Fisher et al., 2017; Cuevas et al., 2021	7
	Costa Rica	Developing	Peters & Carroll, 2012; Peters et al., 2013; Peters, 2014; Caudill et al., 2017; Young & Hunter, 2018; Galbraith et al., 2020	6
	India	Developing	Boreux et al., 2013a; Boreux et al., 2013b; Gaira, 2016; Krishnan et al., 2018; Pavageau et al., 2018; Magrach et al., 2019	6
	Brazil	Developing	Marco Jr & Coelho, 2004; Dáttilo et al., 2012; Matos et al., 2016; Neto et al., 2021	4
	Ethiopia	Developing	Samnegård et al., 2014; Berecha et al., 2015; Geeraert et al., 2019	3
	Uganda	Developing	Munyuli, 2012a; Munyuli, 2012b; Munyuli, 2014a	3
	Burkina Faso	Developing	Lassen et al., 2018; Delaney et al., 2020	2
	Ecuador	Developing	Olschewski et al., 2006; Veddeler et al., 2006	2

	Ghana	Developing	Frimpong et al., 2011; Morel et al., 2019	2
	Philippines	Developing	Hass et al., 2018; Barrera Jr et al., 2021	2
	Puerto Rico	Developed	Prado et al., 2019; Prado et al., 2021	2
	Belize	Developing	Schüepp et al., 2012	1
	Colombia	Developing	Bravo-Monroy et al., 2015	1
	Ivory Coast	Developing	Vanhove et al., 2020	1
	Jamaica	Developing	Arnold et al., 2018	1
	Tanzania	Developing	Classen et al., 2014	1
	Tobago	Developing	Arnold et al., 2018	1
	Trinidad	Developing	Arnold et al., 2018	1
	Bangladesh	Developing	Amin et al., 2015; Amin et al., 2018	2
Subtropical	Egypt	Developing	Norfolk et al., 2016	1
	United Kingdom	Developed	Varah et al., 2020; Staton et al., 2021;	2
Temperate	Canada	Developed	Moisan-DeSerres et al., 2015	1
	Japan	Developed	Ushiyama et al., 2009	1
	New Zealand	Developed	McAneney et al., 1984	1
	Switzerland	Developed	Kay et al., 2020	1
	United States of America	Developed	Graham & Nassauer, 2019	1

Table S3. Type of research methodology used to study pollination dynamics in agroforestry systems.

Nature of method	**References**	**Number of published papers**
Observational	McAneney et al., 1984; Philpott et al., 2006; Veddeler et al., 2006; Bos et al., 2007a; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Hoehn et al., 2010; Jha & Vandermeer, 2010; Fierro et al., 2012; Munyuli, 2012a; Munyuli, 2012b; Peters & Carroll, 2012; Schüepp et al., 2012; Boreux et al., 2013a; Boreux et al., 2013b; Samnegård et al., 2014; Amin et al., 2015; Berecha et al., 2015; Bravo-Monroy et al., 2015; Moisan-DeSerres et al., 2015; Gaira et al., 2016; Matos et al., 2016; Norfolk et al., 2016; Caudill et al., 2017; Fisher et al., 2017; Amin et al., 2018; Arnold et al., 2018; Hass et al., 2018; Krishnan, 2018; Pavageau et al., 2019; Geeraert et al., 2019; Morel et al., 2019; Prado et al., 2019; Delaney et al., 2020; Galbraith et al., 2020; Varah et al., 2020; Cuevas et al., 2021; Neto et al., 2021; Prado et al., 2021; Staton et al., 2021	40
Experimental	Klein et al., 2002; Klein et al., 2003a; Klein et al., 2003b; Klein et al., 2003c; Klein et al., 2004; Marco Jr & Coelho, 2004; Bos et al., 2007b; Sporn et al., 2007; Hoehn et al., 2008; Tylianakis et al., 2008; Groeneveld et al., 2010; Frimpong et al., 2011; Dáttilo et al., 2012; Peters et al., 2013; Classen et al., 2014; Munyuli, 2014a; Peters, 2014; Lassen et al., 2018; Young & Hunter, 2018; Vanhove et al., 2020; Barrera Jr et al., 2021; Tarigan et al., 2021; Toledo-Hernández et al., 2021	23
Review	Norton, 1988; Ya, 2000; Perfecto et al., 2007; Klein et al., 2008; Tscharntke et al., 2008; Tscharntke et al., 2011; Sridhar & Vinesh, 2016; Dubeux Jr et al., 2017; Isbell et al., 2017; Toledo-Hernández et al., 2017; Reed et al., 2017; Barrios et al., 2018; Kuyah et al., 2018; Roy et al., 2018; Bentrup et al., 2019; Chain-Guadarrama et al., 2019; Sollen-Norrlin et al., 2020	17
Modeling	Olschewski et al., 2006; Priess et al., 2007; Ushiyama et al., 2009; Kay et al., 2018; Du et al., 2019; Graham & Nassauer, 2019; Magrach et al., 2019; Kay et al., 2020	8
Meta-analysis	Staton et al., 2019	1

Table S4. Crop(s) studied in agroforestry systems. They may have been the object of study, or the plant with which a pollinator was interacting. Note that studies may appear several times in this table since there may have been more than one study crop per study.

Crop	**Pollinator dependency**	**References**	**Number of published papers**
Arabica coffee	Modest	Klein et al., 2003a; Klein et al., 2003b; Marco Jr & Coelho, 2004; Philpott et al., 2006; Veddeler et al., 2006; Priess et al., 2007; Tylianakis et al., 2008; Jha & Vandermeer, 2009a; Tscharntke et al., 2011; Peters & Carroll, 2012; Classen et al., 2014; Samnegård et al., 2014; Berecha et al., 2015; Bravo-Monroy et al., 2015; Caudill et al., 2017; Geeraert et al., 2019; Prado et al., 2019; Prado et al., 2021	18
Cocoa	Essential	Bos et al., 2007b; Sporn et al., 2007; Klein et al., 2008; Groeneveld et al., 2010; Hoehn et al., 2010; Frimpong et al., 2011; Tscharntke et al., 2011; Fierro et al., 2012; Toledo-Hernández et al., 2017; Young & Hunter, 2018; Morel et al., 2019; Vanhove et al., 2020; Toledo-Hernández et al., 2021	13
Robusta coffee	High	Klein et al., 2003a; Klein et al., 2003c; Jha & Vandermeer, 2009a; Tscharntke et al., 2011; Boreux et al., 2013b; Munyuli, 2014a; Krishnan et al., 2018; Magrach et al., 2019; Prado et al., 2019; Prado et al., 2021	10
Coffee	Modest	Klein et al., 2002; Olschewski et al., 2006; Perfecto et al., 2007; Klein et al., 2008; Jha & Vandermeer, 2009b; Munyuli, 2012b; Fisher et al., 2017; Pavageau et al., 2018; Chain-Guadarrama et al., 2019	9
Corn	None	Ushiyama et al., 2009; Du et al., 2019	2
Mango	High	Amin et al., 2015; Amin et al., 2018	2
Shea tree	Modest	Lassen et al., 2018; Delaney et al., 2020	2
Almond	High	Norfolk et al., 2016	1
Apple	High	Staton et al., 2021	1
California poppy	Unknown	Varah et al., 2020	1
Cardamom	High	Gaira et al., 2016	1
Cherry	High	Kay et al., 2020	1
Coconut	Modest	Barrera Jr et al., 2021	1
Jambolanum	Unknown	Dáttilo et al., 2012	1

Kiwifruit	Essential	McAneney et al., 1984	1
Pumpkin	Essential	Hoehn et al., 2008	1

Table S5. Focal pollinators, which were either the specific object of study or a vector seen interacting with plants. Note that studies may appear several times in this table since there may have been more than one focal pollinator per study.

Pollination vector	References	Number of published papers
Bees	McAneney et al., 1984; Ya, 2000; Klein et al., 2002; Klein et al., 2003a; Klein et al., 2003b; Klein et al., 2003c; Klein et al., 2004; Marco Jr & Coelho, 2004; Olschewski et al., 2006; Veddeler et al., 2006; Bos et al., 2007a; Perfecto et al., 2007; Priess et al., 2007; Hoehn et al., 2008; Klein et al., 2008; Tscharntke et al., 2008; Tylianakis et al., 2008; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Hoehn et al., 2010; Jha & Vandermeer, 2010; Tscharntke et al., 2011; Dáttilo et al., 2012; Fierro et al., 2012; Peters & Carroll, 2012; Schüepp et al., 2012; Boreux et al., 2013a; Boreux et al., 2013b; Peters et al., 2013; Classen et al., 2014; Munyuli, 2014a; Peters, 2014; Samnegård et al., 2014; Amin et al., 2015; Berecha et al., 2015; Bravo-Monroy et al., 2015; Moisan-DeSerres et al., 2015; Gaira et al., 2016; Matos et al., 2016; Norfolk et al., 2016; Sridhar & Vinesh, 2016; Caudill et al., 2017; Fisher et al., 2017; Hass et al., 2018; Krishnan et al., 2018; Lassen et al., 2018; Pavageau et al., 2018; Bentrup et al., 2019; Chain-Guadarrama et al., 2019; Geeraert et al., 2019; Graham & Nassauer, 2019; Magrach et al., 2019; Prado et al., 2019; Staton et al., 2019; Delaney et al., 2020; Galbraith et al., 2020; Kay et al., 2020; Varah et al., 2020; Barrera Jr et al., 2021; Cuevas et al., 2021; Neto et al., 2021; Prado et al., 2021; Staton et al., 2021; Tarigan et al., 2021	64
Other insects	Philpott et al., 2006; Bos et al., 2007b; Sporn et al., 2007; Klein et al., 2008; Groeneveld et al., 2010; Frimpong et al., 2011; Tscharntke et al., 2011; Munyuli, 2012a; Munyuli, 2012b; Classen et al., 2014; Peters, 2014; Amin et al., 2015; Moisan-DeSerres et al., 2015; Norfolk et al., 2016; Toledo-Hernández et al., 2017; Arnold et al., 2018; Young & Hunter, 2018; Bentrup et al., 2019; Geeraert et al., 2019; Morel et al., 2019; Staton et al., 2019; Vanhove et al., 2020; Varah et al. 2020; Cuevas et al., 2021; Toledo-Hernández et al., 2021	25
Not specified	Norton, 1988; Dubeux Jr et al., 2017; Isbell et al., 2017; Reed et al., 2017; Amin et al., 2018; Barrios et al., 2018; Kay et al., 2018; Kuyah et al., 2018; Roy et al., 2018; Sollen-Norrlin et al., 2020	10
Abiotic	Ushiyama et al., 2009; Du et al., 2019	2
Birds	Peters, 2014	1

Table S6. Main pollinator species observed by the authors. Note that studies may appear several times in this table since there may have been more than one main pollinator species per study.

Organism	Family[1]	Species[1]	References	Number of published papers
Bees	-	-	Olschewski et al., 2006; Bos et al., 2007a; Perfecto et al., 2007; Klein et al., 2008; Tscharntke et al., 2011; Peters 2014; Bentrup et al., 2019	7
	Andrenidae	-	Moisan-DeSerres et al., 2015; Staton et al., 2019	2
		Andrena sp.	Norfolk et al., 2016	1
		Andrena barbilabris	Kay et al., 2020	1
		Andrena flavipes	Kay et al., 2020	1
		Andrena labialis	Varah et al., 2020	1
		Andrena vaga	Kay et al., 2020	1
		Andrena wilkella	Varah et al., 2020	1
	Apidae	-	Klein et al., 2003b; Klein et al., 2003c; Hoehn et al., 2008; Hoehn et al., 2010; Jha & Vandermeer, 2010; Peters et al., 2013; Moisan-DeSerres et al., 2015; Matos et al., 2016; Hass et al., 2018; Chain-Guadarrama et al., 2019; Staton et al., 2019	11
		Apis spp.	Ya, 2000; Sridhar & Vinesh, 2016	2
		Apis cerana	Klein et al., 2003a; Boreux et al., 2013a; Boreux et al., 2013b; Gaira et al., 2016; Krishnan et al., 2018; Magrach et al., 2019	6
		Apis dorsata	Klein et al., 2003a; Klein et al., 2008; Boreux et al., 2013a; Boreux et al., 2013b; Krishnan et al., 2018; Pavageau et al., 2018; Magrach et al., 2019	7
		Apis florea	Krishnan et al., 2018	1
		Apis mellifera	Marco Jr & Coelho, 2004; Veddeler et al., 2006; Perfecto et al., 2007; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Dáttilo et al.,	23

			2012; Peters & Carroll, 2012; Peters et al., 2013; Classen et al., 2014; Samnegård et al., 2014; Amin et al., 2015; Berecha et al., 2015; Bravo-Monroy et al., 2015; Norfolk et al., 2016; Caudill et al., 2017; Lassen et al., 2018; Geeraert et al., 2019; Prado et al., 2019; Delaney et al., 2020; Galbraith et al., 2020; Cuevas et al., 2021; Prado et al., 2021; Staton et al., 2021	
		Apis nigrocinta	Klein et al., 2003a	1
		Anthophora spp.	Norfolk et al., 2016	1
		Anthophora furcata	Varah et al., 2020	1
		Anthophora marginata	Cuevas et al., 2021	1
		Bombus spp.	Gaira et al., 2016; Sridhar & Vinesh, 2016; Staton et al., 2019; Varah et al., 2020; Cuevas et al., 2021	5
		Braunsapis spp.	Delaney et al., 2020	1
		Cephalotrigona capitata	Veddeler et al., 2006	1
		Ceratina spp.	Jha & Vandermeer, 2009a; Galbraith et al., 2020; Neto et al., 2021	3
		Ceratina eximia	Jha & Vandermeer, 2009a	1
		Ceratina ignara	Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b	2
		Ceratina trimaculata	Jha & Vandermeer, 2009b	1
		Compsomelissa spp.	Delaney et al., 2020	1
		Compsomelissa borneri	Lassen et al., 2018	1
		Epicharis spp.	Galbraith et al., 2020	1
		Euglossa spp.	Galbraith et al., 2020	1
		Eulaema cingulata	Jha & Vandermeer, 2009a	1
		Exomalopsis spp.	Peters et al., 2013	1
		Heterotrigona	Klein et al., 2003a	1
		Hypotrigona spp.	Lassen et al., 2018	1
		Hypotrigona gribodoi	Munyuli, 2014a	1
		Hypotrigona ruspoli	Delaney et al., 2020	1
		Lepidotrigona terminata	Klein et al., 2003a	1
		Liotrigona bottegoi	Lassen et al., 2018	1

		Melipona spp.	Prado et al., 2019	1
		Melipona beecheii	Jha & Vandermeer, 2009a	1
		Melipona mimetica	Veddeler et al., 2006	1
		Meliponula ferrugínea	Munyuli, 2014a	1
		Meliponula nebulata	Munyuli, 2013	1
		Nannotrigona mellaria	Veddeler et al., 2006	1
		Nannotrigona perilampoides	Veddeler et al., 2006	1
		Nannotrigona testaceicornis	Jha & Vandermeer, 2009a	1
		Oxytrigona mediorufa	Fierro et al., 2012	1
		Partamona peckolti	Veddeler et al., 2006	1
		Plebeia	Jha & Vandermeer, 2009a	1
		Plebeia frontalis	Jha & Vandermeer, 2009b	1
		Scaptotrigona spp.	Dáttilo et al., 2012	1
		Scaptotrigona mexicana	Jha & Vandermeer, 2009a; Fierro et al., 2012	2
		Scaptotrigona pectoralis	Fierro et al., 2012	1
		Tetragonisca	Dáttilo et al., 2012	1
		Tetragonisca angustula	Marco Jr & Coelho, 2004; Veddeler et al., 2006; Fierro et al., 2012; Caudill et al., 2017	4
		Tetragonula biroi	Barrera Jr et al., 2021	1
		Tetragonula iridipennis	Boreux et al., 2013a; Boreux et al., 2013b; Krishnan et al., 2018; Magrach et al., 2019	4
		Trigona spp.	Dáttilo et al., 2012; Prado et al., 2019; Galbraith et al., 2020	3
		Trigona almathea	Veddeler et al., 2006	1
		Trigona fulviventris	Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Fierro et al., 2012	3
		Trigona spinipes	Marco Jr & Coelho, 2004	1
		Trigonisca schulthessi	Jha & Vandermeer, 2009b	1
		Xylocopa spp.	Marco Jr & Coelho, 2004; Galbraith et al., 2020	2
		Xylocopa pubescens	Amin et al., 2015	1
		Xylocopa sulcatipes	Norfolk et al., 2016	1
		Xylocopa tabaniformis	Jha & Vandermeer 2009a	1
	Colletidae	-	Moisan-DeSerres et al., 2015; Staton et al., 2019	2

	Halictidae	-	Klein et al., 2003b; Klein et al., 2003c; Hoehn et al., 2008; Jha & Vandermeer, 2010; Peters et al., 2013; Moisan-DeSerres et al., 2015; Hass et al., 2018; Staton et al., 2019	8
		Augochlora aurifera	Jha & Vandermeer, 2009a	1
		Augochlora nigrocyanea	Jha & Vandermeer, 2009a	1
		Chloralictus spp.	Marco Jr & Coelho, 2004	1
		Dialictus spp.	Jha & Vandermeer, 2009a; Neto et al., 2021	2
		Halictus spp.	Jha & Vandermeer, 2009a	1
		Halictus hesperus	Jha & Vandermeer, 2009a	1
		Lassioglossum spp.	Delaney et al., 2020	1
		Lasioglossum (*Evylaeus*) spp.	Cuevas et al., 2021	1
		Thectochlora alaris	Neto et al., 2021	1
	Megachilidae	-	Klein et al., 2003b; Klein et al., 2003c; Hoehn et al., 2008; Peters et al., 2013; Moisan-DeSerres et al., 2015; Matos et al., 2016; Hass et al., 2018; Staton et al., 2019	8
		Chelostema florisomne	Kay et al., 2020	1
		Chelostema rapunculi	Kay et al., 2020	1
		Heriades spp.	Klein et al., 2003a	1
		Heriades fulvescens	Klein et al., 2004	1
		Megachile spp.	Klein et al., 2002; Sridhar & Vinesh, 2016	2
		Megachile atrata	Klein et al., 2003a	1
		Megachile terminalis	Klein et al., 2002	1
		Osmia spp.	Varah et al., 2020	1
	Melittidae	*Melitta leporina*	Varah et al., 2020	1
Wasps	-	-	Bos et al., 2007a; Schüepp et al., 2012; Peters, 2014; Bentrup et al., 2019	4
	Chrysididae	-	Matos et al., 2016	1
	Crabronidae	-	Matos et al., 2016	1
	Sphecidae	*Chalybion bengalense*	Klein et al., 2002	1
		Pison spp.	Klein et al., 2002	1
		Trypoxylon spp.	Klein et al., 2002	1
	Vespidae	*Antherhyncium fulvipenne*	Klein et al., 2002	1
		Epsilon manifestum	Klein et al., 2002	1

		Rhyncium haemorrhoidale	Klein et al., 2002	1
		Rhyncium atrum	Klein et al., 2002	1
		Subancistrocerus clavicornis	Klein et al., 2002	1
		Vespa vulgaris	Jha & Vandermeer, 2009b; Amin et al., 2015	2
Ants	Formicidae	*Technomyrmex* spp.	Toledo-Hernández et al., 2021	1
		Azteca instabilis	Philpott et al., 2006	1
		Azteca sp.	Philpott et al., 2006	1
		Brachymyrmex spp.	Philpott et al., 2006	1
		Camponotus senex textor	Philpott et al., 2006	1
		Crematogaster sp.	Philpott et al., 2006	1
		Dolichoderinae sp.	Philpott et al., 2006	1
		Pheidole sp.	Philpott et al., 2006	1
		Solenopsis germinata	Philpott et al., 2006	1
		Solenopsis sp.	Philpott et al., 2006	1
		Wasmannia auropunctata	Philpott et al., 2006	1
Diptera	-	-	Tscharntke et al., 2011; Young & Hunter, 2018; Bentrup et al., 2019	3
	Callophoridae	*Calliphora erythrocephala*	Amin et al., 2015	1
	Ceratopogonidae	-	Bos et al., 2007b; Sporn et al., 2007; Klein et al., 2008; Groeneveld et al., 2010; Frimpong et al., 2011; Toledo-Hernández et al., 2017; Arnold et al., 2018; Morel et al., 2019	8
		Forcipomyia spp.	Vanhove et al., 2020	1
	Muscidae	*Musca domestica*	Amin et al., 2015	1
	Sciaridae	-	Toledo-Hernández et al., 2021	1
	Syrphidae	-	Classen et al., 2014; Varah et al., 2020	2
		Allobaccha brevis	Geeraert et al., 2019	1
		Eristalinus aeneus	Norfolk et al., 2016	1
		Eristalinus quinquelineatus	Geeraert et al., 2019	1
		Eristalis spp.	Cuevas et al., 2021	1
		Eupeodes corrolae	Norfolk et al., 2016	1
		Syrphus spp.	Amin et al., 2015; Cuevas et al., 2021	2
	Tabanidae	*Tabanus* spp.	Amin et al., 2015	1
Coleoptera	Scarabaeidae	*Tropinota* spp.	Norfolk et al., 2016; Bentrup et al., 2019	2
Lepidoptera	-	-	Munyuli, 2012a; Munyuli, 2012b; Classen et al., 2014;	5

			Peters, 2014; Bentrup et al., 2019	
	Pieridae	*Colias eurytheme*	Amin et al., 2015	1
Hummingbirds	Trochilidae	-	Peters, 2014	1
Wind	-	-	Du et al., 2019	1

[1] Hyphen (-) indicates that the species and/or family was not specified and only a higher taxonomic level was described.

Table S7. Agroforestry management practices. Note that studies may appear several times in this table since there may have been more than one type of management practice per study.

Type of management	References	Number of published papers
Organic	Philpott et al., 2006; Veddeler et al., 2006; Peters & Carroll et al., 2012; Peters et al., 2013; Peters, 2014; Samnegård et al., 2014; Bravo-Monroy et al., 2015; Norfolk et al., 2016; Caudill et al., 2017; Varah et al., 2020; Staton et al., 2021	11
Non-organic	Groeneveld et al., 2010; Frimpong et al., 2011; Classen et al., 2014; Samnegård et al., 2014; Geeraert et al., 2019; Prado et al., 2019; Galbraith et al., 2020; Kay et al., 2020; Vanhove et al., 2020; Cuevas et al., 2021	10
Not specified	McAneney et al., 1984; Klein et al., 2003a; Klein et al., 2003b; Klein et al., 2003c; Klein et al., 2004; Marco Jr & Coelho, 2004; Olschewski et al., 2006; Bos et al., 2007a; Bos et al., 2007b; Priess et al., 2007; Sporn et al., 2007; Hoehn et al., 2008; Tylianakis et al., 2008; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Ushiyama et al., 2009; Hoehn et al., 2010; Jha & Vandermeer, 2010; Dáttilo et al., 2012; Fierro et al., 2012; Munyuli, 2012a; Munyuli, 2012b; Schüepp et al., 2012; Boreux et al., 2013a; Boreux et al., 2013b; Munyuli, 2014a; Amin et al., 2015; Berecha et al., 2015; Moisan-DeSerres et al., 2015; Gaira et al., 2016; Matos et al., 2016; Fisher et al., 2017; Amin et al., 2018; Arnold et al., 2018; Hass et al., 2018; Kay et al., 2018; Krishnan et al., 2018; Lassen et al., 2018; Pavageau et al., 2018; Young & Hunter, 2018; Du et al., 2019; Magrach et al., 2019; Morel et al., 2019; Delaney et al., 2020; Barrera Jr et al., 2021; Neto et al., 2021; Prado et al., 2021; Tarigan et al., 2021; Toledo-Hernández et al., 2021	49

Table S8. Effects of agroforestry management on pollination services. Note that studies may appear several times in this table since more than one management practice may have been evaluated per study.

No.	Agroforestry management practice	Pollination service	Effect*	References	Number of published papers
1	Increased shade-tree cover	Pollinator diversity	+	Bos et al., 2007a; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2009b; Jha & Vandermeer, 2010; Samnegård et al., 2014; Bravo-Monroy et al., 2015; Delaney et al., 2020; Toledo-Hernández et al., 2021	8
			=	Caudill et al., 2017	1
			–	Klein et al., 2003b	1
		Pollinator behavior	+	Klein et al., 2004	1
		Pollinator traits	–	Klein et al., 2004	1
		Crop production	+	Amin et al., 2015	1
2	Increased local floral resources	Pollinator diversity	+	Klein et al., 2003c; Veddeler et al., 2006; Tylianakis et al., 2008; Jha & Vandermeer, 2009a; Jha & Vandermeer, 2010; Peters et al., 2013; Samnegård et al., 2014; Gaira et al., 2016; Norfolk et al., 2016; Caudill et al., 2017; Arnold et al., 2018; Staton et al., 2021; Toledo-Hernández et al., 2021	13
		Crop production	+	Gaira et al., 2016; Norfolk et al., 2016; Staton et al., 2021	3
			=	Staton et al., 2021	1
3	Increased crop management intensity	Pollinator diversity	=	Cuevas et al., 2021	1
			–	Klein et al., 2002; Berecha et al., 2015; Geeraert et al., 2019	3
		Crop production	–	Bos et al., 2007b; Priess et al., 2007; Munyuli, 2014a; Geeraert et al., 2019	4
4	Reduced distance of the agroforestry fragment to a nearby natural forest	Pollinator diversity	+	Klein et al., 2003b; Klein et al., 2003c; Boreux et al., 2013a; Bravo-Monroy et al., 2015; Moisan-DeSerres et al., 2015	5
			=	Frimpong et al., 2011	1
		Crop production	+	Klein et al., 2003c; Boreux et al., 2013a; Bravo-Monroy et al., 2015	3
			=	Frimpong et al., 2011; Krishnan et al., 2018	2
5	Increased irrigation	Pollinator diversity	+	Boreux et al., 2013b; Krishnan et al., 2018	2
6	Increased rainfall	Pollinator diversity	+	Amin et al., 2018	1
		Crop production	–	Peters & Carroll, 2012	1

7	Increased pollinator management	Crop production	+	Klein et al., 2003a; Groeneveld et al., 2020; Lassen et al., 2018	3
8	Addition of organic inputs	Crop production	+	Young & Hunter, 2018; Morel et al., 2019; Vanhove et al., 2020	3
9	Type of windbreak	Pollen dynamics	NA[2]	McAneney et al., 1984; Du et al., 2019; Ushiyami et al., 2019	3

[1] Effect indicates an increment (+), reduction (–), or no effect (=) in the pollination service in response to each agroforestry management practice. In the case of the traits, signs represent the direction of the modification in a way to become suitable for better and worse pollination efficiency or quality, respectively.

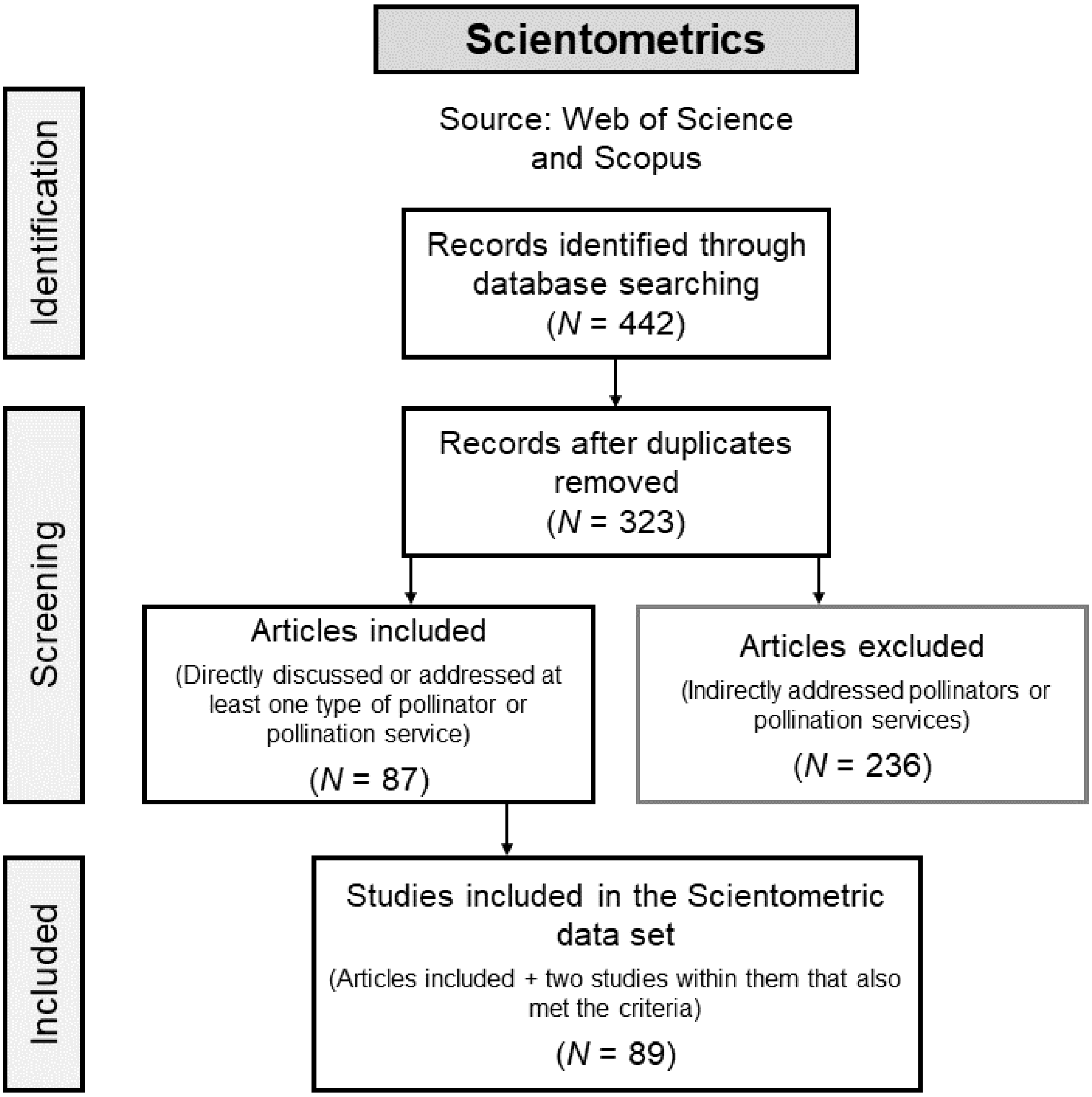
[2] Not applicable.

Table S9. Effects of agroforestry systems versus conventional agroecosystems on pollination services. Note that studies may appear several times in this table since effects on more than one pollination variable may have been evaluated per study.

No.	**Pollination service**		**Effect***	**References**	**Number of published papers**
1	Pollinator diversity		+	Hoehn et al., 2010; Munyuli, 2012b; Varah et al., 2020; Neto et al., 2021	4
			=	Matos et al., 2016; Tarigan et al., 2021	2
			–	Galbraith et al., 2020	1
2	Pollination services	Pollinator behavior	+	Fierro et al., 2012; Kay et al., 2018; Pavageau et al., 2019; Kay et al., 2020	4
		Plant traits	+	Prado et al., 2019; Kay et al., 2020	2
		Pollen dynamics	–	Barrera Jr et al.., 2021	1
		Crop production	+	Philpott et al. 2006; Varah et al., 2020	2
			=	Hoehn et al., 2008	1
			–	Olscheweski et al., 2006	1

*Positive (+), negative (–) or neutral (=) effects indicate a higher, lower, or similar, respectively, pollination service in agroforestry systems in comparison with conventional agroecosystems. In the case of the traits, represents the direction of the modification in a way to become more or less suitable for pollination efficiency or quality, respectively, in agroforestry systems in comparison with conventional agroecosystems.

Fig. S1. Flow diagram representing the body of literature examined in this review of pollination dynamics in agroforestry systems, including the source counts when filtering our findings and establishing the final dataset. Search arguments used in the Web of Science and Scopus: (1) agroforest* AND pollinat*; (2) windbreak* AND pollinat*; (3) silvopast* AND pollinat*; (4) “alley cropping” AND pollinat*; (5) “forest farming” AND pollinat*. This diagram is based on The PRISMA Statement: Preferred Reporting Items for Systematic Reviews and Meta-Analyses (*sensu* Moher et al. 2009; http://www.prisma-statement.org/PRISMAStatement/FlowDiagram).



4. CAPÍTULO 2: Shaping pollinator diversity through coffee agroforestry management: A meta-analytical approach

Diego Centeno-Alvarado, Ariadna Valentina Lopes, Xavier Arnan

https://doi.org/10.1111/icad.12755

Insect Conservation and Diversity:

- Qualis CAPES (Classificações de periódicos quadriênio 2017-2020: Biodiversidade): A2
- Impact Factor: 3.5
- Percentile SCOPUS: 92%

Received: 19 October 2023 | Accepted: 7 May 2024
DOI: 10.1111/icad.12755

REVIEW

Insect Conservation and Diversity
Royal Entomological Society

Shaping pollinator diversity through coffee agroforestry management: A meta-analytical approach

Diego Centeno-Alvarado[1] | Ariadna Valentina Lopes[2] | Xavier Arnan[1,3]

[1]Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife, Brazil

[2]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Brazil

[3]Universidade de Pernambuco, Garanhuns, Brazil

Correspondence
Diego Centeno-Alvarado, Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife, PE, 52171-900, Brazil.
Email: centenoalvaradodiego@gmail.com

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Numbers: 309505/2018-6, 307385/2020-5; Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco, Grant/Award Number: IBPG-0068-2.05/21

Editor: Manu Saunders and Associate Editor: Bethanne Bruninga-Socolar

Abstract

1. Pollinator diversity plays an important role in improving the resilience of pollination services. However, agricultural intensification is causing declines in pollinator diversity. Such losses could be mitigated and even reversed by agroforestry systems, whose structural complexity exceeds that of intensive agricultural systems. Research, primarily conducted in tropical regions, suggests that efficiently managing agroforestry systems can increase pollinator diversity.
2. We performed a global meta-analysis to explore how coffee agroforestry management practices affect the diversity of bee pollinators. We employed 137 sets of results from 20 studies that had been conducted at widely distributed locations across four of the seven continents. More specifically, we investigated the impact of augmenting floral resources (60 sets of results) and shade-tree cover (43 sets of results) and reducing the distance to natural forests (34 sets of results). Additionally, we examined key moderating factors, including climatic conditions, pollinator sociality, the metrics used to describe pollinator diversity, pollinator sampling methods, the metrics used to characterise the effects of management practices and floral resource type.
3. We observed that bee pollinator diversity broadly increased as local floral resources increased in tropical coffee agroforestry systems. Shade-tree cover and proximity to natural forests did not broadly influence bee pollinator diversity. However, the strength and direction of the relationships between the agroforestry management practices and bee pollinator diversity were moderated by different factors, mainly climatic conditions and pollinator sociality.
4. Our findings underscore the importance of managing coffee agroforestry systems to maximise bee diversity, which is crucial for coffee plant pollination. The broader objective should be to ensure the availability of resources that promote pollinator fitness, effective pollination and, as a consequence, crop yields.

KEYWORDS
agricultural management, agroecological systems, ecosystem services, pollination services, pollinator habitat enhancement

INTRODUCTION

Ecosystem services are ecological processes that create conditions and resources that sustain and benefit human populations (Burkhard et al., 2012; Díaz et al., 2018; Fu et al., 2013). Socioeconomic systems rely on these services, which furnish food, fibres, drinking water and clean air, all essential elements of human health and well-being (Burkhard et al., 2012; Fu et al., 2013; Häyhä & Franzese, 2014). Pollination is an ecosystem service of enormous economic value—approximately 75% of food crops and 90% of wild flowering plants worldwide require some degree of animal pollination (e.g., Ollerton et al., 2011; Potts et al., 2016). Most pollinated food crops depend largely on the activity of bees (Hymenoptera: Apiformes) (e.g., Klein et al., 2007). The European honey bee (*Apis mellifera* L.) in particular is often assumed to play a key role, given that it is a highly effective and globally distributed pollinator with a long domestication history (Papa et al., 2022). However, this assumption may not always hold true. Indeed, it might be risky to rely exclusively on a single species for pollination services. For example, honey bees are important pollinators but are also frequently exposed to chemical pesticides, parasites and pathogens (Abay et al., 2023; Henry et al., 2012). Furthermore, the contributions made by wild pollinators are often vastly underestimated, even though these species provide the majority of pollination services for crop and non-crop species alike (Breeze et al., 2011; Garibaldi et al., 2013; Hutchinson et al., 2021). Additionally, wild pollinators can greatly enhance crop quality and quantity (Klein et al., 2007; Oldroyd, 2012; Winfree et al., 2011).

The recent burgeoning demand for food, fibres and fuels has resulted in agricultural intensification worldwide, leading to the transformation and fragmentation of natural ecosystems (Gibbs et al., 2010; Sabino et al., 2022). High levels of agrochemicals, dramatic modifications to natural systems, the acceleration of climate change and pronounced habitat loss are among the factors driving declines in the abundance and richness of wild pollinators (Aizen et al., 2008; Potts et al., 2016). Although the resulting risks and impacts may vary geographically, knowledge remains spotty for certain regions (Dicks et al., 2021; Potts et al., 2016), and farmers, companies and policymakers lack clear guidance when it comes to effective management practices (Russillo & Pintér, 2009). First, most records come from North America and northwestern Europe, whereas fewer data are available for Latin America, Africa, Asia and Oceania (Potts et al., 2016). Second, much more general and specific information is needed regarding how to implement effective management practices (e.g., decisions around the density and type of floral resources or trees, and the maximum distance to natural vegetation) (Russillo & Pintér, 2009). It is necessary to preserve natural habitats through sustainability-oriented public policies in order to safeguard pollinator biodiversity and food production (Koch et al., 2019; Sabino et al., 2022).

Pollinators have highly active lifestyles, and their well-being is dependent on having certain needs met, including access to specific nesting locations, shelter and food resources (Bohart, 1972). To address the ongoing losses of native pollinators, efforts have been made to increase the structural and taxonomic diversity of wild plants and floral resources in crop systems, an approach that has shown great promise (e.g., Isbell et al., 2017). However, such diversity is typically lacking in conventional crop monoculture or intensive livestock systems (Varah et al., 2020). A better solution may lie in agroforestry systems, in which trees or shrubs are intentionally incorporated into crop or livestock systems, thus generating positive impacts on the environment, economy and society (Food and Agriculture Organization of the United Nations, 2017; United States Department of Agriculture (USDA), 2019). Agroforestry systems are more structurally complex than intensively farmed landscapes (Varah et al., 2020) and can, therefore, provide nests, shelter and food for pollinators while simultaneously furnishing humans with fruits, nuts and timber, in addition to other products and services (Varah et al., 2020). Furthermore, the broader availability of spatial and temporal resources within agroforestry systems enhances niche complementarity, which fuels ecosystem functioning (Staton et al., 2021). Indeed, compared with intensive agricultural systems, agroforestry systems host greater levels of functional and taxonomic pollinator diversity (Briggs et al., 2013; Hass et al., 2018). Moreover, research on pollination services in agroforestry systems primarily focuses on tropical regions, where the majority of agroforests are found (Centeno-Alvarado et al., 2023; Food and Agriculture Organization of the United Nations, 2020; Kletty et al., 2023). Coffee agroforestry systems prevail as the most common agroforestry crop in the tropics (e.g., Centeno-Alvarado et al., 2023; Food and Agriculture Organization of the United Nations, 2022). In addition, coffee crops offer benefits like climate resilience, price stability and high profitability (Centeno-Alvarado et al., 2023; Food and Agriculture Organization of the United Nations, 2022; Somarriba & Lopez-Sampson, 2018; Vaast et al., 2015). Additionally, more diverse pollinator communities enhance coffee harvest volume and quality by boosting outcrossing among plants, which results in larger and more robust fruit (Ricketts, 2004).

A range of management practices can enhance productivity (e.g., biomass and crop yields) in agroforestry systems and conventional agricultural systems alike (Chavan et al., 2018). Crop productivity may be boosted via synergistic strategies (Chavan et al., 2018), notably by addressing deficits in pollinator diversity by tackling constraints on flower visitation (Garibaldi et al., 2016). In particular, past research suggests that pollinator diversity can be increased within coffee agroforestry systems by augmenting local floral resources and shade-tree cover while reducing the distance to natural forests (e.g., Bravo-Monroy et al., 2015; Hipólito et al., 2018). First, high levels of diverse and complementary floral resources encourage the presence of diverse pollinators, including both rare and common species (Centeno-Alvarado et al., 2023; Isbell et al., 2017). Second, increased amounts of shade-tree cover in coffee agroecosystems can improve microclimatic conditions, notably by maintaining more favourable temperatures and reducing wind speed (Lin, 2010), thus facilitating pollinator foraging (Prado et al., 2021). Shade-tree cover could also indirectly amplify pollinator presence by enhancing floral resources. For instance, flower availability in coffee agroecosystems may increase when microclimatic conditions become shadier (Lin, 2008). Additionally, shade trees can provide nesting habitat for certain cavity-nesting pollinators (Gardner et al., 2020). Third, if coffee agroforestry systems are found closer to natural forest, pollinator diversity may be positively affected because the trade-off between food resources and nesting habitat is less dramatic. More specifically, the shorter distance means pollinators do not need to travel as far between foraging areas (i.e., agroforestry systems) and nesting habitats (i.e., natural forest) (Rahimi et al., 2022). While theoretical research has strongly suggested that the above management practices improve pollinator diversity, the evidence from field studies is mixed; some provide support (e.g., Samnegård et al., 2014), whereas others do not (e.g., Klein et al., 2002). Therefore, it is important to comprehensively assess available information on this topic to determine how generalised these patterns are and to identify the factors underlying the variability observed.

Climate and biodiversity can shape how coffee agroforestry management affects pollination services, including pollinator diversity (Byers, 2017; Genung et al., 2017; Krishnan et al., 2018). For instance, temperature and precipitation have major impacts on plant physiology and phenology and, thus, alter plant–pollinator interactions (Descamps et al., 2018; Lawson & Rands, 2019). Furthermore, climate-mediated shifts in nectar volume and sugar concentration can lead to changes in resource attractiveness, modifying pollinator abundance and activity (Descamps et al., 2018; Descamps et al., 2021; Lawson & Rands, 2019). Within coffee agroforestry systems, the primary pollinators are bees (Ngo et al., 2011). The latter are affected by management practices in variable ways depending on their degree of sociality, which shapes responses to environmental change (Antoine & Forrest, 2020; Grüter & Hayes, 2022; Gutiérrez-Chacón et al., 2018; Klein et al., 2008; Wcislo & Fewell, 2017). For example, during mass flowering events, social bees predominate because they communicate extensively and recruit numerous nestmates; in contrast, when individual coffee plants are flowering, solitary bees are more common (Klein et al., 2008). The pruning of shade trees may also affect these groups differently: eusocial bees often nest aboveground (e.g., in tree cavities), whereas many solitary bees nest on the ground, with some preferring exposed habitats (Antoine & Forrest, 2020; Gutiérrez-Chacón et al., 2018; Wcislo & Fewell, 2017). Additionally, social bees tend to forage over longer distances than do solitary bees, which means that greater distances between natural forests and agroforestry sites may pose less of a challenge to social bees (Grüter & Hayes, 2022). Also, the varying facets of pollinator diversity may not be affected in similar ways by environmental changes, given that ecological drivers operate at contrasting spatial scales. For example, pollinator richness can be explained at finer scales, by factors such as local floral resources and nesting habitat, while pollinator abundance can be explained at coarser scales, by factors such as canopy cover (Grundel et al., 2010; Shackelford et al., 2013).

In addition, the sampling method chosen can influence the relationship seen between management practices and pollination. Passive methods, namely pan traps and trapping at nests, can sample a broad range of pollinators; however, they do not provide specific information about the associations between pollinators and flowers (Hutchinson et al., 2021; Westphal et al., 2008). Active methods, including observations within plots or along transects, yield direct data on pollinators and floral visits and, therefore, provide more reliable information on pollination effectiveness (Garibaldi et al., 2019; Hutchinson et al., 2021). Furthermore, different studies may use different metrics to quantify the effects of management practices. For example, local floral resources and shade-tree cover may be measured in different ways, as illustrated by studies that have characterised local floral resources in cocoa plantations (a similarly structured system to coffee agroforests) using the number of flowering plants versus the mean number of flowers (e.g., Bravo-Monroy et al., 2015; Toledo-Hernández et al., 2021) or others that have quantified shade-tree cover employing either light intensity or percent canopy cover (e.g., Klein et al., 2002; Samnegård et al., 2014). Such variation in methodology can affect research conclusions. Finally, increasing different types of floral resources within a given area (i.e., the target crop versus complementary flowers) might have different implications for pollinators and plants. On the one hand, increasing the number of crop flowers can attract more pollinators, resulting in better crop pollination and, potentially, higher yields (e.g., Boreux, Kushalappa, et al., 2013). On the other hand, increasing the number of complementary flowers by boosting flowering plant diversity can provide additional resources for pollinators, especially when the target crop is not in bloom (e.g., Winfree et al., 2007).

In this study, we used a global meta-analysis to assess how coffee agroforestry management practices influence pollinator diversity. We tested the following hypotheses: (1) higher levels of local floral resources (i.e., abundance and diversity) should increase pollinator diversity (i.e., richness and abundance) by increasing foraging opportunities; (2) greater amounts of shade-tree cover should increase pollinator diversity by increasing the availability of sheltering and nesting sites and (3) shorter distances to natural forests should increase pollinator diversity by increasing habitat connectivity. We also explored how different factors moderate the relationship observed between coffee agroforestry management practices and pollinator diversity. We focused on climate (i.e., mean annual temperature and precipitation), pollinator sociality (i.e., social or solitary), the pollinator diversity metric (i.e., richness or abundance), pollinator sampling methods (i.e., passive or active), the metric used to characterise local floral resources (e.g., number of flowers or inflorescences), the metric used to characterise shade-tree cover (e.g., percent canopy cover or light intensity) and floral resource type (i.e., coffee plant flowers or complementary flowers).

MATERIALS AND METHODS

Literature search, study selection and data extraction

Meta-analyses are becoming increasingly common in ecology and evolution because they use powerful, informative and unbiased tools to identify trends and summarise results from different studies on the same topic (Koricheva & Gurevitch, 2013). Our meta-analysis began with a systematic search of references in the Web of Science (administered by Clarivate Analytics) and Scopus (administered by Elsevier). We adopted the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) protocol (sensu Moher et al., 2009: www.prisma-statement.org/PRISMAStatement/FlowDiagram) (Figure S1). Specifically, we compiled published studies evaluating the influence of coffee agroforestry management practices on pollinator diversity, richness (i.e., number of species) and abundance (i.e., number of individuals). We exclusively focused on bees because they are the most common and effective pollinators of coffee plants (Ngo et al., 2011; Imbach et al., 2017). Hereafter, we use the term pollinator diversity to refer solely to bee diversity. We also looked at whether there was an effect of methodology (i.e., passive methods, such as flight, pan, vane, or malaise traps, versus active methods, such as visual observations and counts, sweep netting, or net sampling). We centred our analysis on the following coffee agroforestry practices: (1) managing the abundance and diversity of local floral resources; (2) managing levels of shade-tree cover and (3) modifying the distance to natural forests. They consequently became the focus of our analyses.

We employed a Boolean search with the following arguments and terms (appearing in the title, keywords, and/or abstract): (1) agroforest* AND pollinat*, (2) 'forest farming' AND pollinat*, (3) silvopast* AND pollinat* and (4) coffee* AND pollinat*. The terms 'forest farming' and silvopast* (referring to silvopasture or silvopastoral systems) were included to broaden the search results, as they refer to different types of coffee agroforestry systems (Atangana et al., 2014; Cardinael et al., 2015; Jose & Dollinger, 2019; Mosquera-Losada et al., 2009). Our search covered a timespan from the earliest available digital records through January 2023; we applied no language restrictions.

The search returned a total of 635 individual studies, of which 20 met our criteria for inclusion in the meta-analysis (Figure S1; Appendix S1): they evaluated the effects of local floral resources (e.g., number of flowers or inflorescences), shade-tree cover (e.g., percent canopy cover) and/or distance to natural forests (e.g., in meters) on pollinator diversity (i.e., richness and/or abundance) in coffee agroforestry systems. For each publication, we extracted certain types of data. We treated the management practices as explanatory variables and pollinator diversity as the response variable. In studies where management practices were ordinally classified (e.g., low vs. high levels of shade-tree cover), we noted the sample size for each management practice class and the mean and dispersion of pollinator diversity. In studies where management practices were described by continuous values, we noted R^2, F statistic, or T statistic and total sample size for the regression analyses and the correlation coefficient and total sample size for correlation analyses. When studies only reported their values graphically, we extracted the relevant data using the package *metaDigitise* (v. 1.0; Pick et al., 2019, 2020) in R (v. 4.1.3; R Core Team, 2022). We also collected information about study site location (i.e., using the geographical coordinates indicated in the study or location name) and about potential moderating factors: pollinator sociality (i.e., social or solitary), the pollinator diversity metric used (i.e., richness and/or abundance), pollinator sampling methods (i.e., passive or active methods [explained above]), the metric used to characterise local floral resources within the agroforestry area (i.e., percentage of flowers, number of flowers or inflorescences, number of individuals flowering, or number of sites flowering), the metric used to characterise shade-tree cover (i.e., percent canopy cover, light intensity, shade-tree composition or forest index [based on variables reflecting shade-tree structure]) and floral resource type (i.e., coffee plant flowers or complementary flowers from herbs, shrubs and/or trees). Certain studies did not classify bees according to their degree of sociality; their results were subsequently excluded from the moderator analyses because this moderating factor was undefined. Other moderating factors were mean annual temperature and precipitation, which we determined for each agroforestry system using the R package *raster* (v. 2.0-12; Hijmans & Etten, 2012) and a 2.5-min spatial resolution (Table S1). Their ranges were 17.2–26.1°C (mean ± standard error: 21.68 ± 0.64°C) and 522–4002 mm (2218.56 ± 247.93 mm), respectively.

Of the 20 studies included in this meta-analysis, some reported more than one set of results. For instance, Klein et al. (2002) evaluated how the percent of coffee plants in flower influenced the abundance of (1) social bees and (2) solitary bees, generating two sets of results. In such situations, we analysed the sets of observations separately. Thus, after extracting all the data from these 20 studies, we had 137 sets of results to include in the meta-analysis.

Statistical analyses

Effect sizes

The above data were transformed into effect sizes, which made it possible to compare results from different studies by placing them on the same scale (Rosenberg et al., 2013). Effect sizes quantitatively describe the direction and magnitude of the relationship between two variables (Harrer et al., 2021). Since coffee agroforestry management practices could be categorical or continuous in nature, we used five approaches to calculate effect sizes: (1) we calculated standardised mean difference or Cohen's *d* (*d*) from categorical means (Formula S1, Appendix S2); (2) we computed Cohen's *d* (*d*) from the *T* statistic from regression analyses (Formula S2, Appendix S2); (3) we calculated Fisher's *z* from the F statistic from regression analyses (Formula S3, Appendix S2); (4) we calculated the correlation coefficient from the R-squared (R^2) from regression analyses (Formula S4, Appendix S2); and (5) we calculated Fisher's *z* from the correlation coefficients (Formula S5, Appendix S2). Finally, to obtain comparable, reliable and interpretable effect sizes, we converted all the effect size measures to Fisher's *z* (Formulae S1–S6, Appendix S2; Table S1), which we considered to be an appropriate metric, given that it measures associations between two continuous variables (Rosenberg et al., 2013). Positive Fisher's *z* values supported our hypotheses: they indicated that higher levels of local floral resources, greater percentages of shade-tree cover, or shorter distances to natural forests promoted pollinator diversity. In contrast, negative Fisher's *z* values indicated the opposite. We also ran three-level meta-analytical random-effects models to capture the degree of between- and within-study dependence among effect sizes (Borenstein et al., 2009).

Meta-analysis using random-effects models

We used a meta-analysis model to determine the general association between each coffee agroforestry management practice and pollinator diversity (i.e., richness or abundance). These models used robust variance estimation, which was implemented via the R package *robumeta* (v. 2.0; Fisher et al., 2017). This method addresses interdependence among effect sizes calculated with data from the same study without underestimating the confidence intervals, and it adjusts the assumed degree of correlation (Hedges et al., 2010). Meta-analysis models estimate an overall effect size from individual effect sizes (Harrer et al., 2021; Li et al., 2018). When effect sizes are highly heterogenous, there may be characteristics or variables that act as moderators—conditioning the direction or strength of the relationship between the explanatory and response variables (Sharma et al., 1981; King, 2013). We, thus, calculated T^2 and I^2 statistics, which quantify the degree of heterogeneity. T^2 expresses variability among effect sizes, and I^2 indicates the proportion of T^2 attributable to true variability, not sampling-error-based variability (Borenstein et al., 2009; Borenstein et al., 2017). When I^2 exceeds 75% (Higgins & Thompson, 2002; Higgins et al., 2003), heterogeneity is high, and moderators should be analysed (Blut et al., 2015).

Sensitivity analysis for publication bias

To address publication bias in our meta-analysis, we adopted the method described by Mathur and VanderWeele (2020a), which can be implemented using the R package *PublicationBias* (Mathur & VanderWeele, 2020b). Publication bias exists when statistically significant findings are more likely to be published than non-significant results, which may lead to incorrect conclusions (Lin & Chu, 2017). The above method performs a meta-analysis using only the studies in which negative or 'non-significant' results were found, which yields a worst-case scenario (i.e., with maximal publication bias; Mathur & VanderWeele, 2020a). When the two sets of results are compared (primary = main model vs. worst case = model assuming maximum publication bias), the analysis indicates the degree to which the non-significant effect sizes are systematically smaller than overall effect sizes. If there is a pronounced degree of difference, the primary results are sensitive to publication bias; if there is little difference, the primary results are robust (Mathur & VanderWeele, 2020a).

Moderator analysis: Boosted regression trees

To test the relative influence of moderators (see list in the section Literature search, study selection and data extraction) on effect size heterogeneity, we performed boosted regression tree (BRT) analyses using the R package *gbm* (v. 2.1.5; Greenwell et al., 2019). We employed the recommended parameter values (Elith et al., 2008): bag fraction = 0.75, cross-validation = 10, tree complexity = 2 and learning rate = 0.001. Because Fisher's *z* is a continuous variable, we used a Gaussian distribution of errors. In BRT analyses, variables are scaled such that their summed influences equal 100, where higher proportional values mean greater influence (Hastie et al., 2009). Before proceeding to BRTs, we assessed whether the climatic variables were correlated using a Pearson product–moment correlation analysis (*r*). Employing a significance threshold of $r > 0.70$, we found no evidence of a correlation ($r = -0.02$, $p = 0.95$). We only performed moderator analyses for meta-analysis models with robust results (i.e., no publication bias) and high levels of variability (I^2 exceeding 75%; Higgins & Thompson, 2002; Higgins et al., 2003). Finally, we simplified the set of predictor moderators by identifying and excluding irrelevant moderators, following the approach outlined by Elith et al. (2008). In this approach, after the model's initial run, the two least important predictor variables are removed, and the model is then re-run. There is considered to be an improvement in model fit if a more parsimonious model results (i.e., the contributions of the remaining predictors shift slightly). Some predictors have only a minimal impact on prediction and are deemed non-informative. To enhance the performance of BRTs, we removed the least important variables from the original model without affecting predictive performance.

RESULTS

The 20 studies included in the meta-analysis had taken place in eight tropical countries located across four of the seven continents, North America, South America, Africa and Asia (Figure 1). The research had been conducted in Mexico (21% of the sets of research results), followed by Costa Rica and Indonesia (19% of sets), Uganda (16% of sets), Ethiopia and India (10% of sets), Colombia (3% of sets) and Ecuador (2% of sets) (Table S1). Several of these countries are among the world's top 10 coffee producers (i.e., ranked as follows: Colombia, Indonesia, Ethiopia, India and Mexico) (Food and Agriculture Organization of the United Nations, 2022). In addition, these studies were conducted at an elevational range (199–2215 m) that is representative of coffee farming conditions (Table S1).

Meta-analysis using random-effects models

In the meta-analysis models, pollinator diversity was significantly positively influenced by local floral resources (average effect size [95% confidence intervals]: 0.17 [0.01–0.33]) but was unaffected by shade-tree cover (−0.06 [−0.27 to 0.15]) and distance to natural forests (0.31 [−0.10 to 0.72]) (Table 1 and Figure 2). The models also revealed that the three management practices displayed a high degree of unexplained variability in effect sizes among studies, which was explored via the moderator analyses (Table S2).

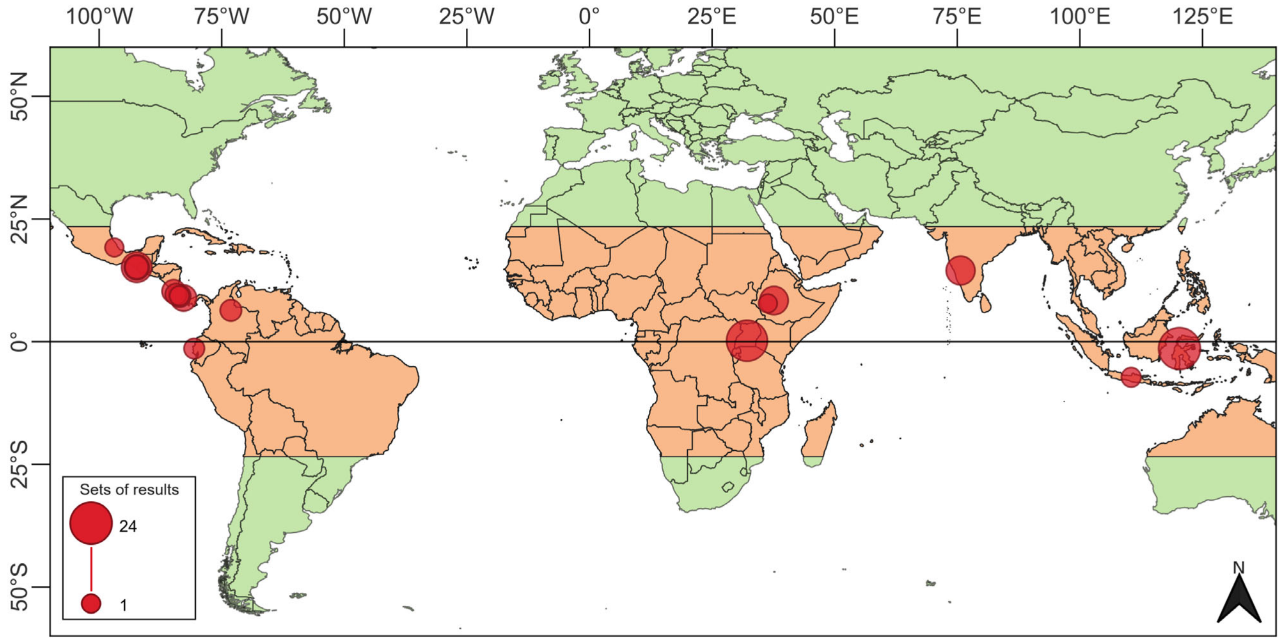


FIGURE 1 Global distribution of the research sites in the 20 studies included in the meta-analysis. The tropics are indicated in orange, while areas outside the tropics are indicated in green. The size of the points represents the number of sets of results per study.

TABLE 1 Results of the primary meta-analysis models and the sensitivity analysis.

	Estimate	SE	95% CI (lower)	95% CI (upper)	*p* value	df[a]
Local floral resources						
Primary	0.17	0.08	0.01	0.33	0.04[a]	13
Sensitivity	0.17	0.06	0.05	0.29	0.01[a]	50.85
Shade-tree cover						
Primary	−0.06	0.10	−0.27	0.15	0.54	11
Sensitivity	−0.06	0.08	−0.22	0.09	0.44	40.54
Distance to natural forests						
Primary	0.31	0.15	−0.10	0.72	0.11	4.91
Sensitivity	0.18	0.08	−0.001	0.36	0.05	23.43

Abbreviations: CI, confidence interval; df, degrees of freedom; SE, standard error.

[a] If the degrees of freedom were greater than or equal to four, the alpha was 0.05. If the degrees of freedom were less than four, the alpha was 0.01, as type I error is usually higher in such cases (sensu Tanner-Smith et al., 2016).

Sensitivity analysis for publication bias

We found no substantial differences between the results of the sensitivity analysis and the results of the primary meta-analysis for the relationship of pollinator diversity with local floral resources, shade-tree cover and distance to natural forests (Table 1). This finding indicates that there was no significant publication-related bias for these three coffee agroforestry management practices.

Moderator analysis: Boosted regression trees

Mean annual temperature was the most important moderator of the relationship between local floral resources and pollinator diversity (relative influence: 35.9%). Other, less significant moderators were pollinator sociality (31.5%), mean annual precipitation (17.6%), the metric used to characterise local floral resources (11.8%) and local floral resource type (3.3%). Pollinator sampling method and the metric used to describe pollinator diversity had no influence on the relationship between pollinator diversity and local floral resources. For temperature, the effect size was positive from 17.2 to 22.9°C and negative from 23.6 to 25.7°C (Figure 3a), which indicates that the impact of increasing local floral resources was negative in environments with higher temperatures. With regards to pollinator sociality, social bees exhibited positive effect sizes, whereas solitary bees exhibited negative effect sizes (Figure 3b). For precipitation, the effect size was negative between 522 and 1250 mm, was positive between 1254 and 2818 mm, dropped to its most negative value at 2938 mm,

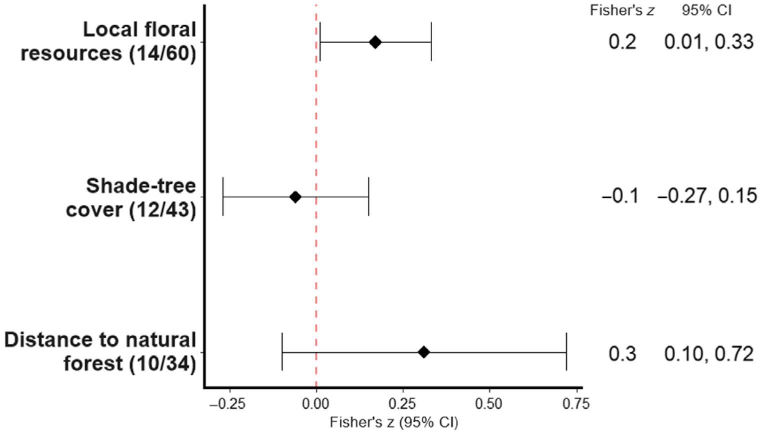


FIGURE 2 Mean effect sizes (Fisher's *z*; represented by squares) and 95% confidence intervals (95% CI; represented by horizontal lines) for each set of results providing information about how pollinator diversity was influenced by local floral resources, shade-tree cover, and the distance to natural forests. The management-related metrics (the number of papers/number of sets of results) are shown in parentheses, and the mean effect sizes (Fisher's *z* and 95% CI values) are on the right. The red dashed vertical line indicates a situation of zero effects.

and then became positive and stable (Figure 3c). In other words, the positive impact of providing more local floral resources was intensified in regions with higher levels of precipitation, up until a certain threshold. Regarding the metric used to characterise local floral resources, the number of individuals flowering had a relatively null effect size (Figure 3d). The effect sizes were negative for flower percentage and number of sites flowering and positive for flower and inflorescence number (Figure 3d). In other words, the increase in pollinator diversity associated with local floral resources was greater when flower or inflorescence number was used as the metric. In contrast, the increase was weaker when flower percentage or number of sites flowering was used. For floral resource type, the effect size was slightly positive for complementary flowers and slightly negative for coffee plant flowers (Figure 3e). In other words, the effect of increasing floral resources is greater when considering complementary flowers and is weaker when considering coffee plant flowers.

With respect to the relationship between shade-tree cover and pollinator diversity, the most important moderator was temperature (58.8%), followed by precipitation (17%), pollinator sociality (12.4%) and the metric used to characterise shade-tree cover (11.8%). The rest of the moderators were considered irrelevant. For temperature, the effect size was negative from 18.6 to 21.5°C, abruptly reached a peak at 22.9°C, and then remained consistently positive (Figure 3f). In short, in areas with higher temperatures, increased shade-tree cover had amplified effects. For precipitation, the effect size decreased as precipitation increased, achieving its most negative value at 2938 mm. It then sharply increased all the way to 3581 mm and subsequently hovered near zero (Figure 2g). In other words, there was less of an effect of increasing shade-tree cover on pollinator diversity in areas with more precipitation (up to 2938 mm). With regards to pollinator sociality, effect sizes were positive for social bees and negative for solitary bees (Figure 3h).

For the relationship between the distance to natural forests and pollinator diversity, the most important moderator was precipitation (50.1%), followed by the metric for describing pollinator diversity (49.9%). None of the other moderators was relevant. For precipitation, the effect size was positive between 614 and 2818 mm; afterward, it became negative, continuing to drop until it reached a minimum stable negative value (Figure 3j). In other words, the effect of increasing proximity to natural forest was diminished in areas with more precipitation.

DISCUSSION

In general, we found that higher levels of local floral resources within coffee agroforestry systems enhanced pollinator diversity (i.e., richness and abundance). This finding aligns with results obtained in other types of agroecosystems (e.g., Staton et al., 2021). In general, the relationship appears to be moderated by (i) temperature, (ii) pollinator sociality, (iii) precipitation, (iv) the metric used to characterise local floral resources and (iv) floral resource type. While past research has found that greater shade-tree cover and proximity to natural forests promote pollinator diversity in different types of agroecosystems (e.g., Carvalheiro et al., 2010; Hipólito et al., 2018), our meta-analysis showed that those coffee agroforestry management practices did not broadly influence pollinator diversity. Notably, the effect of increasing shade-tree cover seemed to depend on (i) temperature, (ii) precipitation, (iii) pollinator sociality and (iv) the metric used to characterise shade-tree cover. In contrast, the effect of the distance to natural forest appeared to be moderated largely by (i) precipitation, and, to a lesser extent, (ii) the metric used to describe pollinator diversity. We expand on these overall findings below.

Local floral resources and pollinator diversity

Boosting local floral resources is an agricultural management strategy that has been shown to improve pollinator habitat suitability in several

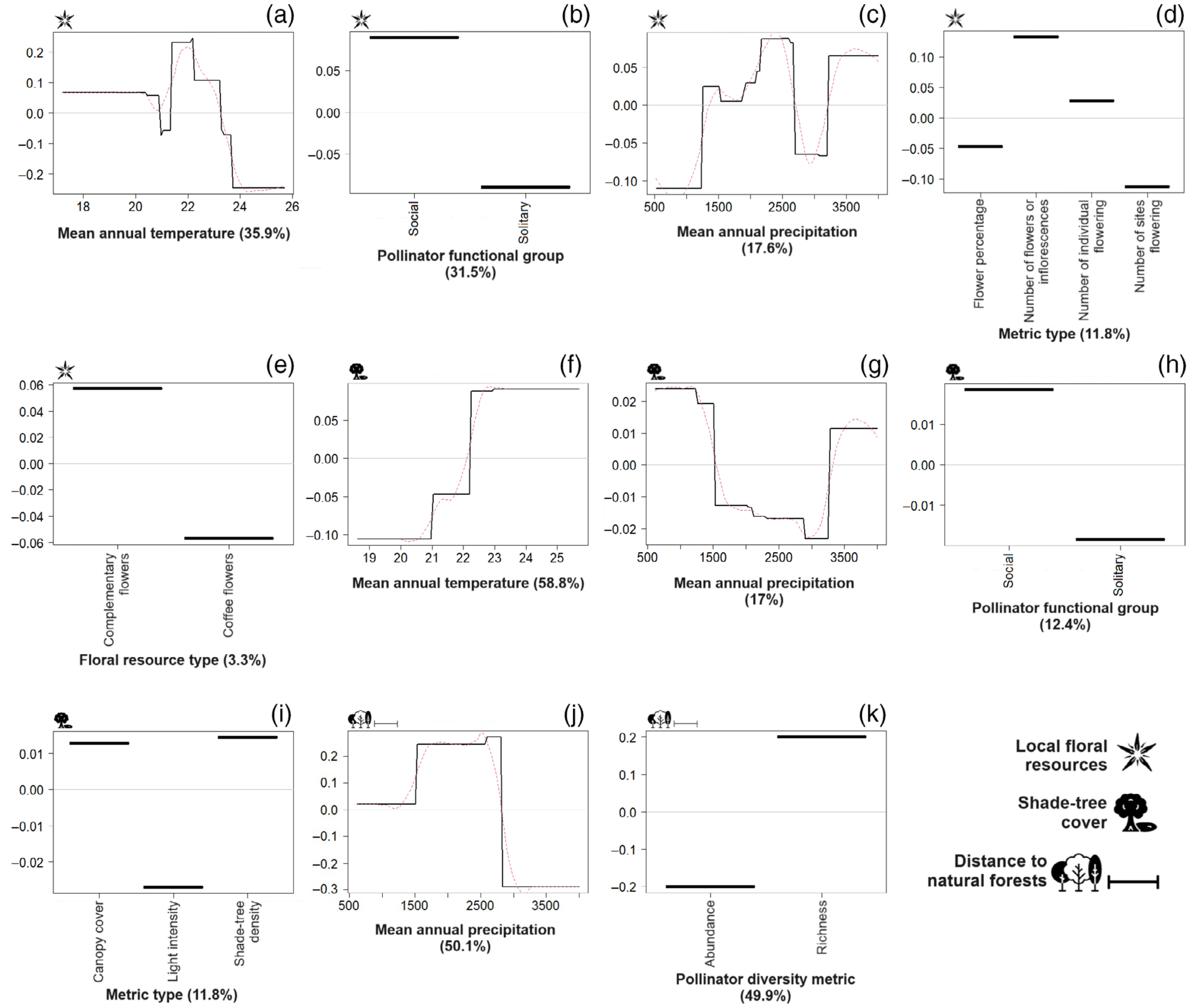


FIGURE 3 Boosted regression tree partial dependence plots showing the contributions of moderators to Fisher's *z* for the relationships of pollinator diversity (i.e., richness and abundance) with local floral resources (a–e), shade-tree cover (f–i), and distance to natural forests (j and k). For continuous moderators, the fitted function is in black, and the smoothed function is in red. For categorical moderators, the lines convey sample density. Moderators that did not contribute to the relationships are not shown.

agroecosystems. It increases pollinator diversity and the number of floral visits; they, in turn, increase the quantity and quality of crop yields (Greenleaf & Kremen, 2006; Wratten et al., 2012). The underlying cause of higher diversity might be increased ecological opportunities since better environmental conditions can lead to the greater availability of fundamental niche space as well as niche discordance, where competing species adopt different patterns of resource usage (Wellborn & Langerhans, 2015; Vacher et al., 2016; Wandrag et al., 2019). Establishing habitats with improved floral resources within or around crop fields expands the range of pollen and nectar sources, enhancing foraging efficacy and pollinator fitness by augmenting colony pollen stores, colony size, pollinator overwintering success and the occurrence of rare species (Wratten et al., 2012). To attract more pollinators, floral resource management should focus on amplifying the spatial continuity of flowers from the focal crop within years and should expand the presence of alternative flowering species (Feltham et al., 2015; Mitchell et al., 2009). Other studies in non-forestry-based agroecosystems have found similar results: increased floral resources fostered pollinator occurrence and diversity in temperate regions (e.g., Brittain et al., 2013; Feltham et al., 2015; Pisanty et al., 2015), tropical regions (e.g., Muñoz et al., 2021) and worldwide (e.g., Eilers et al., 2011). Our study underscores the omnipresence of this relationship, at least for tropical coffee agroforestry systems.

Temperature had the following moderating effects: the association between levels of floral resources and pollinator diversity was negative in warmer regions and positive in colder regions. This pattern might be associated with climate-related shifts in flower development and pollinator behaviour. In warmer areas, increased temperatures could boost flower quantity while reducing flower quality due to heat-induced changes (Descamps et al., 2021; Khodorova & Boitel-Conti, 2013).

These alterations may render floral resources less attractive to pollinators, potentially leading to a decline in pollinator diversity (Descamps et al., 2021). Conversely, in colder regions, the milder temperatures could have positive impacts on both flower quantity and quality (Khodorova & Boitel-Conti, 2013). Consequently, as long as local floral resources remain attractive to pollinators, pollinator diversity should be maintained.

Moderating effects varied for social versus solitary pollinators, potentially as a result of differences in foraging behaviours. For levels of floral resources, there seemed to be a positive effect for social bees, but a negative effect for solitary bees. Social bees can engage in extensive communication, which might have led to the recruitment of numerous individuals during mass flowering events (Klein et al., 2008). In contrast, solitary bees are known to forage and predominate when individual coffee plants are flowering; they consequently may be negatively affected by mass flowering events (Klein et al., 2008).

In the case of precipitation, higher values enhanced the effect of local floral resources on pollinator diversity. This pattern likely arises from the correlation between plant diversity and rainfall (e.g., Yao et al., 2022). Thus, it is reasonable to infer that diverse plant communities yield diverse floral resources. In turn, a greater diversity of floral resources should result in more diverse assemblages of pollinators (e.g., Greenleaf & Kremen, 2006; Wratten et al., 2012). Surprisingly, when mean annual precipitation was between 1254 and 2818 mm, it had a negative influence on the relationship between local floral resources and pollinator diversity, a trend that must be explored in future studies.

The increase in pollinator diversity resulting from local floral resources was greater when the number of flowers or inflorescences was employed as a metric. A weaker effect was seen when flower percentage and number of sites flowering were used as metrics. When the number of flowers or inflorescences is used as a metric, it likely provides a more accurate representation of the actual abundance of floral resources available to pollinators. For instance, the metric ‘percentage of flowers’ refers to the ratio of individual flowering plants in a particular area, among a particular number of individuals, or for another defined group. Furthermore, the metric ‘number of flowering sites’ does not necessarily reveal differences between sites with few flowers versus many flowers.

Finally, floral resource type (i.e., coffee plant flowers vs. complementary flowers) influenced the relationship between local floral resources and pollinator diversity because of the role of floral resource type in supporting pollinators. For example, the presence of a diverse array of complementary flowering plants can have a significant impact on pollinator diversity. These plants often provide additional floral resources necessary for the health and reproductive needs of pollinators, thereby fostering greater diversity (Winfree et al., 2007; Albrecht et al., 2020; Jones & Rader, 2022). In contrast, when we exclusively consider coffee flowers, certain pollinators may exhibit specific preferences for particular flower types. In such cases, a single crop may not offer sufficient resources to sustain its population (Jones & Rader, 2022).

Shade-tree cover and pollinator diversity

Past research has posited that shade-tree cover can promote pollinator diversity by improving microclimatic conditions in agroforestry systems, primarily by moderating temperatures and wind speed (e.g., Corbet et al., 1993; Kwon & Saeed, 2003; DaMatta et al., 2007; Lin, 2010; Prado et al., 2021). We found, however, that shade-tree cover in coffee agroforestry systems did not have a significant overall effect on pollinator diversity. That said, this management practice can have a conditional impact that largely depends on precipitation, temperature and pollinator sociality.

Increasing temperature had a positive influence on the link between shade-tree cover and pollinator diversity (Garcia et al., 2022), likely because of plant physiological responses to warming (Hatfield & Prueger, 2015). Specifically, for equal levels of shade-tree cover, plant growth may be greater (Garcia et al., 2022) in warmer regions compared with cooler regions. This finding underscores that increasing shade-tree cover could help coffee-growing regions adapt to climate change, primarily because increasing shade increases cooling. Useful strategies could include minimising pruning frequency and intensity for existing shade trees, introducing a greater diversity of tree species, or employing a combination of the two (Lara-Estrada et al., 2023). That said, it is crucial to acknowledge that excessive levels of shade may intensify competition among coffee plants, which can adversely affect coffee yields (Lara-Estrada et al., 2023).

Increased levels of precipitation had a negative effect on the relationship between shade-tree cover and pollinator diversity. This pattern could also arise from the correlation between plant diversity and rainfall (e.g., Yao et al., 2022), where more precipitation leads to more floral resources that pollinators can exploit (e.g., Greenleaf & Kremen, 2006; Wratten et al., 2012), regardless of shade-tree cover. Therefore, shade-tree cover may have a lesser impact on pollinator diversity in wetter regions than in drier regions.

The moderating role of pollinator sociality in the relationship between shade-tree cover and pollinator diversity is likely influenced by nesting behaviour. As expected, solitary bees showed negative responses to shade-tree cover, possibly because they tend to be ground nesters with a preference for exposed habitats (Klein et al., 2008; Wcislo & Fewell, 2017; Gutiérrez-Chacón et al., 2018; Antoine & Forrest, 2020). Conversely, social bees, and primarily honey bees, showed positive responses, as they may be attracted by both foraging resources and nesting resources (e.g., tree cavities; Antoine & Forrest, 2020; Gutiérrez-Chacón et al., 2018; Klein et al., 2008; Wcislo & Fewell, 2017).

It is worth considering that shade-tree flowering could underlie the effects of shade-tree cover. However, we could not assess this hypothetical relationship because the studies did not contain information about shade-tree flowering. If this mechanism is at play, it seems likely that the flowering period of the shade trees would overlap with that of the coffee crop, leading to interactive influences. Many shade tree species might also produce flowers that attract bee foragers (e.g., Mach & Potter, 2018), further emphasising the potential impacts of shade trees on pollinator diversity.

Distance to natural forests and pollinator diversity

Some previous studies have suggested that pollinator diversity in agroforestry systems increases as distance to natural forests decreases (Klein et al., 2003a; Klein et al., 2003b; Ricketts, 2004; Boreux, Krishnan, et al., 2013; Bravo-Monroy et al., 2015), whereas others have found no such relationship (Caudill et al., 2017; Toledo-Hernández et al., 2021). Only one showed that the effect was seasonal (Vergara & Badano, 2009). Furthermore, a recent meta-analysis found that pollinator abundance and richness increased in diversified farming systems when the distance from natural and semi-natural habitats was increased (Sánchez et al., 2022). That said, our results indicate that, in the case of coffee agroforestry systems, closer proximity to natural forests did not broadly enhance pollinator diversity. Instead, the effect was moderated by precipitation and the metric used to describe pollinator diversity.

The relationship between distance to natural forests and pollinator diversity may be negatively affected by increased levels of precipitation, which could affect hydrological conditions, and thus habitat quality, in agroforestry systems and adjacent natural areas (Ganuza et al., 2022). Prolonged rainfall can lead to excessive soil moisture (Dai et al., 2022), potentially causing plants to allocate more resources to survival than reproduction, which could lead to reduced numbers of flowers (Dai et al., 2022). Moreover, extreme precipitation events can impose mechanical and energetic constraints on pollinators during their foraging and nesting activities (Lawson & Rands, 2019). Consequently, as the distance from natural forests increases, pollinators could face larger differences in resources and greater constraints. Ultimately, such conditions might make it less likely for pollinators to traverse the distance between natural forests and agroforestry systems, potentially leading to reduced pollinator diversity.

The impact of the diversity metric type on the relationship between distance to natural forests and pollinator diversity is multifaceted. Pollinator abundance tends to show a weaker relationship with distance to natural forests than pollinator richness. In essence, while proximity to natural forests may indeed lead to a more diverse pollinator community, it might not necessarily result in a dramatic increase in the total number of individual pollinators (abundance) (e.g., Klein, 2009). Instead, it may be fostering a higher variety of pollinator species (richness), each adapted to different aspects of the forest environment (e.g., Klein, 2009).

Overall conclusions

Using the vast range of research available to date, our meta-analysis explored how pollinator diversity may be influenced by the major management practices used in coffee agroforestry systems. We found strong overall support for the idea that increased local floral resources enhance bee pollinator diversity. This effect on local floral resources can be significantly moderated by climatic conditions, pollinator sociality and the metric used to characterise floral resources. Pollinator diversity did not appear to be influenced by shade-tree cover and the distance to natural forests, but this relationship may largely depend on climatic conditions.

Agroforestry systems show clear ecological responses to climatic conditions (Luedeling et al., 2014), which our results indicate are accentuated by coffee agroforestry management practices. Our results highlight that there is an abrupt change in patterns at the temperature and precipitation thresholds that mark the transition from dry to wet tropical forests, based on the Holdridge life zone classification scheme (Holdridge, 1964). This finding implies that biome type will influence how pollinator diversity responds to coffee agroforestry management practices, information that should inform the strategies that are ultimately applied. These findings should also be considered in the light of future climate change scenarios. For instance, in certain regions, hotter temperatures in wetter areas could lead to even greater precipitation, erasing the positive effects of local floral resources and shade-tree cover on pollinator diversity. As a result, coffee agroforestry management strategies could become less effective. While temperature will rise globally, changes in precipitation will be region-specific (Collins et al., 2013), which means that local floral resources, shade-tree cover and distance to natural forests may have shifting relationships with pollinator diversity over time depending on geographical location. In the future, the effectiveness of certain techniques for managing pollinator diversity and crop production in coffee agroforestry systems may change dramatically, and more research is needed that focuses specifically on upcoming climatic, social and economic challenges. Furthermore, as indicated by our results, there are compelling reasons for adopting increases in shade-tree cover to adapt to climate change, especially given that shade-tree cover had a stronger positive impact on pollinator diversity at higher temperatures, likely because of its cooling effects.

In conclusion, our study emphasises the importance of managing coffee agroforestry systems to create suitable pollinator habitats. The broader objective should be ensuring the availability of resources that promote pollinator fitness, effective pollination and, as a consequence, crop yields. Our results have considerable relevance given policies around agricultural production and food security in tropical regions. For instance, sustainable efforts to improve land productivity are underway in the form of Brazil's National Policy on Climate Change, the Central American Agriculture Policy and various public policies in tropical Asia (United Nations Economic and Social Commission for Asia and the Pacific, 2009; Inter-American Institute for Cooperation on Agriculture, 2019; Sotta et al., 2021). By incorporating current knowledge on floral resource management, policies could better promote pollinator diversity and pollination success in coffee agroforestry systems. Simultaneously, shade tree-cover should be increased in a targeted fashion, focusing on areas with compatible climatic conditions. Finally, it could be helpful to explore the utility of other management practices, such as irrigation, landscape configuration and agrochemical treatments, to determine the reproducibility and repeatability of past work.

AUTHOR CONTRIBUTIONS

Diego Centeno-Alvarado: Conceptualization; methodology; data curation; investigation; validation; formal analysis; writing – review and

editing; writing – original draft. **Ariadna Valentina Lopes:** Validation; writing – review and editing; supervision. **Xavier Arnan:** Validation; writing – review and editing; funding acquisition; supervision.

ACKNOWLEDGEMENTS

We are grateful to Jean C.G. Ortega (Post-Graduate Program in Ecology, Federal University of Pará, Brazil) and Tim Whitfield (Division of Psychiatry, University College London, UK) for providing helpful guidance on our statistical analyses. We would also like to thank Jessica Pearce-Duvet for her English-editing services.

FUNDING INFORMATION

This study was supported by the Foundation for the Support of Science and Technology of the State of Pernambuco (Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco; FACEPE; grant number: IBPG-0068-2.05/21; PhD fellowship awarded to Diego Centeno-Alvarado) and productivity grants from the Brazilian Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico; CNPq; PQ-1D grant number 309505/2018-6 awarded to Ariadna Valentina Lopes; PQ-2 grant number 307385/2020-5 awarded to Xavier Arnan).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Mendeley Data at https://doi.org/10.17632/f4py97mdy4.1.

ORCID

Diego Centeno-Alvarado https://orcid.org/0000-0003-0273-8538
Ariadna Valentina Lopes https://orcid.org/0000-0001-5750-5913
Xavier Arnan https://orcid.org/0000-0002-9904-274X

REFERENCES

Abay, Z., Bezabeh, A., Gela, A. & Tassew, A. (2023) Evaluating the impact of commonly used pesticides on honeybees (Apis mellifer) in North Gonder of Amhara region, Ethiopia. *Journal of Toxicology*, 2023, 2634158.

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current Biology*, 18, 1572–1575.

Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R. et al. (2020) The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecology Letters*, 23, 1488–1498.

Antoine, C.M. & Forrest, J.R.K. (2020) Nesting habitat of ground-nesting bees: a review. *Ecological Entomology*, 46, 143–149.

Atangana, A., Khasa, D., Chang, S. & Degrande, A. (2014) Agroforestry for soil conservation. In: Atangana, A., Khasa, D., Chang, S. & Degrande, A. (Eds.) *Tropical agroforestry*. Dordrecht: Springer, pp. 203–216.

Blut, M., Chowdhry, N., Mittal, V. & Brock, C. (2015) E-service quality: a meta-analytic review. *Journal of Retailing*, 91, 679–700.

Bohart, G.E. (1972) Management of wild bees for the pollination of crops. *Annual Review of Entomology*, 17, 287–312.

Borenstein, M., Hedges, L.V., Higgins, J. & Rothstein, H.R. (2009) *Introduction to meta-analysis*. New Jersey: John Wiley & Sons.

Borenstein, M., Higgins, J.P.T., Hedges, L.V. & Rothstein, H.R. (2017) Basics of meta-analysis: I^2 is not an absolute measure of heterogeneity. *Research Synthesis Methods*, 8, 5–18.

Boreux, V., Krishnan, S., Cheppudira, K.G. & Ghazoul, J. (2013) Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agroforests. *Agriculture, Ecosystems & Environment*, 172, 42–48.

Boreux, V., Kushalappa, C.G., Vaast, P. & Ghazoul, J. (2013) Interactive effects among ecosystem services and management practices on crop production: pollination in coffee agroforestry systems. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 8387–8392.

Bravo-Monroy, L., Tzanopoulos, J. & Potts, S.G. (2015) Ecological and social drivers of coffee pollination in Santander, Colombia. *Agriculture, Ecosystems & Environment*, 211, 145–154.

Breeze, T.D., Bailey, A.P., Balcombe, K.G. & Potts, S.G. (2011) Pollination services in the UK: how important are honeybees? *Agriculture, Ecosystems & Environment*, 142, 137–143.

Briggs, H.M., Perfecto, I. & Brosi, B.J. (2013) The role of the agricultural matrix: coffee management and Euglossine bee (Hymenoptera: Apidae: *Euglossini*) communities in southern Mexico. *Environmental Entomology*, 42, 1210–1217.

Brittain, C., Kremen, C. & Klein, A.M. (2013) Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology*, 19, 540–547.

Burkhard, B., Kroll, F., Nedkov, S. & Müller, F. (2012) Mapping ecosystem service supply, demand and budgets. *Ecological Indicators*, 21, 17–29.

Byers, D.L. (2017) Studying plant-pollinator interactions in a changing climate: a review of approaches. *Applications in Plant Sciences*, 5, 1700012.

Cardinael, R., Mao, Z., Prieto, I., Stokes, A., Dupraz, C., Kim, J.H. et al. (2015) Competition with winter crops induces deeper rooting of walnut trees in a Mediterranean alley cropping agroforestry system. *Plant and Soil*, 391, 219–235.

Carvalheiro, L.G., Seymour, C.L., Veldtman, R. & Nicolson, S.W. (2010) Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, 47(4), 810–820.

Caudill, S., Brokaw, J., Doublet, D. & Rice, R. (2017) Forest and trees: shade management, forest proximity and pollinator communities in southern Costa Rica coffee agriculture. *Renewable Agriculture and Food Systems*, 32, 417–427.

Centeno-Alvarado, D., Lopes, A.V. & Arnan, X. (2023) Fostering pollination through agroforestry: a global review. *Agriculture, Ecosystems & Environment*, 351, 108478.

Chavan, S.B., Kumar, N., Uthappa, A.R., Keerthika, A., Handa, A.K., Sridhar, K.B. et al. (2018) Tree management practices in agroforestry. In: Sood, K.K. & Mahajan, V. (Eds.) *Forests, climate change and biodiversity*. Negar: Kalyani Publishers, pp. 89–100.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.L., Fichefet, T., Friedlingstein, P. et al. (2013) Long-term climate change: projections, commitments and irreversibility. In: Stocker, T.F., Qin, D., Plattner, G. K., Tignor, M., Allen, S.K. & Boschung, J. (Eds.) *Climate change 2013: the physical science basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press.

Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A. et al. (1993) Temperature and the pollinating activity of social bees. *Ecological Entomology*, 18, 17–30.

Dai, W., Yang, Y., Patch, H.M., Grozinger, C.M. & Mu, J. (2022) Soil moisture affects plant–pollinator interactions in an annual flowering plant. *Philosophical Transactions of the Royal Society B*, 377, 20210423.

DaMatta, F.M., Ronchi, C.P., Maestri, M. & Barros, R.S. (2007) Ecophysiology of coffee growth and production. *Brazilian Journal of Plant Physiology*, 19, 485–510.

Descamps, C., Jambrek, A., Quinet, M. & Jacquemart, A.L. (2021) Warm temperatures reduce flower attractiveness and bumblebee foraging. *Insects*, 12, 493.

Descamps, C., Quinet, M., Baijot, A. & Jacquemart, A.L. (2018) Temperature and water stress affect plant-pollinator interactions in Borago officinalis (Boraginaceae). *Ecology and Evolution*, 8, 3443–3456.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z. et al. (2018) Assessing nature's contributions to people: recognizing culture, and diverse source of knowledge, can improve assessments. *Science*, 359, 270–272.

Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A. et al. (2021) A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution*, 5, 1453–1461.

Eilers, R.J., Kremen, C., Greenleaf, S.S., Garber, A.K. & Klein, A.M. (2011) Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS One*, 6, e21363.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802–813.

Feltham, H., Park, K., Minderman, J. & Goulson, D. (2015) Experimental evidence that wildflower strips increase pollinator visits to crops. *Ecology and Evolution*, 5, 3523–3530.

Fisher, Z., Tipton, E. & Zhipeng, H. (2017) *Robumeta*. R package version 2.0. Available from: https://cran.r-project.org/web/packages/robumeta/ [Accessed 7th March 2022].

Food and Agriculture Organization of the United Nations. (2017) *Sustainable woodfuel for food security—a smart choice: green renewable and affordable*. Rome: Food and Agriculture Organization of the United Nations.

Food and Agriculture Organization of the United Nations. (2020) *Global forest resources assessment 2020: main report*. Rome: Food and Agriculture Organization of the United Nations.

Food and Agriculture Organization of the United Nations. (2022) *FAOSTAT online database*. Rome: Food and Agriculture Organization of the United Nations.

Fu, B., Wang, S., Su, C. & Forsius, M. (2013) Linking ecosystem processes and ecosystem services. *Current Opinion in Environmental Sustainability*, 5, 4–10.

Ganuza, C., Redlich, S., Uhler, J., Tobisch, C., Rojas-Botero, S., Peters, M.K. et al. (2022) Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. *Science Advances*, 8(18), eabm9359.

Garcia, F.C., Warfield, R. & Yvon-Durocher, G. (2022) Thermal traits govern the response of microbial community dynamics and ecosystem functioning to warming. *Frontiers in Microbiology*, 13, 906252.

Gardner, E., Breeze, T.D., Clough, Y., Smith, H.G., Baldock, K.C.R., Campbell, A. et al. (2020) Reliably predicting pollinator abundance: Challenges of calibrating process-based ecological models. *Methods in Ecology and Evolution*, 11(12), 1673–1689.

Garibaldi, L.A., Carvalheiro, L.G., Vaissière, B.E., Gemmill-Herren, B., Hipólito, J., Freitas, B.M. et al. (2016) Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, 351, 388–391.

Garibaldi, L.A., Pérez-Méndez, N., Garratt, M.P., Gemmill, B., Miguez, F.E. & Dicks, L.V. (2019) Policies for ecological intensification of crop production. *Trends in Ecology & Evolution*, 34, 282–286.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A. et al. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339, 1608–1611.

Genung, M.A., Fox, J., Williams, N.M., Kremen, C., Ascher, J., Gibbs, J. et al. (2017) The relative importance of pollinator abundance and species richness for the temporal variance of pollination services. *Ecology*, 98(7), 1807–1816.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N. et al. (2010) Tropical forests were the primary source of new agricultural land in 1980s and 1990s. *Proceedings of the National Academy of Sciences*, 107, 16732–16737.

Greenleaf, S.S. & Kremen, C. (2006) Wild bees enhance honey bee's pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences*, 103, 13890–13895.

Greenwell, B., Boehmke, B., Cunningham, J. & GBM Developers. (2019) *gbm: generalized boosted regression models*. R package version 2.1.5. Available from: https://cran.r-project.org/package=gbm/ [Accessed 7th March 2020].

Grundel, R., Jean, R.P., Frohnapple, K.J., Glowacki, G.A., Scott, P.E. & Pavlovic, N.B. (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications*, 20, 1678–1692.

Grüter, C. & Hayes, L. (2022) Sociality is a key driver of foraging ranges in bees. *Current Biology*, 32, 5390–5397.

Gutiérrez-Chacón, C., Dormann, C.F. & Klein, A.M. (2018) Forest-edge associated bees benefit from the proportion of tropical forest regardless of its edge length. *Biological Conservation*, 220, 149–160.

Harrer, M., Cuijpers, P., Furukawa, T.A. & Eebert, D.D. (2021) *Doing meta-analysis with R: a hands-on guide*. Boca Raton: Chapman & Hall/CRC.

Hass, A.L., Liese, B., Heong, K.L., Settele, J., Tscharntke, T. & Westphal, C. (2018) Plant-pollinator interactions and bee functional diversity are driven by agroforests in rice-dominated landscapes. *Agriculture, Ecosystems and Environment*, 253, 140–147.

Hastie, T., Tibshirani, R. & Friedman, J. (2009) *The elements of statistical learning: data mining, inference, and prediction*. New York: Springer.

Hatfield, J.L. & Prueger, J.H. (2015) Temperature extremes: effect on plant growth and development. *Weather and Climate Extremes*, 10, 4–10.

Häyhä, T. & Franzese, P.P. (2014) Ecosystem services assessment: a review under an ecological-economic and systems perspective. *Ecological Modelling*, 289, 124–132.

Hedges, L.V., Tipton, E. & Johnson, M.C. (2010) Robust variance estimation in meta-regression with dependent effect size estimates. *Research Synthesis Methods*, 1, 39–65.

Henry, M., Beguin, M., Requier, F., Rollin, O., Odoux, J.F., Aupinel, P. et al. (2012) A common pesticide decreases foraging success and survival in honey bees. *Science*, 336, 348–350.

Higgins, J. & Thompson, S.G. (2002) Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, 21, 1539–1558.

Higgins, J., Thompson, S.G., Deeks, J.J. & Altman, D.G. (2003) Measuring inconsistency in meta-analyses. *British Medical Journal*, 6, 557–560.

Hijmans, R.J. & Etten, J. (2012) *raster: geographic analysis and modeling with raster data*. R package version 2.0-12. Available from: http://cran.r-project.org/package=raster [Accessed on 7th March 2022].

Hipólito, J., Boscolo, D. & Viana, B.F. (2018) Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms. *Agriculture, Ecosystems and Environment*, 256, 218–225.

Holdridge, L.R. (1964) *Life zone ecology*. San José: Tropical Science Center.

Hutchinson, L.A., Oliver, T.H., Breeze, T.D., Bailes, E.J., Brünjes, L., Campbell, A.J. et al. (2021) Using ecological and field survey data to establish a national list of the wild bee pollinator of crops. *Agriculture, Ecosystems & Environment*, 315, 107447.

Hutchinson, L.A., Oliver, T.H., Breeze, T.D., O'Connor, R.S., Potts, S.G., Roberts, S.P.M. et al. (2021) Inventorying and monitoring crop pollinating bees: evaluating the effectiveness of common sampling methods. *Insect Conservation and Diversity*, 15, 299–311.

Imbach, P., Fung, E., Hannah, L., Navarro-Racines, C.E., Roubik, D.W. & Ricketts, T.H. (2017) Coupling of pollination services and coffee suitability under climate change. *Proceedings of the National Academy of Sciences*, 114, 10438–10442.

Inter-American Institute for Cooperation on Agriculture. (2019) *Agricultural policy for the SICA region 2019–2030*. San José: IICA.

Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C. et al. (2017) Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology*, 105, 871–879.

Jones, J. & Rader, R. (2022) Pollinator nutrition and its role in merging the dual objectives of pollinator health and optimal crop production. *Philosophical Transactions of the Royal Society B*, 377, 20210170.

Jose, S. & Dollinger, J. (2019) Silvopasture: a sustainable livestock production systems. *Agroforestry Systems*, 93, 1–9.

Khodorova, N., Boitel-Conti, M. (2013) The role of temperature in the growth and flowering of geophytes. *Plants*, 2(4), 699–711.

King, P.S. (2013) Moderators/moderating factors. In: Gellman, M.D. & Turner, J.R. (Eds.) *Encyclopedia of behavioral medicine*. New York: Springer.

Klein, A.M. (2009) Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness. *Forest Ecology and Management*, 258(9), 1838–1845.

Klein, A.M., Cunningham, S.A., Bos, M. & Steffan-Dewenter, I. (2008) Advance in pollination ecology from tropical plantation crops. *Ecology*, 89, 935–943.

Klein, A.M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology*, 16, 1003–1014.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003a) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B*, 270, 955–961.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003b) Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology*, 40, 837–845.

Klein, A.M., Viassière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. et al. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, 274, 303–313.

Kletty, F., Rozan, A. & Habold, C. (2023) Biodiversity in temperate silvoarable systems: a systematic review. *Agriculture, Ecosystems & Environment*, 351, 108480.

Koch, N., Ermgassen, E.K.H.J., Wehkamp, J., Oliveira, F.J.B. & Schwerhoff, G. (2019) Agricultural productivity and forest conservation: evidence from the Brazilian Amazon. *American Journal of Agricultural Economic*, 101, 919–940.

Koricheva, J. & Gurevitch, J. (2013) Place of meta-analysis among other methods of research synthesis. In: Koricheva, J., Gurevitch, J. & Mengersen, K. (Eds.) *Handbook of meta-analysis in ecology and evolution*. Oxford: Princeton University Press, pp. 105–206.

Krishnan, S., Cheppudira, K.G. & Ghazoul, J. (2018) Pollinator services in coffee agroforests of the Western Ghats. In: Dagar, J.C. & Tewari, V. P. (Eds.) *Agroforestry: anecdotal to modern sciences*. Cham: Springer, pp. 771–995.

Kwon, Y.J. & Saeed, S. (2003) Effect of temperature on the foraging activity of *Bombus terrestris* L. (Hymenoptera: Apidae) on greenhouse hot pepper (*Capsicum annuum* L.). *Applied Entomology and Zoology*, 38, 275–280.

Lara-Estrada, L., Rasche, L., Schneider, U.A. (2023) Exploring the cooling effect of shading for climate change adaptation in coffee areas. *Climate Risk Management*, 42, 100562.

Lawson, D.A. & Rands, S.A. (2019) The effects of rainfall on plant-pollinator interactions. *Arthropod-Plant Interactions*, 13, 561–569.

Li, D. (2018) The plant functional traits of arid and semiarid grassland plants under warming and precipitation change. In: Ratnadewo, D. (Ed.) *Plant growth and regulation—alterations to sustain unfavorable conditions*. London: IntechOpen.

Lin, B.B. (2008) Microclimate effects on flowering success in coffee agroforestry systems. *American-Eurasian Journal of Agricultural and Environmental Sciences*, 3, 148–152.

Lin, B.B. (2010) The role of agroforestry in reducing water loss through soil evaporation and crop transpiration in coffee agroecosystems. *Agricultural and Forest Meteorology*, 150, 510–518.

Lin, L. & Chu, H. (2017) Quantifying publication bias in meta-analysis. *Biometrics*, 74, 785–794.

Luedeling, E., Kindt, R., Huth, N.I. & Koening, K. (2014) Agroforestry systems in a changing climate—challenges in project future performance. *Current Opinion in Environmental Sustainability*, 6, 1–7.

Mach, B.M. & Potter, D.A. (2018) Quantifying bee assemblages and attractiveness of flowering woody landscape plants for urban pollinator conservation. *PLoS One*, 13, e0208428.

Mathur, M.B. & VanderWeele, T.J. (2020a) *PublicationBias*. R package version 2.2. Available from: https://cran.r-project.org/web/packages/PublicationBias/ [Accessed 7th March 2022].

Mathur, M.B. & VanderWeele, T.J. (2020b) Sensitivity analysis for publication bias in meta-analyses. *Applied Statistics*, 69, 1091–1119.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D. (2009) New frontiers in competition for pollination. *Annals of Botany*, 103, 1403–1413.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G. (2009) Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *PLoS Medicine*, 6(7), e1000097.

Mosquera-Losada, M.R., McAdam, J.H., Romero-Franco, R., Santiago-Freijanes, J.J. & Rigueiro-Rodríguez, A. (2009) Definitions and components of agroforestry practices in Europe. In: Rigueiro-Rodríguez, A., McAdam, J. & Mosquera-Losada, M.R. (Eds.) *Agroforestry in Europe*. Dordrecht: Springer, pp. 3–19.

Muñoz, A.E., Amouroux, P. & Zaviezo, T. (2021) Native flowering shrubs promote beneficial insects in avocado orchards. *Agricultural and Forest Entomology*, 23, 463–472.

Ngo, H.T., Mojica, A.C. & Packer, L. (2011) Coffee plant—pollinator interactions: a review. *Canadian Journal of Zoology*, 89(8), 647–660.

Oldroyd, B.P. (2012) Domestication of honey bees was associated with expansion of genetic diversity. *Molecular Ecology*, 21, 4409–4411.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals. *Oikos*, 120, 321–326.

Papa, G., Maier, R., Durazzo, A., Lucarini, M., Karabagias, I.K., Plutino, M. et al. (2022) The honey bee *Apis mellifera*: an insect at the interface between human and ecosystem health. *Biology*, 11, 233.

Pick, J.L., Nakagawa, S. & Noble, D.W.A. (2019) Reproducible, flexible and high-throughput data extraction from primary literature: the metaDigitise R package. *Methods in Ecology and Evolution*, 10, 426–431.

Pick, J.L., Nakagawa, S. & Noble, D.W.A. (2020) *metaDigitise*. R package version 1.0.1. Available from: https://cran.r-project.org/web/packages/metaDigitise/ [Accessed 7th March 2020].

Pisanty, G., Afik, O., Wajnberg, E. & Mandelik, Y. (2015) Watermelon pollinators exhibit complementarity in both visitation rate and single-visit pollination efficiency. *Journal of Applied Ecology*, 53, 360–370.

Potts, S.G., Imperatriz-Fonseca, V. & Ngo, H.T. (2016) *The assessment report on pollinators, pollination and food production of the intergovernmental science-policy platform on biodiversity and ecosystem services*. Bonn: IPBES.

Prado, S.G., Collazo, J.A., Marand, M.H. & Irwin, R.E. (2021) The influence of floral resources and microclimate on pollinator visitation in and agroecosystem. *Agriculture, Ecosystems and Environment*, 307, 107196.

R Core Team. (2022) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: https://www.r-project.org/

Rahimi, E., Barghjelveh, S. & Dong, P. (2022) Amount, distance-dependent and structural effects of forest patches on bees in agricultural landscapes. *Agriculture & Food Security*, 11, 10.

Ricketts, T.H. (2004) Tropical forest enhance pollinator activity in nearby coffee crops. *Conservation Biology*, 18, 1262–1271.

Rosenberg, M.S., Rothstein, H.R. & Gurevitch, J. (2013) Effect sizes: conventional choices and calculations. In: Koricheva, J., Gurevitch, J. & Mengersen, K. (Eds.) *Handbook of meta-analysis in ecology and evolution*. Oxford: Princeton University Press, pp. 61–71.

Russillo, A. & Pintér, L. (2009) *Linking farm-level measurment systems to environmental sustainability outcomes: challenges and ways forward*. Manitoba: International Institute for Sustainable Development.

Sabino, W., Costa, L., Andrade, T., Teixeira, J., Araújo, G., Acosta, A.L. et al. (2022) Status and trends of pollination services in Amazon agroforestry systems. *Agriculture, Ecosystems & Environment*, 335, 108012.

Samnegård, U., Hambäck, P.A., Nemomissa, S. & Hylander, K. (2014) Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia. *Journal of Tropical Ecology*, 30, 401–408.

Sánchez, A.C., Jones, S.K., Purvis, A., Estrada-Carmona, N., De Palma, A. (2022) Landscape complexity and functional groups moderate the effect of diversified farming on biodiversity: A global meta-analysis. *Agriculture, Ecosystems & Environment*, 332, 107933.

Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C. et al. (2013) Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biological Reviews*, 88, 1002–1021.

Sharma, S., Durand, R.M. & Gur-Arie, O. (1981) Identification and analysis of moderator variables. *Journal of Marketing Research*, 18, 291–300.

Somarriba, E. & Lopez-Sampson, A. (2018) *Coffee and cocoa agroforestry systems: pathways to deforestation, reforestation, and tree cover change*. Turrialba: CATIE.

Sotta, E.D., Sampaio, F.G., Marzall, K. & Silva, W.G. (2021) *Adapting to climate change: strategies for Brazilian agricultural and livestock systems*. Livestock and Food Supply, Brasília: Ministry of Agriculture.

Staton, T., Walters, R., Smith, J., Breeze, T. & Girling, R. (2021) Management to promote flowering understoreys benefits natural enemy diversity, aphid suppression and income in an agroforestry system. *Agronomy*, 11, 651.

Tanner-Smith, E.E., Tipton, E. & Polanin, J.R. (2016) Handling complex meta-analytic data structures using robust variance estimates; a tutorial in R. *Journal of Developmental and Life-Course Criminology*, 2, 85–112.

Toledo-Hernández, M., Tscharntke, T., Tjoa, A., Anshary, A., Cyio, B. & Wanger, C. (2021) Landscape and farm-level management for conservation of potential pollinators in Indonesian cocoa agroforests. *Biological Conservation*, 257, 109106.

United Nations Economic and Social Commission for Asia and the Pacific. (2009) *Sustainable agriculture and food security in Asia and the Pacific*. Bangkok: ESCAP.

United States Department of Agriculture (USDA). (2019) *Agroforestry strategic framework: fiscal years 2019–2024*. Washington, DC: USDA.

Vaast, P., Harmand, J.M., Rapidel, B., Jagoret, P. & Deheuvels, O. (2015) Coffee and cocoa production in agroforestry—a climate-smart agriculture model. In: Torquebiau, E. (Ed.) *Climate change and agriculture worldwide*. Cham: Springer, pp. 209–224.

Vacher, C., Tamaddoni-Nezhad, A., Kamenova, S., Peyrard, N., Moalic, Y., Sabbadin, R. et al. (2016) Learning ecological networks from next-generation sequencing data. In: Woodward, G. & Bohan, D.A. (Eds.) *Ecosystem services: from biodiversity to society, part 2*. London: Elsevier, pp. 1–39.

Varah, A., Jones, H., Smith, J. & Potts, S.G. (2020) Temperate agroforestry systems provide greater pollination service than monoculture. *Agriculture, Ecosystems and Environment*, 301, 107031.

Vergara, C.H. & Badano, E.I. (2009) Pollinator diversity increases fruit production in Mexican coffee plantations: the importance of rustic management systems. *Agriculture, Ecosystems and Environment*, 129, 117–123.

Wandrag, E.M., Catford, J.A. & Duncan, R.P. (2019) Quantifying niche availability, niche overlap and competition for recruitment sites in plant populations without explicit knowledge of niche axes. *Journal of Ecology*, 107, 1791–1803.

Wcislo, W. & Fewell, J.H. (2017) Sociality in bees. In: Rubenstein, D.R. & Abbot, P. (Eds.) *Comparative Social Evolution*. Cambridge: Cambridge University Press, pp. 50–93.

Wellborn, G.A. & Langerhans, R.B. (2015) Ecological opportunity and the adaptive diversification of lineages. *Ecology and Evolution*, 5, 176–195.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T. et al. (2008) Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, 78, 653–671.

Winfree, R., Bartomeus, I. & Cariveau, D.P. (2011) Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics*, 42, 1–22.

Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. (2007) Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, 10, 1105–1113.

Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E. & Desneux, N. (2012) Pollinator habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems & Environment*, 159, 112–122.

Yao, Z., Xin, Y., Yang, L., Zhao, L. & Ali, A. (2022) Precipitation and temperature regulate species diversity, plant coverage and aboveground biomass through opposing mechanisms in large-scale grasslands. *Frontiers in Plant Science*, 13, 999636.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting information.

Appendix S1. References of articles included in this meta-analysis.

Appendix S2. Formulae used in this meta-analysis.

Formula S1. Standardized mean difference or Cohen's d (*d*) from categorical means to Fisher's z.

Formula S2. Standardized mean difference or Cohen's d (*d*) from T statistic (*T*) from regression analyses to Fisher's z.

Formula S3. Fisher's z from F statistic (*F*) from regression analyses.

Formula S4. Correlation coefficient (*r*) from coefficient of determination (R^2) to Fisher's z.

Formula S5. Fisher's z from correlation data (*r*).

Table S1. List of studies included in the meta-analysis, along with the country, management practice evaluated, mean annual temperature and mean annual precipitation of the study area, pollinator functional group, diversity metric, metric type, or variable measured for the management practice, floral resource type, calculated effect sizes and variances of the effect sizes, and the statistic used to calculate effect sizes and the location of the statistic in the reference paper.

Table S2. Heterogeneity statistics for the three-level meta-analytical random-effects models.

Figure S1. Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) flow diagram of the literature search on the effect of management practices within coffee agroforestry systems on pollinator diversity, showing the records obtained by our search and the number of records that were eliminated according to our exclusion criteria.

How to cite this article: Centeno-Alvarado, D., Lopes, A.V. & Arnan, X. (2024) Shaping pollinator diversity through coffee agroforestry management: A meta-analytical approach. *Insect Conservation and Diversity*, 1–14. Available from: https://doi.org/10.1111/icad.12755

SUPPORTING INFORMATION

Shaping pollinator diversity through coffee agroforestry management: A meta-analytical approach

Diego Centeno-Alvarado[1], Ariadna Valentina Lopes[2], Xavier Arnan[1,3]

[1]Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil

[2]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[3]Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

***Corresponding author:** centenoalvaradodiego@gmail.com

This document contains 2 appendices, 2 tables and 1 figure.

Appendix S1. References of articles included in this meta-analysis.

Banks, J.E., Hannon, L., Hanson, P., Dietsch, T., Castro, S., Urena, N. *et al.*, 2013. Effects of proximity to forest habitat on hymenoptera diversity in a Costa Rican coffee agroecosystem. *The Pan-Pacific Entomologist,* **89**, 60–68.

Berecha, G., Aerts, R., Muys, B., Honnay, O., 2015. Fragmentation and management of Ethiopian moist evergreen forest drive compositional shifts of insect communities visiting wild arabica coffee flowers. *Environmental Management,* **55**, 372–382.

Boreux, V., Krishnan, S., Cheppudira, K.G., Ghazoul, J., 2013a. Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agroforests. *Agriculture, Ecosystems & Environment,* **172**, 42–48.

Boreux, V., Kushalappa, C.G., Vaast, P., Ghazoul, J., 2013b. Interactive effects among ecosystem services and management practices on crop production: Pollination in coffee agroforestry systems. *Proceedings of the National Academy of Sciences of the United States of America,* **110**, 8387–8392.

Bravo-Monroy, L., Tzanopoulos, J., Potts, S.G., 2015. Ecological and social drivers of coffee pollination in Santander, Colombia. *Agriculture, Ecosystems & Environment,* **211**, 145–154.

Caudill, S., Brokaw, J., Doublet, D., Rice, R., 2017. Forest and trees: Shade management, forest proximity and pollinator communities in southern Costa Rica coffee agriculture. *Renewable Agriculture and Food Systems,* **32**, 417–427.

Fisher, K., Gonthier, D.J., Ennis, K.K., Perfecto, I., 2017. Floral resource availability from groundcover promotes bee abundance in coffee agroecosystems. *Ecological Applications,* **27**, 1815–1826.

Jha, S., Vandermeer, J.H., 2009. Contrasting bee foraging in response to resource scale and local habitat management. *Oikos,* **118**, 1174–1180.

Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. *Biological Conservation,* **143**, 1423–1431.

Klein, A.M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology,* **16**, 1003–1014.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003a. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B,* **270**, 955–961.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003b. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology,* **40**, 837–845.

Munyuli, T., 2011. Factors governing flower visitation patterns and quality of pollination services delivered by social and solitary bee species to coffee in central Uganda. *African Journal of Ecology,* **49**, 501–509.

Ngo, H.T., Gibbs, J., Griswold, T., Packer, L., 2013. Evaluating bee (Hymenoptera: Apoidea) diversity using Malaise traps in coffee landscapes of Costa Rica. *The Canadian Entomologist,* **145**, 435 – 453.

Peters, V.E., Carroll, C.R., Cooper, R.J., Greenberg, R., Solis, M., 2013. The contribution of plant species with a steady-state flowering phenology to native bee conservation and bee pollination services. *Insect Conservation and Diversity,* **6**, 45–56.

Ricketts, T.H., 2004. Tropical forest enhance pollinator activity in nearby coffee crops. *Conservation Biology,* **18**, 1262–1271.

Samnegård, U., Hambäck, P.A., Nemomissa, S., Hylander, K., 2014. Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia. *Journal of Tropical Ecology,* **30**, 401–408.

Setyawati, A.I., Supriyadi, Pardono, Wijayanti, R., Putri, B.A., 2018. The role of flowering plants, *Hibiscus sabdariffa* and *Crotalaria juncea* in coffee ecosystem to diversity of insect pollinators and coffee fruit set. *AIP Conference Proceedings,* **2014**, 020027.

Veddeler, D., Klein, A.M., Tscharntke, T., 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos,* **112**, 594–601.

Vergara, C.H., Badano, E.I., 2009. Pollinator diversity increases fruit production in Mexican coffee plantations: The importance of rustic management systems. *Agriculture, Ecosystems and Environment,* **129**, 117–123.

Appendix S2. Formulae used in this meta-analysis.

Formula S1. Standardized mean difference or Cohen's d (*d*) from categorical means to Fisher's z.

(1) Categorical means to standardized mean difference or Cohen's d (*d*) (Hedges, 1981; Borenstein, 2009)

$$d = \frac{\bar{Y}_1 - \bar{Y}_2}{S_{within}}$$

where $\bar{Y}_1$ and $\bar{Y}_2$ are the sample means in the two groups and S_{within} is the within-groups standard deviation.

$$S_{within} = \sqrt{\frac{(n_1){S_1}^2 + (n_2){S_2}^2}{n_1 + n_2 - 2}}$$

where n_1 and n_2 are the sample size in the two groups and S_1 and S_2 are the standard deviation in the two groups.

(2) Standardized mean difference or Cohen's d (*d*) to correlation coefficient (*r*) (Lajeunesse, 2013)

$$r = \frac{d}{\sqrt{d^2 + a}}$$

where a is a correction factor.

$$a = \frac{(n_1 + n_2)^2}{n_1 n_2}$$

(3) Correlation coefficient to Fisher's z (*z*) (Rosenberg et al., 2013)

$$z = \frac{1}{2} ln \frac{(1 + r)}{(1 - r)}$$

(4) Variance of Fisher's z (v_z) (Rosenberg et al., 2013)

$$v_z = \frac{1}{n - 3}$$

where n is the sample size (or $n_1 + n_2$).

Formula S2. Standardized mean difference or Cohen's d (*d*) from T statistic (*T*) from regression analyses to Fisher's z.

(1) T statistic to standardized mean difference or Cohen's d (*d*) (Rosenthal, 1994; Howell, 2013)

$$d = \frac{T}{\sqrt{n}}$$

where n is the sample size (or $n_1 + n_2$).

(2) Standardized mean difference or Cohen's d (*d*) to correlation coefficient (*r*) (Lajeunesse, 2013)

$$r = \frac{d}{\sqrt{d^2 + a}}$$

where a is a correction factor.

$$a = \frac{(n_1 + n_2)^2}{n_1 n_2}$$

(3) Correlation coefficient to Fisher's z (*z*) (Rosenberg et al., 2013)

$$z = \frac{1}{2} ln \frac{(1 + r)}{(1 - r)}$$

(4) Variance of Fisher's z (v_z) (Rosenberg et al., 2013)

$$v_z = \frac{1}{n - 3}$$

where n is the sample size (or $n_1 + n_2$).

Formula S3. Fisher's z from F statistic (*F*) from regression analyses.

(1) Fisher's z (*z*) (Schwarzenberg-Czerny & Beaulieu, 2006)

$$z = \frac{1}{2} \log (F)$$

(2) Variance of Fisher's z (v_z) (Rosenberg et al., 2013)

$$v_z = \frac{1}{n - 3}$$

where n is the sample size (or $n_1 + n_2$).

Formula S4. Correlation coefficient (*r*) from coefficient of determination (R^2) to Fisher's z.

(3) Correlation coefficient (*r*) (Rosenberg et al., 2013)

$$r = \sqrt{R^2}$$

(4) Fisher's z (*z*) (Rosenberg et al., 2013)

$$z = \frac{1}{2} ln \frac{(1 + r)}{(1 - r)}$$

(5) Variance of Fisher's z (v_z) (Rosenberg et al., 2013)

$$v_z = \frac{1}{n-3}$$

where n is the sample size (or $n_1 + n_2$).

Formula S5. Fisher's z from correlation data (*r*).

(6) Fisher's z (*z*) (Rosenberg et al., 2013)

$$z = \frac{1}{2} ln \frac{(1+r)}{(1-r)}$$

(7) Variance of Fisher's z (v_z) (Rosenberg et al., 2013)

$$v_z = \frac{1}{n-3}$$

where n is the sample size (or $n_1 + n_2$).

References

Borenstein, M. (2009) Effect sizes for continuous data. In: *The handbook of research synthesis and meta-analysis* (eds H. M. Cooper, L. V. Hedges and J. C. Valentine), pp. 221–237. New York, NY: Russell Sage Foundation.

Hedges, L.V. (1981) Distribution theory for Glass's estimator of effect size and related estimators. *Journal of Educational Statistics,* **6**, 107– 128.

Howell, D.C. (2013) *Statistical methods for psychologists*. California, USA: Wadsworth.

Lajeunesse, M.J. (2013) Recovering missing or partial data from studies: A survey of conversions and imputations for meta-analysis. In: *Handbook of Meta-Analysis in Ecology and Evolution* (eds J. Koricheva, J. Gurevitch and K. Mengersen), pp. 195– 206. Oxford, UK: Princeton University Press.

Rosenberg, M. S., Rothstein, H. R. & Gurevitch, J. (2013) Effect sizes: Conventional choices and calculations. In: *Handbook of Meta-Analysis in Ecology and Evolution* (eds J. Koricheva, J. Gurevitch and K. Mengersen), pp. 61– 71. Oxford, UK: Princeton University Press.

Rosenthal, R. (1994) Parametric measures of effect size. In: *The handbook of research synthesis* (eds. H. M. Cooper, L.V. Hedges and J. C. Valentine), pp. 231–244. New York, NY: Russell Sage Foundation.

Schwarzenberg-Czerny, A., Beaulieu, J.P. (2006). Efficient analysis in planet transit surveys. *Monthly Notices of the Royal Astronomical Society*, **365**, 165–170.

Table S1. List of studies included in the meta-analysis, along with the country, management practice evaluated, mean annual temperature and mean annual precipitation of the study area, pollinator functional group, diversity metric, metric type, or variable measured for the management practice, floral resource type, calculated effect sizes and variances of the effect sizes, and the statistic used to calculate effect sizes and the location of the statistic in the reference paper.

No.	Study	Country	Elevation (m)	Management practice	Temperature (°C)	Precipitation (mm)	Pollinator functional group	Diversity metric	Pollinator sampling method	Metric type	Floral resource type	Statistic used to calculate effect size	Source in the reference paper	Sample size			Effect size (Fisher's *z*)	Variance of Fisher's *z*
														Total	Treatment	Control		
1	Klein et al. (2002)	Indonesia	1219	Local floral resources	20.5	1820	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Regression (F-statistic)	Table 4	30	NA	NA	0.38	0.04
2	Klein et al. (2002)	Indonesia	1219	Local floral resources	20.5	1820	Social	Abundance	Active	Flower percentage	Target crop	Regression (F-statistic)	Table 4	30	NA	NA	-0.09	0.04
3	Klein et al. (2002)	Indonesia	1219	Local floral resources	20.5	1820	Solitary	Abundance	Active	Number of flowers or inflorescences	Target crop	Regression (F-statistic)	Table 4	30	NA	NA	0.10	0.04
4	Klein et al. (2002)	Indonesia	1219	Local floral resources	20.5	1820	Solitary	Abundance	Active	Flower percentage	Target crop	Regression (F-statistic)	Table 4	30	NA	NA	-0.20	0.04
5	Klein et al. (2003b)	Indonesia	1219	Local floral resources	20.5	1820	No data	Richness	Active	Flower percentage	Complementary flowers	Regression (T-statistic)	Table 1	15	NA	NA	0.46	0.08
6	Klein et al. (2003b)	Indonesia	1219	Local floral resources	20.5	1820	No data	Richness	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	15	NA	NA	-0.32	0.08
7	Klein et al. (2003b)	Indonesia	1219	Local floral resources	20.5	1820	No data	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	15	NA	NA	0.38	0.08
8	Klein et al. (2003b)	Indonesia	1219	Local floral resources	20.5	1820	Social	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	15	NA	NA	0.29	0.08
9	Klein et al. (2003b)	Indonesia	1219	Local floral resources	20.5	1820	Solitary	Richness	Active	Flower percentage	Complementary flowers	Regression (T-statistic)	Table 1	15	NA	NA	0.48	0.08
10	Klein et al. (2003b)	Indonesia	1219	Local floral resources	20.5	1820	Solitary	Richness	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	15	NA	NA	-0.37	0.08
11	Klein et al. (2003b)	Indonesia	1219	Local floral resources	20.5	1820	Solitary	Abundance	Active	Flower percentage	Complementary flowers	Regression (T-statistic)	Table 1	15	NA	NA	0.26	0.08
12	Veddeler et al. (2006)	Ecuador	280	Local floral resources	23.7	522	Social	Abundance	Active	Flower percentage	Target crop	Regression (R^2)	Figure 2	22	NA	NA	-0.64	0.05
13	Veddeler et al. (2006)	Ecuador	280	Local floral resources	23.7	522	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Regression (R^2)	Figure 3	55	NA	NA	0.67	0.02
14	Veddeler et al. (2006)	Ecuador	280	Local floral resources	23.7	522	Social	Richness	Active	Number of flowers or inflorescences	Target crop	Regression (R^2)	Figure 3	55	NA	NA	0.31	0.02
15	Jha & Vandermeer (2009)	Mexico	987	Local floral resources	24.3	4002	Solitary	Abundance	Active	Flower percentage	Target crop	Regression (R^2)	Results section (Text)	67	NA	NA	-0.34	0.02
16	Jha & Vandermeer (2009)	Mexico	987	Local floral resources	24.3	4002	Social	Abundance	Active	Flower percentage	Target crop	Regression (R^2)	Results section (Text)	67	NA	NA	-0.31	0.02

17	Jha & Vandermeer (2009)	Mexico	987	Local floral resources	24.3	4002	Social	Abundance	Active	Flower percentage	Target crop	Regression (R^2)	Results section (Text)	57	NA	NA	0.36	0.02
18	Jha & Vandermeer (2010)	Mexico	1165	Local floral resources	22.9	3581	No data	Richness	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Figure 5	NA	14	10	0.46	0.05
19	Jha & Vandermeer (2010)	Mexico	1165	Local floral resources	22.9	3581	Solitary	Abundance	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Figure 6	NA	11	13	0.57	0.05
20	Jha & Vandermeer (2010)	Mexico	1165	Local floral resources	22.9	3581	Social	Abundance	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Figure 6	NA	11	13	0.57	0.05
21	Munyuli (2011)	Uganda	1191	Local floral resources	21.5	1254	Social	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	30	NA	NA	0.36	0.04
22	Munyuli (2011)	Uganda	1191	Local floral resources	21.5	1254	Social	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	30	NA	NA	0.23	0.04
23	Munyuli (2011)	Uganda	1191	Local floral resources	21.5	1254	Social	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	30	NA	NA	0.60	0.04
24	Munyuli (2011)	Uganda	1191	Local floral resources	21.5	1254	Social	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	30	NA	NA	0.41	0.04
25	Munyuli (2011)	Uganda	1191	Local floral resources	21.5	1254	Solitary	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	30	NA	NA	0.23	0.04
26	Munyuli (2011)	Uganda	1191	Local floral resources	21.5	1254	Solitary	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	30	NA	NA	0.20	0.04
27	Munyuli (2011)	Uganda	1191	Local floral resources	21.5	1254	Solitary	Abundance	Active	Flower percentage	Target crop	Regression (T-statistic)	Table 1	30	NA	NA	0.44	0.04
28	Peters et al. (2013)	Costa Rica	1225	Local floral resources	21.3	2859	No data	Abundance	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Table 3	NA	3	3	-1.21	0.33
29	Peters et al. (2013)	Costa Rica	1225	Local floral resources	21.3	2859	No data	Abundance	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Table 3	NA	3	3	-0.50	0.33
30	Peters et al. (2013)	Costa Rica	1225	Local floral resources	21.3	2859	Social	Abundance	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Table 3	NA	3	3	0.85	0.33
31	Peters et al. (2013)	Costa Rica	1225	Local floral resources	21.3	2859	Social	Abundance	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Table 3	NA	3	3	0.48	0.33
32	Peters et al. (2013)	Costa Rica	1225	Local floral resources	21.3	2859	No data	Richness	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Table 3	NA	3	3	-1.19	0.33
33	Peters et al. (2013)	Costa Rica	1225	Local floral resources	21.3	2859	No data	Richness	Passive	Number of individuals flowering	Complementary flowers	Means (categories)	Table 3	NA	3	3	-0.38	0.33
34	Boreux et al. (2013a)	India	544	Local floral resources	25.7	614	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure 2	NA	94	32	-0.74	0.01
35	Boreux et al. (2013a)	India	544	Local floral resources	25.7	614	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure 2	NA	94	32	-0.72	0.01

36	Boreux et al. (2013a)	India	544	Local floral resources	25.7	614	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure 2	NA	94	32	-0.02	0.01
37	Boreux et al. (2013b)	India	544	Local floral resources	25.7	614	Social	Abundance	Active	Number of sites flowering	Target crop	Means (categories)	Results section (Text)	NA	91	28	-0.54	0.01
38	Boreux et al. (2013b)	India	544	Local floral resources	25.7	614	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Regression (chi-squared)	Table 1	113	NA	NA	0.21	0.01
39	Samnegård et al. (2014)	Ethiopia	2215	Local floral resources	17.2	1907	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Regression (T-statistic)	Results section (Text)	19	NA	NA	0.32	0.06
40	Setyawati et al. (2014)	Indonesia	447	Local floral resources	23.6	2543	Social	Abundance	Active	Number of individuals flowering	Complementary flowers	Means (categories)	Table 1	NA	3	1	0.42	1
41	Setyawati et al. (2014)	Indonesia	447	Local floral resources	23.6	2543	Solitary	Abundance	Active	Number of individuals flowering	Complementary flowers	Means (categories)	Table 1	NA	3	1	0.49	1
42	Berecha et al. (2015)	Ethiopia	1635	Local floral resources	19.8	1250	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	0.86	0.06
43	Berecha et al. (2015)	Ethiopia	1635	Local floral resources	19.8	1250	No data	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	-0.17	0.06
44	Berecha et al. (2015)	Ethiopia	1635	Local floral resources	19.8	1250	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	-0.12	0.06
45	Berecha et al. (2015)	Ethiopia	1635	Local floral resources	19.8	1250	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	1.42	0.06
46	Berecha et al. (2015)	Ethiopia	1635	Local floral resources	19.8	1250	No data	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	-0.28	0.06
47	Berecha et al. (2015)	Ethiopia	1635	Local floral resources	19.8	1250	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	-0.19	0.06
48	Bravo-Monroy et al. (2015)	Colombia	1668	Local floral resources	20.4	2380	Social	Abundance	Active	Number of flowers or inflorescences	Target crop	Regression (R^2)	Figure S4 (Supplementary Material)	112	NA	NA	0.60	0.01
49	Bravo-Monroy et al. (2015)	Colombia	1668	Local floral resources	20.4	2380	Social	Abundance	Active	Number of individuals flowering	Complementary flowers	Regression (R^2)	Figure S5 (Supplementary Material)	14	NA	NA	0.62	0.09
50	Bravo-Monroy et al. (2015)	Colombia	1668	Local floral resources	20.4	2380	Social	Abundance	Active	Number of individuals flowering	Complementary flowers	Regression (R^2)	Figure S5 (Supplementary Material)	14	NA	NA	0.63	0.09
51	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	No data	Richness	Mixed	Flower percentage	Target crop	Correlation coefficient	Table 1	22	NA	NA	0.44	0.05

52	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	No data	Richness	Mixed	Flower percentage	Complementary flowers	Correlation coefficient	Table 1	22	NA	NA	0.11	0.05
53	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	No data	Richness	Mixed	Number of individuals flowering	Complementary flowers	Correlation coefficient	Table 1	22	NA	NA	0.39	0.05
54	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	Social	Abundance	Mixed	Flower percentage	Target crop	Correlation coefficient	Table 1	22	NA	NA	0.23	0.05
55	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	Solitary	Abundance	Mixed	Flower percentage	Target crop	Correlation coefficient	Table 1	22	NA	NA	0.29	0.05
56	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	Solitary	Abundance	Mixed	Number of individuals flowering	Complementary flowers	Correlation coefficient	Table 1	22	NA	NA	0.46	0.05
57	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	Solitary	Abundance	Mixed	Flower percentage	Complementary flowers	Correlation coefficient	Table 1	22	NA	NA	0.20	0.05
58	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	Social	Abundance	Mixed	Flower percentage	Target crop	Correlation coefficient	Table 1	22	NA	NA	0.74	0.05
59	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	Social	Abundance	Mixed	Number of individuals flowering	Complementary flowers	Correlation coefficient	Table 1	22	NA	NA	0.10	0.05
60	Fisher et al. (2017)	Mexico	930	Local floral resources	22.9	3581	Social	Abundance	Mixed	Flower percentage	Complementary flowers	Correlation coefficient	Table 1	22	NA	NA	0.33	0.05
61	Klein et al. (2002)	Indonesia	1219	Shade-tree cover	20.5	1820	Social	Abundance	Active	Light intensity	NA	Regression (F-statistic)	Table 4	30	NA	NA	-0.44	0.04
62	Klein et al. (2002)	Indonesia	1219	Shade-tree cover	20.5	1820	Solitary	Abundance	Active	Light intensity	NA	Regression (F-statistic)	Table 4	30	NA	NA	-0.43	0.04
63	Klein et al. (2003a)	Indonesia	1219	Shade-tree cover	20.5	1820	Solitary	Richness	Active	Light intensity	NA	Regression (R^2)	Figure 2	24	NA	NA	-1.12	0.05
64	Klein et al. (2003a)	Indonesia	1219	Shade-tree cover	20.5	1820	Solitary	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 2	24	NA	NA	-0.38	0.05
65	Klein et al. (2003a)	Indonesia	1219	Shade-tree cover	20.5	1820	Social	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 2	24	NA	NA	0.55	0.05
66	Klein et al. (2003b)	Indonesia	1219	Shade-tree cover	20.5	1820	Solitary	Richness	Active	Light intensity	NA	Regression (R^2)	Figure 1	15	NA	NA	-0.91	0.08
67	Klein et al. (2003b)	Indonesia	1219	Shade-tree cover	20.5	1820	Social	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	15	NA	NA	0.68	0.08
68	Klein et al. (2003b)	Indonesia	1219	Shade-tree cover	20.5	1820	No data	Richness	Active	Light intensity	NA	Regression (T-statistic)	Table 1	15	NA	NA	-0.63	0.08
69	Klein et al. (2003b)	Indonesia	1219	Shade-tree cover	20.5	1820	Solitary	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	15	NA	NA	-0.48	0.08
70	Jha & Vandermeer (2009)	Mexico	987	Shade-tree cover	24.3	4002	No data	Abundance	Active	Canopy cover	NA	Means (categories)	Results section (Text)	NA	67	57	0.47	0.02
71	Jha & Vandermeer (2009)	Mexico	987	Shade-tree cover	24.3	4002	Solitary	Abundance	Active	Canopy cover	NA	Means (categories)	Figure 2	NA	67	57	0.20	0.02
72	Jha & Vandermeer (2009)	Mexico	987	Shade-tree cover	24.3	4002	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure 2	NA	67	57	0.29	0.02

73	Jha & Vandermeer (2009)	Mexico	987	Shade-tree cover	24.3	4002	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure 2	NA	67	57	0.30	0.02
74	Jha & Vandermeer (2010)	Mexico	1165	Shade-tree cover	22.9	3581	No data	Abundance	Passive	Canopy cover	NA	Means (categories)	Figure 5	NA	12	12	0.58	0.05
75	Jha & Vandermeer (2010)	Mexico	1165	Shade-tree cover	22.9	3581	Solitary	Abundance	Passive	Canopy cover	NA	Means (categories)	Figure 6	NA	18	13	0.54	0.04
76	Jha & Vandermeer (2010)	Mexico	1165	Shade-tree cover	22.9	3581	Solitary	Abundance	Passive	Canopy cover	NA	Means (categories)	Figure 6	NA	18	11	0.29	0.04
77	Munyuli (2011)	Uganda	1191	Shade-tree cover	21.5	1254	Social	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.46	0.04
78	Munyuli (2011)	Uganda	1191	Shade-tree cover	21.5	1254	Social	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.28	0.04
79	Munyuli (2011)	Uganda	1191	Shade-tree cover	21.5	1254	Social	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.37	0.04
80	Munyuli (2011)	Uganda	1191	Shade-tree cover	21.5	1254	Social	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	30	NA	NA	0.31	0.04
81	Munyuli (2011)	Uganda	1191	Shade-tree cover	21.5	1254	Solitary	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	30	NA	NA	0.14	0.04
82	Munyuli (2011)	Uganda	1191	Shade-tree cover	21.5	1254	Solitary	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.19	0.04
83	Munyuli (2011)	Uganda	1191	Shade-tree cover	21.5	1254	Solitary	Abundance	Active	Light intensity	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.28	0.04
84	Boreux et al. (2013a)	India	544	Shade-tree cover	25.7	614	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure 2	NA	32	94	0.74	0.01
85	Boreux et al. (2013a)	India	544	Shade-tree cover	25.7	614	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure 2	NA	32	94	0.72	0.01
86	Boreux et al. (2013a)	India	544	Shade-tree cover	25.7	614	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure 2	NA	32	94	0.02	0.01
87	Boreux et al. (2013b)	India	544	Shade-tree cover	25.7	614	Social	Abundance	Active	Shade tree density	NA	Regression (χ^2)	Table 1	113	NA	NA	0.25	0.01
88	Boreux et al. (2013b)	India	544	Shade-tree cover	25.7	614	Social	Abundance	Active	Shade tree density	NA	Regression (χ^2)	Table 1	113	NA	NA	0.32	0.01
89	Ngo et al. (2013)	Costa Rica	754	Shade-tree cover	23	2938	No data	Richness	Passive	Canopy cover	NA	Means (categories)	Table 2	NA	4	4	-0.62	0.20
90	Ngo et al. (2013)	Costa Rica	754	Shade-tree cover	23	2938	No data	Abundance	Passive	Canopy cover	NA	Means (categories)	Table 2	NA	4	4	-1.31	0.20
91	Berecha et al. (2015)	Ethiopia	1635	Shade-tree cover	19.8	1250	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	-0.86	0.06
92	Berecha et al. (2015)	Ethiopia	1635	Shade-tree cover	19.8	1250	No data	Abundance	Active	Canopy cover	NA	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	0.17	0.06
93	Berecha et al. (2015)	Ethiopia	1635	Shade-tree cover	19.8	1250	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	0.12	0.06

94	Berecha et al. (2015)	Ethiopia	1635	Shade-tree cover	19.8	1250	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	-1.42	0.06
95	Berecha et al. (2015)	Ethiopia	1635	Shade-tree cover	19.8	1250	No data	Abundance	Active	Canopy cover	NA	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	0.28	0.06
96	Berecha et al. (2015)	Ethiopia	1635	Shade-tree cover	19.8	1250	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Figure S1 (Supplementary Material)	NA	10	10	0.19	0.06
97	Caudill et al. (2017)	Costa Rica	1354	Shade-tree cover	18.6	2818	Social	Richness	Active	Canopy cover	NA	Means (categories)	Table 2	NA	9	9	0.14	0.07
98	Caudill et al. (2017)	Costa Rica	1354	Shade-tree cover	18.6	2818	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Table 2	NA	9	9	-0.05	0.07
99	Caudill et al. (2017)	Costa Rica	1354	Shade-tree cover	18.6	2818	Social	Abundance	Active	Canopy cover	NA	Means (categories)	Table 2	NA	9	9	-0.34	0.07
100	Fisher et al. (2017)	Mexico	930	Shade-tree cover	22.9	3581	No data	Richness	Mixed	Canopy cover	NA	Correlation coefficient	Table 1	22	NA	NA	-0.29	0.05
101	Fisher et al. (2017)	Mexico	930	Shade-tree cover	22.9	3581	Social	Abundance	Mixed	Canopy cover	NA	Correlation coefficient	Table 1	22	NA	NA	-0.27	0.05
102	Fisher et al. (2017)	Mexico	930	Shade-tree cover	22.9	3581	Solitary	Abundance	Mixed	Canopy cover	NA	Correlation coefficient	Table 1	22	NA	NA	-0.27	0.05
103	Fisher et al. (2017)	Mexico	930	Shade-tree cover	22.9	3581	Social	Abundance	Mixed	Canopy cover	NA	Correlation coefficient	Table 1	22	NA	NA	0.11	0.05
104	Klein et al. (2003a)	Indonesia	1219	Distance to natural forest	20.5	1820	Social	Richness	Active	Forest distance	NA	Regression (R^2)	Figure 2	24	NA	NA	1.39	0.05
105	Klein et al. (2003b)	Indonesia	1219	Distance to natural forest	20.5	1820	Social	Richness	Active	Forest distance	NA	Regression (R^2)	Figure 1	15	NA	NA	1.17	0.08
106	Klein et al. (2003b)	Indonesia	1219	Distance to natural forest	20.5	1820	No data	Richness	Active	Forest distance	NA	Regression (T-statistic)	Table 1	15	NA	NA	0.28	0.08
107	Klein et al. (2003b)	Indonesia	1219	Distance to natural forest	20.5	1820	Social	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	16	NA	NA	0.58	0.08
108	Ricketts et al. (2004)	Costa Rica	689	Distance to natural forest	22.9	2801	Social	Richness	Active	Forest distance	NA	Means (categories)	Figure 2	NA	4	4	1.90	0.2
109	Ricketts et al. (2004)	Costa Rica	689	Distance to natural forest	22.9	2801	Social	Richness	Active	Forest distance	NA	Means (categories)	Figure 2	NA	4	4	1.75	0.2
110	Ricketts et al. (2004)	Costa Rica	689	Distance to natural forest	22.9	2801	Social	Richness	Active	Forest distance	NA	Means (categories)	Figure 2	NA	4	4	0.60	0.2
111	Ricketts et al. (2004)	Costa Rica	689	Distance to natural forest	22.9	2801	Social	Richness	Active	Forest distance	NA	Means (categories)	Figure 2	NA	4	4	1.14	0.2
112	Ricketts et al. (2004)	Costa Rica	689	Distance to natural forest	22.9	2801	Social	Richness	Active	Forest distance	NA	Means (categories)	Figure 2	NA	4	4	0.67	0.2
113	Jha & Vandermeer (2009)	Mexico	987	Distance to natural forest	24.3	4002	No data	Abundance	Active	Forest distance	NA	ANCOVA (F-statistic)	Table 2	375	NA	NA	0.25	0.003

114	Vergara-Badano et al. (2009)	Mexico	1079	Distance to natural forest	19.6	1868	Social	Richness	Active	Forest distance	NA	Regression (R^2)	Results section (Text)	16	NA	NA	0.73	0.08
115	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Social	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	0.61	0.04
116	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Social	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.18	0.04
117	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Social	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	0.19	0.04
118	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Social	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.18	0.04
119	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Social	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	0.29	0.04
120	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Solitary	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	0.29	0.04
121	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Solitary	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.25	0.04
122	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Solitary	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	0.31	0.04
123	Munyuli (2011)	Uganda	1191	Distance to natural forest	21.5	1254	Solitary	Abundance	Active	Forest distance	NA	Regression (T-statistic)	Table 1	30	NA	NA	-0.23	0.04
124	Banks et al. (2013)	Costa Rica	199	Distance to natural forest	26.1	3257	Social	Richness	Passive	Forest distance	NA	Means (categories)	Figure 2	NA	3	3	-0.76	0.33
125	Banks et al. (2013)	Costa Rica	199	Distance to natural forest	26.1	3257	Social	Abundance	Passive	Forest distance	NA	Means (categories)	Figure 3	NA	3	3	-0.91	0.33
126	Banks et al. (2013)	Costa Rica	199	Distance to natural forest	26.1	3257	No data	Abundance	Active	Forest distance	NA	Means (categories)	Figure 4	NA	3	3	0.69	0.33
127	Banks et al. (2013)	Costa Rica	199	Distance to natural forest	26.1	3257	No data	Abundance	Active	Forest distance	NA	Means (categories)	Figure 4	NA	3	3	-0.59	0.33
128	Boreux et al. (2013a)	India	544	Distance to natural forest	25.7	614	Social	Abundance	Active	Forest distance	NA	Means (categories)	Figure 2	NA	32	94	0.74	0.01
129	Boreux et al. (2013a)	India	544	Distance to natural forest	25.7	614	Social	Abundance	Active	Forest distance	NA	Means (categories)	Figure 2	NA	32	94	0.72	0.01
130	Boreux et al. (2013a)	India	544	Distance to natural forest	25.7	614	Social	Abundance	Active	Forest distance	NA	Means (categories)	Figure 2	NA	32	94	0.02	0.01
131	Bravo-Monroy et al. (2015)	Colombia	1668	Distance to natural forest	20.4	2380	Social	Abundance	Active	Forest distance	NA	Regression (R^2)	Figure S3 (Supplementary Material)	12	NA	NA	-0.75	0.11
132	Caudill et al. (2017)	Costa Rica	1354	Distance to natural forest	18.6	2818	Social	Richness	Active	Forest distance	NA	Means (categories)	Table 2	NA	9	9	0.14	0.07
133	Caudill et al. (2017)	Costa Rica	1354	Distance to natural forest	18.6	2818	Social	Richness	Active	Forest distance	NA	Means (categories)	Table 2	NA	9	9	0.73	0.07
134	Caudill et al. (2017)	Costa Rica	1354	Distance to natural forest	18.6	2818	Social	Abundance	Active	Forest distance	NA	Means (categories)	Table 2	NA	9	9	-0.16	0.07
135	Caudill et al. (2017)	Costa Rica	1354	Distance to natural forest	18.6	2818	Social	Abundance	Active	Forest distance	NA	Means (categories)	Table 2	NA	9	9	0.04	0.07
136	Caudill et al. (2017)	Costa Rica	1354	Distance to natural forest	18.6	2818	Social	Abundance	Active	Forest distance	NA	Means (categories)	Table 2	NA	9	9	-0.21	0.07

137	Caudill et al. (2017)	Costa Rica	1354	Distance to natural forest	18.6	2818	Social	Abundance	Active	Forest distance	NA	Means (categories)	Table 2	NA	9	9	-0.40	0.07

Table S2. Heterogeneity statistics for the three-level meta-analytical random-effects models.

Model	τ^2	I^{2*}
Local floral resources	0.03	85.09
Shade-tree cover	0.10	87.46
Distance to natural forests	0.18	81.37

*When I2 exceeds 75% (Higgins & Thompson, 2022; Higgins et al., 2003), heterogeneity is high, and moderators should be analyzed (Blut et al., 2015).

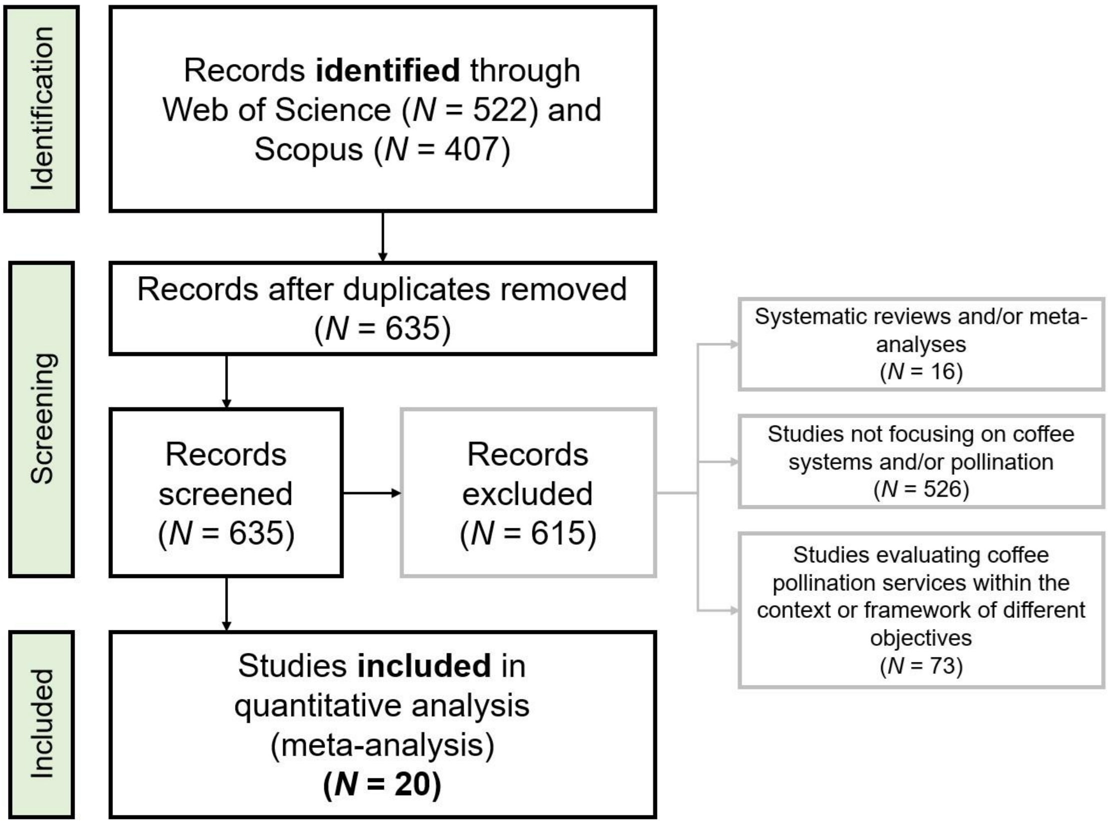
References

Blut, M., Chowdhry, N., Mittal, V., & Brock, C. (2015) E-Service quality: a meta-analytic review. *Journal of Retailing*, **91**, 679–700.

Higgins, J. & Thompson, S.G. (2002) Quantifying Heterogeneity in a Meta-Analysis. *Statistics in Medicine,* **21**, 1539–1558.

Higgins, J., Thompson, S.G., Deeks, J.J., & Altman, D.G. (2003) Measuring Inconsistency in Meta-Analyses. *British Medical Journal,* **6**, 557–60.

Figure S1. Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) flow diagram of the literature search on the effect of management practices within coffee agroforestry systems on pollinator diversity, showing the records obtained by our search and the number of records that were eliminated according to our exclusion criteria.



5. CAPÍTULO 3: Using a response-effect framework to identify agroforestry practices for increasing pollinator functional diversity and improving acerola fruit yield and quality

Diego Centeno-Alvarado, Caroline Souza, Ariadna Valentina Lopes, Xavier Arnan

ID: AGEE39904, Under Review

Agriculture, Ecosystems & Environment:

- Qualis CAPES (Classificações de periódicos quadriênio 2017-2020: Biodiversidade): A1
- Impact Factor: 6.6
- Percentile SCOPUS: 98%

Using a response-effect framework to identify agroforestry practices for increasing pollinator functional diversity and improving acerola fruit yield and quality

Diego Centeno-Alvarado[1], Caroline Souza[2], Ariadna Valentina Lopes[3], Xavier Arnan[1,4]

[1]Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil

[2]Laboratório de Interação Planta-Animal, Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, São Paulo, Brazil

[3]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[4]Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

***Corresponding author:** centenoalvaradodiego@gmail.com; Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife – PE, 52171-900.

Email: centenoalvaradodiego@gmail.com (D. Centeno-Alvarado), carolinesouza.bio@gmail.com (C. Souza), ariadna.lopes@ufpe.br (A.V. Lopes), xavier.arnan@upe.br (X. Arnan).

ORCID

Diego Centeno-Alvarado: https://orcid.org/0000-0003-0273-8538

Caroline Souza: https://orcid.org/0000-0003-4476-4355

Ariadna Valentina Lopes: https://orcid.org/0000-0001-5750-5913

Xavier Arnan: https://orcid.org/0000-0002-9904-274X

Abstract

Pollinators are essential in ecosystems and agricultural systems, but their recent declines are jeopardizing food security. Current research in this area has been exploring questions beyond pollinator taxonomy, such as those focused on functional diversity, in order to clarify how pollinator traits may respond to environmental changes (i.e., response traits) and influence ecosystem functioning (i.e., effect traits). Agroforestry systems can help maintain pollinator diversity and, consequently, food production. Various local and regional management practices could enhance both pollinator diversity and crop yield in agroforestry systems. We applied a response-effect framework to evaluate the influence of management-related variables on the functional diversity of bee pollinators as well as on the yield and quality of acerola (*Malpighia emarginata* DC), a crop of economic and cultural significance in northeastern Brazil. We thus collected data from 10 small agroforestry farms in the Atlantic Forest in the state of Pernambuco. These farms experience a broad diversity of management-related variables at local scales (e.g., floral resources, light intensity) and regional scales (e.g., forest coverage). We characterized bee functional diversity and composition using nine pollination-related traits. To describe fruit yield, we measured fruit set. To describe fruit quality, we measured maximum length and width, fresh mass, firmness, and sugar content. We found that decreased light intensity and increased forest coverage influenced pollinator communities. Notably, they favored the presence of smaller-winged bees. Fruit set increased with higher pollinator visitation rates and the greater presence of oligolectic bees. Additionally, there was a strong association between acerola quality and multiple facets of pollinator trait diversity, trait composition, and visitation rates. Ultimately, the response-effect framework helped identify management approaches that could be used to indirectly boost fruit quality. Our findings highlight the need to consider ecological interactions when designing land management strategies so as to better balance ecological health and system productivity.

Keywords: Agroecology; agroecosystems; plant-pollinator interactions; pollination, West Indian cherry

Introduction

Animal-mediated pollination is a fundamental process in natural and agricultural ecosystems, with impacts on biodiversity, productivity, and global food security (Ollerton, 2017; Katumo et al., 2022). Over 90% of plant species in certain regions exclusively reproduce via animal-mediated pollination, which is carried out by insects, birds, and mammals (Kevan & Baker, 1983; Whelan et al., 2008; Ollerton et al., 2011; Lacker et al., 2019). The result is not only greater plant genetic diversity (Wright, 1946; Wessinger, 2020), but also the increased productivity of crop and non-crop species alike, which means animal-mediated pollination directly shapes ecosystem functionality (Klein et al., 2007; Vanbergen & the Insect Pollinator Initiative, 2013: Sluijs & Vaage, 2016). Yet, this vital ecosystem service is under threat (IPBES, 2017). Worldwide, pollinators are decreasing in abundance and diversity, primarily due to anthropogenic forces (IPBES, 2017). The latter include intensive agriculture, pesticide usage, pathogens, and climate change (Steffan-Dewenter & Westphal, 2008; Potts et al., 2010; Winfree et al., 2011; IPBES, 2017). Pollinator declines are having severe consequences, including lower plant yields (Potts et al., 2010), decreased access to critical resources for human populations (Sluijs & Vaage, 2016), and dramatic volatility in crop prices, leading to significant economic losses (IPBES, 2017).

Previous research on the relationship between pollinators and anthropogenic activities has primarily described pollinator taxonomy and population demography (e.g., Biesmeijer et al., 2006; Brittain et al., 2010; Carvalheiro et al., 2013; Zattara & Aizen, 2021). However, given the concerns listed previously, researchers have shifted their focus to examining functional diversity (Gagic et al., 2015). In general, the objective is to adopt a holistic, functional perspective, otherwise known as a response-effect framework. More specifically, researchers are considering how the phenological, physiological, and behavioral traits of pollinators respond to environmental change (i.e., response traits) and/or influence ecosystem functioning (i.e., effect traits) (Hooper et al., 2000; Tilman, 2001; McGill et al., 2006). Within this framework, if response traits and effect traits fully overlap, then environmental changes should lead to alterations in ecosystem services. Conversely, if there is no overlap, environmental changes should not have a significant impact on ecosystem services.

Understanding pollinator functional diversity is crucial to better understanding levels of ecosystem resilience and sustainability in the face of anthropogenic impacts (Fontaine et al., 2005). For example, environmentally heterogenous agricultural landscapes tend to host a greater diversity of pollinator groups, such as bees and flies, at various spatial and temporal scales (e.g., Hass et al., 2018; Martínez-Núñez et al., 2022; Sciligo et al., 2022). However, more broadly, biodiversity may be positively or negatively impacted depending on consistency or compatibility among landscape features (e.g., topography, soil composition, climate) and species ecological requirements (i.e., related to survival and reproduction) (Dronova, 2017). For instance, biodiversity can be promoted or at least maintained if cover type diversity enhances the availability of food, nesting sites, and dispersal options (Fahrig et al., 2010). Specifically, factors may be operating at local and regional scales. At the local scale, pollinators may benefit from shade trees and diverse floral resources. The former can provide nesting habitat and refuge, ensuring protection against extreme temperatures and intense wind (Ricketts et al., 2004; Prado et al., 2021). The latter generates a consistent and abundant food supply, supporting a broader range of pollinators (e.g., Fründ et al., 2010). At the regional scale, greater amounts of area covered by natural forest (i.e., forest coverage) can offer pollinators a more diverse range of floral resources, non-floral resources, nesting sites, and structural characteristics that may otherwise be lacking (Montagnana et al., 2021; Ulyshen et al., 2023). As a result, environmental factors can influence the composition of pollinator communities and, consequently, the traits represented therein. If specific traits, such as foraging strategies, are favored, the effects could ripple up to shape overall functional diversity within ecosystems.

Management practices could be used to improve pollinator functional diversity in such a way as to boost pollination services (Woodcock et al., 2019; Coutinho et al., 2021). Pollination efficiency is closely linked to the presence of a diverse array of pollinator traits (Phillips et al., 2018; Roquer-Beni et al., 2020; Stavert et al., 2016). For instance, certain pollinators possess traits that allow more effective exploitation of certain flower types and, therefore, higher pollination rates. Thus, a diverse pollinator community will contain a range of traits, which should translate into a broader increase in pollination rates and plant reproductive success (e.g., Woodcock et al., 2019; Coutinho et al., 2021). In this vein, agroforestry systems are known to enhance landscape heterogeneity and promote biodiversity, all while allowing sustainable levels of agricultural productivity (FAO, 2017; USDA, 2019). At the local scale, agroforestry systems provide more abundant and diverse floral resources as well as more extensive shade-tree cover; at the regional scale, they contribute to higher levels of forest coverage (Fahrig et al., 2010; Centeno-Alvarado et al., 2023). One objective of agroforestry management practices is to promote synergies between system productivity and biodiversity conservation (Centeno-Alvarado et al., 2023). Within agroforestry systems, levels of floral resources tend to be positively associated with pollinator diversity and crop production, a relationship that is likely driven by niche complementarity (Centeno-Alvarado et al., 2023). Consequently, increasing resource diversity and quantity seems to create an environment conducive to the coexistence of diverse pollinators (Centeno-Alvarado et al., 2023). Additionally, the presence of shade-tree cover can further amplify pollination services by promoting pollinator diversity, floral visitation rates, and crop production (Centeno-Alvarado et al., 2023). It is important to note that, although infrequent, there are cases in which shade-tree cover and pollinator diversity are negatively related or unrelated (Centeno-Alvarado et al., 2023). Overall, it is evident that the underlying mechanisms and the precise impacts of the above relationships remain to be elucidated.

Generally, agroforestry systems are more common in tropical regions, where their implementation faces fewer social and cultural challenges than in temperate regions. Indeed, these systems have been spreading at a moderate pace in Brazil in recent years, but an absence of guidance on practices and techniques (Martinelli et al., 2019) is hampering system adoption and retention among farmers (Martinelli et al., 2019). This study's objective was thus to determine how local and regional agroforestry management may be affecting the functional diversity of bee pollinators and the latter's impacts on the yield and quality of acerola (*Malpighia emarginata* DC.) in the northeastern Brazilian state of Pernambuco. Acerola is a fruit of great economic and cultural value in this region, and its production largely depends on insect pollination, primarily by bees (EMBRAPA, 2012; Silva et al., 2012; Dias et al., 2018; BPBES & REBIPP, 2019). We hypothesized that 1) management-related variables—namely floral resources, light intensity, and forest coverage—would be positively related to pollinator functional diversity and 2) increased pollinator functional diversity would positively influence acerola fruit yield and quality. This work underscores how a functional diversity approach can help identify effective local and regional agroforestry management practices that can support pollinators, enhance crop production, and promote sustainable agriculture. The application of a response-effect framework can help highlight specific practices capable of optimizing ecosystem services, particularly pollination, while simultaneously preserving agricultural productivity and ecological sustainability.

Materials and Methods

Study sites

Our study was conducted in the northeastern Brazilian state of Pernambuco. This region hosts humid coastal areas dominated by the wet tropical Atlantic Forest. The latter is particularly fragmented in Pernambuco because of extensive sugarcane farming (Ranta et al., 1998; Siqueira Filho et al., 2007). In northeastern Brazil, smallholdings occupy 36.6% of the over 70 million hectares of agricultural lands (Aquino et al., 2020). A smallholding is defined as a farmed surface area of less than 4 fiscal modules (i.e., 1 fiscal module ≤ 90 hectares in this region; Brazilian Family Farming Law 11.326/06). Although 90% of agricultural production in Pernambuco comes from smallholdings, only 3% of farms utilize agroforestry (IBGE, 2017). These farms tend to be concentrated in the state's humid coastal and semi-arid zones (Santos et al., 2023). The Brazilian government is increasingly promoting the implementation of agroforestry systems, as can be seen in the Sectoral Plan for Climate Change Adaptation and Low Carbon Emissions in Agriculture (*Plano ABC+*) 2020–2030 (Ministério de Agricultura, Pecuária e Abastecimento, 2021). This plan describes a national strategy for boosting climate change adaptations and controlling greenhouse gas emissions in Brazilian agricultural systems (Ministério de Agricultura, Pecuária e Abastecimento, 2021). A key objective is to encourage the implementation of agroforestry systems (Ministério de Agricultura, Pecuária e Abastecimento, 2021), which could help protect mean agricultural profitability by mitigating the negative effects of climate change (Schembergue et al., 2017).

We established a total of 10 study sites, each located within a smallholding farm practicing agroforestry on less than 1 hectare of land (Table S1 – Supplementary Materials). These farms were distributed across the municipalities of Igarassu, Recife, Rio Formoso, and Sirinhaém (7.8353–8.6944°S; 34.8806–35.2424°W) (Figs. 1 & S1 – Supplementary Materials). At each study site, we established a 20-m^2 plot. We had permission from the farmers to access their land, and all field research activities were approved by the Brazilian Biodiversity Authorization and Information Systems (SISBIO; license number 86051-1).

Study species

We selected acerola (*Malpighia emarginata* DC., Fam. Malpighiaceae) as our focal study crop because of its dependence on insect pollination and its economic and cultural value in northeastern Brazil. There has been scientific debate as to whether acerola is self-compatible (Freitas et al., 1999; Moura et al., 2018), but it is known that, in the absence of pollination, fruit formation is rare or absent (Freitas et al., 1999). Indeed, acerola strongly relies on insects, mainly bees, for pollination (BPBES & REBIPP, 2019).

Brazil is the foremost producer, consumer, and exporter of acerola (Sazan et al., 2014). Acerola cultivation is particularly widespread in northeastern Brazil because the crop can be grown under various climatic conditions and displays resistance to pests (Freitas et al., 1999; Dias et al., 2018; Moura et al., 2018; Lima et al., 2019). Acerola flowers typically bloom in the early morning, just before dawn, and then persist for one day (Freitas et al., 1999). This species has the remarkable ability to flower year-round (Gomes et al., 2001), ensuring a nearly continuous cash flow for smallholders.

In addition, acerola is a fruit of high nutritional value, whose cultivation could promote regional food security. First, acerola is one of the richest natural sources of ascorbic acid in the world (Prakash & Baskaran, 2018). Second, it possesses substantial levels of phytonutrients with myriad biofunctional properties, such as anti-aging effects and multidrug resistance-reversing activity (Prakash & Baskaran, 2018). Third, it contains high levels of anthocyanins, carotenoids, and vitamin C (EMBRAPA, 2012; Silva et al., 2012; Dias et al., 2018), making it a popular dietary supplement taken by pregnant women, children, athletes, and manual workers, among others (EMBRAPA, 2012).

Local management-related variables

Local management practices frequently affect variables such as shade-tree cover and floral resources. We thus measured light intensity and floral cover in each study plot as proxies. Light intensity was characterized using a luxmeter (KIBOULE, a digital illuminance meter with four measurement ranges from 0 to 1999 W m−2) under standardized conditions. Measurements were obtained at ground level on sunny days between 700 and 1000 hours at 20 randomly selected points within each study plot. A mean value was then calculated (Table S1 – Supplementary Materials). To measure floral cover, we employed a grid-based method. First, each study plot was equally divided into 100 subplots. Next, at each subplot intersection point (i.e., N = 81; Fig. S2 – Supplementary Materials), we assessed flower presence or absence for two distinct strata: (1) the woody layer (i.e., trees and bushes) and (2) the herbaceous layer. Next, we calculated percentage floral cover for each stratum and for the combined strata by dividing the number of intersection points where flowers occurred (Table S1 – Supplementary Materials) by the total number of intersection points sampled. When both strata displayed flowers at a given intersection point, we considered both data points.

We used Spearman rank correlation to examine the associations between stratum-specific levels of floral cover. There was no correlation between floral cover for the woody and herbaceous layers. Given that total floral cover seemed to be largely driven by herbaceous floral cover (Spearman $\rho = 0.86$, $P = 0.001$; Table S2 – Supplementary Materials) and not by woody floral cover (Fig. S3 – Supplementary Materials), we decided to use herbaceous floral cover in the subsequent analyses. There was no correlation between floral cover and light intensity (Spearman ρ = 0.50, *P* = 0.14).

Regional management-related variables

Regional management practices frequently affect landscape configuration. We thus characterized two related metrics in each study plot: (1) natural forest connectivity (effective mesh size in m²) and (2) forest coverage (%). More specifically, effective mesh size estimates landscape connectivity by determining the likelihood that two randomly selected points within a region are connected (i.e., not separated by any physical barriers), indicating that they exist within the same landscape patch (Moser et al., 2007). These two metrics are directly associated with the probability that native pollinator populations can become established, remain viable, and encounter suitable habitat (Kuussaari et al., 2007; Bailey et al., 2014; Griffin & Haddad, 2021; Ganuza et al., 2022). Using the Quantum GIS Landscape Ecology Analysis (LecoS) plugin (v. 2.0.7; Jung, 2016), these metrics were calculated by applying buffer radii of 500 m, 1 km, and 2 km to 2021 MapBiomas land cover maps for Pernambuco (spatial resolution = 30 m; Table S1 – Supplementary Materials) (Souza et al., 2020; MapBiomas Project, 2021). We then used Spearman rank correlation to assess the associations between the landscape metrics across buffer radii. Since the metrics were highly correlated within and across radii (Spearman ρ > 0.7), we decided to only use forest coverage at a buffer radius of 500 m in subsequent analyses (Table S3 – Supplementary Materials). We chose this buffer scale because it corresponds to the typical foraging range of wild bees (Gathmann & Tscharntke, 2002; Steffan-Dewenter et al., 2002; Zurbuchen et al., 2010).

Pollinator surveys

We conducted pollinator surveys between November 2022 and January 2023, with one day allocated to each study site. This time span coincided with the peak flowering period of acerola in the region (Gomes et al., 2001). The daily surveys proceeded as follows. First, we recorded the number of open flowers per individual acerola plant. When there were fewer than 100 open flowers, we used manual counting. Otherwise, we estimated flower number by counting the number of open flowers on five flowering branches and multiplying that figure by the total number of flowering branches. Second, we documented pollinator presence. We randomly selected five individual plants within each study plot and spent 15 min observing all the insects that landed on the flowers and that came in contact with the flowers' reproductive parts. This work was carried out during sunny weather conditions between 700 and 1400 hours. Overall, we conducted 75 minutes of observations per study plot. Following each observation period, insects were captured using sweep nets for subsequent identification. In some cases, we were able to visually identify pollinators in the field. Using the survey data, we calculated the overall abundance of each pollinator species (number of individuals visiting flowers/5 plants/75 minutes) and the overall pollinator visitation rate (number of visits/100 flowers/5 minutes) per study plot.

Acerola fruit yield and quality

To assess pollination services, we measured acerola fruit yield and quality. In each study plot, we randomly selected five acerola plants, which served as a representative sample of the plot's acerola population (i.e., there were never more than 10 acerola plants per plot). We tagged a total of 70 flowers across the 5 plants, which were then monitored to determine the onset of fruit formation (approximately 25 days later; Carrington & King, 2002). Fruit yield was estimated by determining fruit set: we divided the total number of fruits formed by the original number of tagged flowers. Additionally, we collected 50 fruits from the 5 plants (10.9 ± 0.3 fruits per individual), which were all harvested at the same stage of ripening (i.e., when bright red). We then characterized fruit quality, performing all measurements within 3 hours of fruit harvest to ensure consistency in our results and to limit any bias due to water loss and post-harvesting metabolic processes (see Klatt et al., 2014). We specifically measured (1) maximum length, (2) maximum width, (3) fresh mass, (4) firmness, and (5) sugar content, which are established indicators of fruit quality (e.g., Álvarez-Fernández et al., 2003; do Rêgo et al., 2009; Kumar et al., 2010; Garratt et al., 2014). Length and width were measured using a digital caliper, and fresh mass was obtained to the nearest 0.01 g using an EP-05-29 analytical balance. Firmness was quantified using a fruit penetrometer (GY-03), and sugar content was measured using a refractometer (0 to 32 Brix; Kasvi K52-032).

Pollinator functional diversity

We characterized a set of response and effect traits for the acerola pollinators identified during the survey to describe their functional diversity. This response-effect framework can provide valuable insight into how local and regional agroforestry management practices may influence pollinators and pollination services. We chose bee traits that, based on previous research and/or existing knowledge, have a demonstrated influence on pollinator responses to environmental conditions (response: R), pollinator effectiveness (effect: E), or both (response-effect: R-E) (for details, see Table S5 – Supplementary Materials). The response-only traits were forewing aspect ratio (Fig. S4 – Supplementary Materials), nesting location or substrate (i.e., aboveground, belowground, or both), sociality (i.e., social or solitary), and voltinism (i.e., univoltine or multivoltine). Ultimately, we did not use voltinism, as all the species were multivoltines. The effect-only traits were pollen transportation structure (i.e., corbicula or leg scopa) and resource specialization (i.e., resin collector, oil collector, or non-specialist). The response-effect traits were body length (Fig. S4 – Supplementary Materials), intertegular span (Fig. S4 – Supplementary Materials), dietary specialization (i.e., lecty: polylactic or oligolectic), and hairiness (i.e., dense or sparse). For each quantitative trait, we calculated a species-specific mean (n per species: range: 1—13 individuals; mean ± SE: 5 ± 3.6 individuals) using any specimens collected (Table S6 – Supplementary Materials). For the categorical traits, we determined average trait values based on information in the scientific literature (Table S6 – Supplementary Materials). We then calculated the functional dispersion (FDis) values for each individual trait and trait group (i.e., response, effect), which served as a measure of trait diversity. Additionally, we calculated the community-weighted mean (CWM) for each trait as a measure of trait identity. These metrics collectively expressed the functional diversity of acerola pollinators in each study plot. Our calculations were performed in R (v. 4.1.3; R Core Team, 2022) using the function *dbFD* in the package *FD* (v. 1.0-12.1; Laliberté et al., 2022). FDis conveys the mean distance of each species from its community centroid in multidimensional space, which is determined by the values of one or more traits (Laliberté and Legendre, 2010). In our study, FDis was the extent of trait diversity among a particular pollinator community, where higher FDis values indicated that a wider range of traits were present, implying that the pollinator community was more functionally diverse. We calculated FDis values for (1) each individual trait, (2) the response traits (i.e., response traits + response-effect traits), (3) the effect traits (i.e., effect traits + response-effect traits), and (4) the response-effect traits. The CWM expresses the distribution of trait values within a species assemblage (Garnier et al., 2004; Ricotta & Moretti, 2011). In our study, it revealed the dominant traits displayed within a particular pollinator community. For continuous traits, the CWM is the mean trait value across all species within the community and is calculated while accounting for relative species abundance (Ricotta & Moretti, 2001). For categorical traits, the CWM is the proportion or percentage of individuals within each trait category.

Statistical analyses

Applying our response-effect framework, we first analyzed how variables related to agroforestry management practices influenced the functional diversity of bee pollinators. Next, we analyzed how the functional diversity of bee pollinators influenced pollination services by exploring the former's association with acerola fruit yield and quality.

Influence of management-related variables on pollinator functional diversity

To explore the influence of management-related variables on pollinator functional diversity, we ran a set of generalized linear models (GLMs; Gaussian distribution) in which the response variables were as follows: FDis for the individual response traits, FDis for the response traits as a group, FDis for the response-effect traits as a group, and CWM for the individual response traits. Only the model with CWM of nesting location – belowground as a response variable could not be performed because trait values were zero in 8 of the 10 study plots. In all the models, the explanatory variables were light intensity and herbaceous floral cover (i.e., local management-related variables) and forest coverage (i.e., regional management-related variable). The study plots were the replicates. We also included the quadratic term for light intensity in the models because both high and low values could have a negative influence on pollinator visitation rates (Xu et al., 2021).

Influence of pollinator functional diversity on acerola traits

To explore the association between pollinator functional diversity and acerola traits, we employed a combination of GLMs and generalized linear mixed models (GLMMs). We used a Gaussian distribution in all models, with the exception of the fruit set models, in which a binomial distribution was utilized (fruit vs. no fruit). We conducted separate analyses for fruit yield and fruit quality. All the traits tended to have significantly correlated FDis and CWM values (Tables S10-S11 – Supplementary Materials). Consequently, we focused on two FDis to describe trait diversity: one for the effect traits as a group and the other for dietary specialization. To describe trait identity, we focused on two CWMs: one for dietary specialization (specifically oligolectic) and the other for resource specialization (specifically oil collectors). We deemed these traits to be most crucial in the pollination of Malpighiaceae species. Malpighiaceae occupies a unique ecological role since it is one of the oldest plant families known to offer oils as a floral resource (Renner & Schaefer, 2010). Many species within Malpighiaceae rely on bee pollinators that specialize in oil collection, namely those in the tribe Centridini, whose larvae developmentally depend on the oil (Vogel, 1990; Mello et al., 2013). Moreover, these specialist bees often have mutualistic relationships with plant families whose members have oil-producing flowers (Machado, 2004; Mello et al., 2013; Rabelo et al., 2014; Pacheco-Filho et al., 2015).

In the analyses focused on trait diversity, we conducted a GLM in which fruit yield (i.e., fruit set) was the response variable. The explanatory variables were the FDis for the effect traits as a group, the FDis for dietary specialization, and the pollinator visitation rate. The study plots were the replicates. Additionally, we performed a set of GLMMs in which each fruit quality trait was a response variable: maximum length, maximum width, fresh mass, firmness, and sugar content. The explanatory variables in these models were the FDis for the group of effect traits, the FDis for dietary specialization, and the pollinator visitation rate. Plant identity was included as a random factor to control for the multiple measurements taken from individual plants. The fruits were the replicates.

In the analyses focused on trait identity, we again conducted a GLM with fruit yield (i.e., fruit set) as the response variable. The explanatory variables were the CWM for dietary specialization (specifically oligolectic), the CWM for resource specialization (specifically oil collection), and the pollinator visitation rate. The study plots were the replicates. Additionally, we conducted a set of GLMMs in which each fruit quality trait was a response variable. Model structure was the same as described above. Pollinator visitation rate was a covariable in these models, as previous studies have shown that increased flower visitation frequency increases the chances of cross pollination and can therefore influence both fruit formation and quality (Schneider et al., 2009; Chautá-Mellizo et al., 2012; Stein et al., 2017; Boff et al., 2018, MacInnis & Forrest, 2020).

In both the trait diversity and identity models, we included the quadratic terms for the FDis for the effect traits as a group, the FDis for dietary specialization, and the CWM for dietary specialization (specifically oligolectic), in case the relationships were unimodal. We made this choice for several reasons. First, FDis could display unimodal relationships because functional trait space might not follow a linear pattern along environmental gradients (Faith, 1989; Faith, 2015). Second, oligolectic bees could display a unimodal relationship given their pollination efficiency patterns. In certain cases, oligolectic bees have a foraging advantage over polylectic bees because the former’s morphological and behavioral adaptations facilitate the collection of pollen from specific plants (Schlindwein, 2004). However, in other instances, oligolectic bees act as pollen thieves, a behavior that may adversely impact pollination success (Schlindwein, 2004).

We assessed whether assumptions of normality and homoscedasticity were met by graphically evaluating model residuals. In models where these assumptions were not met, the response variables were log transformed. Additionally, we verified that the variance inflation factor (VIF) was lower than 5 for all models. Furthermore, we detected outliers using Cook's distance criterion (outlier = any point with a Cook's distance > 4/*N*; Cook, 1977), and they were excluded from the analyses. A model selection approach was then employed to identify the best-supported models. We started with the full models (i.e., each response variable with all possible combinations of the explanatory variables) and conducted comparisons using Akaike’s information criterion with small-sample correction (AICc) (Burnham & Anderson, 2002) (Table S10 – Supplementary Materials). Models were considered to be well supported when ΔAICc < 2 (Burnham & Anderson, 2002). Afterward, we considered that the variables of greatest relevance were those included in the best-supported models. However, when a null model was one of the best-supported models, then none of the variables were of relevance (Burnham & Anderson, 2002). Finally, we confirmed the absence of any spatial autocorrelation by conducting individual Moran's I tests on the residuals of each full model (Table S13 – Supplementary Materials).

All analyses were conducted in R. The GLMs were performed using the *stats* package (v. 4.4.0; R Core Team, 2022), and the GLMMs were performed with the *nlme* package (v. 3.1-162; Pinheiro et al., 2023). Model selection was carried out using the *MuMIn* package (v. 1.47.5; Bartoń, 2023), and the Moran’s *I* tests were conducted with the *spdep* package (v. 1.2-8; Bivand et al., 2023). During model selection, all relevant relationships were plotted using the *effects* package (v. 4.2-2; Fox, 2003; Fox et al., 2022).

Results

Pollinators

We observed a total of 1,223 bees visiting the acerola flowers (Table S4 – Supplementary Materials). Overall, there were representatives of nine species. Most of these bees (44.89%) were members of three species in the genus *Centris*: *C. analis*, *C. tarsata*, and *C. flavifrons*. The next most abundant species were *Trigona spinipes* (32.38%), *Tetragonisca angustula* (12.10%), and *Plebeia flavocincta* (4.42%). The least abundant species were *Paratetrapedia* sp. (2.94%), *Apis mellifera* (2.70%), and *Frieseomelitta doederleini* (0.57%). However, in terms of occurrence, *Centris analis* was the most abundant species (found in 90% of plots), followed by *Trigona spinipes* (70% of plots), *Centris tarsata* (50% of plots), *Apis mellifera* (50% of plots), and *Paratetrapedia* sp. (30% of plots). Four species—*Centris flavifrons*, *Frieseomelitta* *doederleini*, *Plebeia flavocincta*, and *Tetragonisca angustula*—were found in 20% of plots. Pollinator visitation rate ranged from 0.17 to 4.38 visits/100 flowers/5 min across the study sites (Table S9 – Supplementary Materials).

Acerola fruit yield and quality

Fruit set varied across study sites, ranging from 28.6% to 68.6% (Table S9 – Supplementary Materials). There was also variability in fruit quality (mean ±SE) across study plots. Fruit maximum length ranged from 13.4 ± 0.5 mm to 21 ± 0.3 mm, while fruit maximum width ranged from 17 ± 0.3 mm to 23.8 ± 0.5 mm. Fruit fresh mass ranged from 2.6 ± 0.2 g to 6.9 ± 0.4 g, fruit firmness ranged from 1.1 ± 0.1 kg/cm^2 to 2.4 ± 0.1 kg/cm^2, and sugar content ranged from 5 ± 0.2 Brix to 8.4 ± 0.3 Brix (Figure S5; Table S9 – Supplementary Materials).

Influence of management-related variables on pollinator functional diversity

We only observed one relationship between management-related variables and pollinator functional diversity: light intensity and forest coverage explained the CWM of the forewing aspect ratio (Table S12 – Supplementary Materials). At very low light intensities, there were slightly smaller proportions of bees with larger wings; as light intensities increased, so did proportions of bees with larger wings (Fig. 2A; Tables 1 & S12 – Supplementary Materials). As forest coverage increased, the proportion of bees with larger wings decreased (by ~36%) (Fig. 2B; Tables 1 & S12 – Supplementary Materials).

Influence of pollinator functional diversity on acerola fruit traits

We found that fruit set was explained exclusively by the CWM of oligolectic bees and the pollinator visitation rate (Tables 1 & S12 – Supplementary Materials). A unimodal relationship was observed between fruit set and the CWM of oligolectic bees. Initially, the relationship was negative; however, as the proportion of oligolectic bees reached 0.25, there was a slight increase in fruit set (Fig. 3A). There was a positive association between fruit set and pollinator visitation rate (Fig. 3B).

Acerola quality was explained by all the metrics of pollinator trait diversity and identity as well as by the pollinator visitation rate. Our findings revealed several notable patterns. First, greater trait diversity (FDis for all the effect traits) exhibited a positive and then negative association with fruit maximum length, width, fresh mass, and firmness (Figs. 3C, H, M, Q). Conversely, fruit sugar content initially decreased and then increased (Fig. 3V). Second, diversity in dietary specialization (FDis) mostly had a positive relationship with fruit maximum length, width, fresh mass, and firmness (Figs. 3D, I, N, R). In contrast, there was a largely negative unimodal relationship with fruit sugar content (Fig. 3W). Third, as community proportions of oligolectic bees increased, there was a slight decrease and then increase in fruit maximum length, width, and fresh mass (Figs. 3F, K, O). However, the relationship was reversed for fruit firmness and sugar content (Figs. 3T, Y). Fourth, as community proportions of oil-collecting bees increased, fruit maximum length, maximum width, fresh mass, and firmness decreased (Figs. 3G, L, P, U); in contrast, sugar content increased (Fig. 3Z). Fifth, there was a positive association between pollinator visitation rate and maximum fruit length, width, and firmness (Figs. E, J, S); the association was negative with sugar content (Fig. 3Z); and there was no relationship with fresh mass.

Taken together, these results suggest that management practices are indirectly influencing acerola quality by shaping the functional diversity of bee pollinators. A significant positive correlation was present between the CWM of the forewing aspect ratio and the CWM of oil-collecting bees. The CWM of the forewing aspect ratio changed in response to light intensity and forest coverage, and bee functional diversity was revealed to influence various aspects of acerola quality. There are therefore likely to be significant ties among management practices, pollinator functional diversity, and acerola quality.

Discussion

Overall, we found that variables related to local and regional agroforestry management practices influenced the functional diversity of the bees that pollinate acerola flowers. More specifically, light intensity and forest coverage had different relationships with pollinator functional diversity. Furthermore, reflecting the system’s dynamic interdependence, pollinator functional diversity was associated with acerola fruit yield and quality.

Our results show that local management-related variables can have an influence on pollinator functional diversity. We observed that increasing levels of shade (i.e., reduced levels of light intensity) led to a community shift toward bees with smaller wings, perhaps as a result of bee thermal tolerance. In shadier environments, temperatures may be lower due to reduced radiance (e.g., Armson et al., 2012), and bees with shorter wings may be better able to tolerate lower temperatures as they experience slower rates of energy loss (Peters et al., 2016). Although we did not see a relationship between floral resources and pollinator functional diversity, past research suggests that the relative representation of bee functional traits, such as individual length, individual hairiness, and community diversity, are positively impacted by enhanced floral resources (Hevia et al., 2021; Roquer-Beni et al., 2021). In this vein, effective local management practices include the use of floral strips with melliferous herbaceous plants or the establishment of habitats rich in floral resources (Hevia et al., 2021; Roquer-Beni et al., 2021).

Our results also emphasize that regional management-related variables can affect pollinator functional diversity. Past studies have shown that levels of forest coverage are linked to specific bee traits. Notably, smaller bees appear to be more vulnerable to deforestation (Campbell et al., 2021). Furthermore, the functional trait diversity of bee communities is influenced by forest cover in surrounding areas (Martins et al., 2025). Here, we found that increases in forest coverage were associated with reduced forewing aspect ratio values, which means more forested areas contained communities with a greater relative abundance of smaller-winged bees. It may be that, compared to larger-winged bees, smaller-winged bees can more efficiently maneuver through forested habitats (Mountcastle et al., 2016). Smaller-winged bees may be more effective foragers in more densely vegetated landscapes, given that their compact morphology enables them to better exploit narrow openings in the vegetation (Mountcastle et al., 2016) and access less apparent floral resources. Larger-winged bees might struggle under such environmental conditions, with spatial constraints and complex vegetative structures disrupting their flight patterns (e.g., Murúa et al., 2011) and limiting their foraging effectiveness.

We observed a strong association between the functional traits of the bee pollinators and the traits of acerola fruit. Previous work has underscored this relationship in the context of pollination services, using such metrics as fruit and seed set, fruit mass, and seed mass (e.g., Woodcock et al., 2019; Chase et al., 2023). First, non-overlapping trait distributions were found to be positively associated with fruit yield in oilseed rape (Woodcock et al., 2019). Second, for several plant species worldwide, pollinator body length, diet breadth, nesting patterns, and sociality are traits associated with pollination services (Chase et al., 2023). Increased pollinator trait diversity has been observed to enhance niche segregation (e.g., Fründ et al., 2013), which can, in turn, boost pollination and thereby improve fruit quality (e.g., size and mass). This effect could be mediated by traits such as foraging behavior and dietary preferences (e.g., Woodcock et al., 2019; Chase et al., 2023). However, at a certain point, functional diversity could lead to increased competition. Lower levels of functional diversity imply that there is a greater degree of niche overlap among the species present, which may be experiencing more intense competition for shared resources (e.g., Arceo-

Gómez & Ashman, 2014; Fornoff et al., 2017; Lázaro et al., 2008). The consequences may be reduced fruit size and mass. Here, we found that higher degrees of dietary specialization tended to have positive impacts on fruit quality. If a pollinator community contains species with diverse dietary preferences, resource utilization might be more effective (IPBES, 2017), which can have positive influences on fruit quality, including fruit maximum length, maximum width, fresh mass, and firmness.

It was only in communities where oligolectic bees exceeded 17% representation that we saw benefits for fruit formation, maximum length, maximum width, and fresh mass. Additionally, there was a non-linear relationship between the relative representation of oligolectic bees and the firmness and sugar content of acerola fruit: it first increased, then decreased. Thus, fruit quality could be improved by ensuring that pollinator communities contain a threshold percentage of dietary specialists. The pattern we observed could arise if increased flower homogeneity provokes behavioral changes in more specialized bees, thus enhancing pollination effectiveness (Larsson, 2005; Perfectti et al., 2009; Blüthgen & Klein, 2011). Furthermore, we found that fruit traits were distinctly impacted when there was a greater relative abundance of pollinators specializing in oil collection. The latter have adapted to extract oils from the unique floral structures of Malpighiaceae flowers (Mello et al., 2013). Research on the foraging behavior of these specialists has shown that they dedicate a significant portion of their flights to collecting oil, a resource that is important in both nest construction and offspring rearing (e.g., Aguiar & Gaglianone, 2003; Aguiar & Garófalo, 2004; Camillo, 2005; Oliveira & Schlindwein, 2009; Schäffler & Dötterl, 2011). However, as abundances of oil-collecting bees increase, so could foraging pressure on oil resources, potentially leading to fewer visits by other efficient bee pollinators and, subsequently, diminished overall levels of pollination. In turn, fruit size, mass, and firmness could decline. Pollination dynamics have also been found to influence the nutritional composition of fruit (Samnegård et al., 2019). For instance, in apples, mass can influence concentrations of potassium, zinc, and magnesium because of resource allocation dynamics (Samnegård et al., 2019). We suggest that, here, the greater relative presence of oil-collecting bees might have had indirect impacts on acerola development, where reductions in fruit size, mass, and firmness led to shifts in resource allocation patterns, leading to higher sugar content.

Pollinator visitation rates also influenced acerola fruit yield and quality. Higher visitation rates can exert diverse effects on plant reproductive success and fruit traits. Pollinators play a vital role in transferring pollen among flowers, leading to successful fertilization and fruit formation (Klein et al., 2007; Garibaldi et al., 2011; Ollerton et al., 2011). Higher levels of pollination result in a greater number of flowers successfully transforming into fully developed fruits (Chautá-Mellizo et al., 2012), which ultimately leads to larger fruit yields (e.g., Klatt et al., 2014). Pollination influences the maturation of fruit tissues because it has effects on important cellular mechanisms, such as cell division and expansion, and could thus drive the development of heavier, firmer fruits (e.g., Klatt et al., 2014). However, fruit traits are also impacted by certain plant-specific metabolic shifts, such as those related to ovary enlargement (Shinozaki et al., 2020). These dynamics can potentially result in lower levels of sugar accumulation within the fruits. This finding contrasts with those of research demonstrating that pollination could increase sugar concentrations in cucumber (Gajc-Wolska et al., 2011), muskmelon (Al-Mefleh, Samarah, Zaitoun, & Al-Ghzawi, 2012), oilseed rape (Bommarco, Marini, & Vaissière, 2012), strawberries (Klatt et al., 2014), and watermelon (Sawe et al., 2020).

In conclusion, this study has delved into the multifaceted ways that agroforestry management practices could affect agricultural production using the acerola study system. We observed that the functional diversity of bee pollinator communities displayed different responses to variables related to local and regional agroforestry management practices and that, in turn, pollinator trait diversity influenced fruit quality in a complex manner. Our response-effect framework has revealed that management practices could have significant indirect effects on fruit quality. This work thus offers practical guidance to farmers: agroforestry management practices could be used to enhance acerola fruit quality by strategically shaping pollinator functional diversity. Pollinator community diversity can be augmented by increasing amounts of shade (i.e., reducing light intensity) and maintaining varying levels of forest coverage in surrounding areas. Going forward, it is imperative to conduct research focused on other species of economic and cultural significance in northeastern Brazil, such as cajá (*Spondias lutea*), mango (*Mangifera indica*), pitanga (*Eugenia uniflora*), and seriguela (*Spondias purpurea*) (Cerqueira et al., 2009). In this way, we can develop broader food security strategies and design more effective agroforestry regimes. The latter must be carefully tailored to preserve biodiversity and ensure crop production resilience in the face of ongoing ecosystem changes.

Funding

This study was funded by the Organization for Tropical Studies (OTS) and the Hovore-Horn Entomology Fund (523/573, fellowship number: 1439). In addition, support came in the form of a PhD grant (IBPG-0068-2.05/21) awarded to DC-A and XA by *Fundação de Amparo à Ciência e Tecnologia do Estado de*

Pernambuco (FACEPE), a technical training grant (2021/13297-8) awarded to CS by *Fundação de Amparo à Pesquisa do Estado de São Paulo* (FAPESP), and research productivity grants awarded to AVL (PQ-1D: 309505/2018-6) and XA (PQ-2: 307385/2020-5) by the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq).

Acknowledgments

We thank the OTS, Hovore-Horn Entomology Fund 523/573, FACEPE, FAPESP, and CNPq for their essential financial support, the *Centro de Desenvolvimento Agroecológico Sabiá* for connecting us with the agroforestry farmers, the agroforestry farmers who generously allowed us access to their lands, Daniele R. Parizotto for validating our identification of the bee species, and Jessica Pearce-Duvet for providing English editing services.

References

Aguiar, C.M.L, Gaglione, M.C., 2003. Nesting biology of *Centris* (*Centris*) *aenea* Lepeletier (Hymenoptera, Apidae, Centridini). Revista Brasileira de Zoologia. 20(4). https://doi.org/10.1590/S0101-81752003000400006

Aguiar, C.M.L., Garófalo, C.A., 2004. Nesting biology of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera, Apidae, Centridini). Revista Brasileira de Zoologia. 21(4). https://doi.org/10.1590/S0101-81752004000300009

Al-Mefleh, N.K., Samarah, N., Zaitoun, S., Al-Ghzawi, A., 2012. Effect of irrigation levels on fruit characteristics, total fruit yield and water use efficiency of melon under drip irrigation system. Journal of Food, Agriculture & Environment. 10, 540–545. https://doi.org/10.1234/4.2012.3050

Allouche, O., Kalyuzhny, M., Moreno-Ruega, G., Pizarro, M., Kadmon, R., 2012. Area-heterogeneity tradeoff and the diversity of ecological communities. Proceedings of the National Academy of Sciences of the United States. 109, 17495–17500. https://doi.org/10.1073/pnas.1208652109

Álvarez-Fernández, A., Paniagua, P., Abadía, J., Abadía, A., 2003. Effect of Fe deficiency chlorosis on yield and fruit quality in peach (*Prunus persica* L. Batsch). Journal of Agricultural and Food Chemistry. 51(19), 5738–5744. https://doi.org/10.1021/jf034402c

Aquino, J.R., Alves, M.O., Vidal, M.F., 2020. Agriculture familiar no Nordeste: Um breve panorama dos seus ativos produtivos e da sua importância regional. Boletim Regional, Urbano e Ambiental. 23, 97–110.

Arceo-Gómez, G., Ashman, T.L. (2014). Co-flowering community context influences female fitness and alters the adaptive value of flower longevity in *Mimulus guttatus*. The American Naturalist. 83, E50–E63. https://doi.org/10.1086/674358

Armson, D., Stringer, P., Ennos, A.R., 2012. The effect of tree shade and grass on surface and globe temperatures in an urban area. Urban Forestry & Urban Greening. 11(3), 245-255. https://doi.org/10.1016/j.ufug.2012.05.002

Bailey, S., Requier, F., Nusillard, B., Roberts, S.P.M., Potts, S.G., Bouget, C., 2014. Distance from forest edge affects bee pollinators in oilseed rape fields. Ecology and Evolution. 4, 370–380. https://doi.org/10.1002/ece3.924

Bartoń, K., 2023. MuMIn: Multi-Model inference (v.1.47.5). The R Project for Statistical Computing, CRAN Repository. Available from: https://cran.r-project.org/web/packages/MuMIn/

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T. *et al.*, 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science. 313(5785), 351–354. https://doi.org/10.1126/science.1127863

Bivand, R., Altman, M., Anselin, L., Assunção, R., Berke, O., Blanchet, G. *et al.*, 2023. spdep: Spatial dependence: weighting schemes, statistics (v. 1.2-8). Available from: https://cran.r-project.org/web/packages/spdep/

Bluethgen, N., Klein, A.M., 2011. Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. Basic and Applied Ecology. 12(4), 282–291. https://doi.org/10.1016/j.baae.2010.11.001

BPBES, REBIPP, 2019. Relatório temático sobre polinização, polinizadores e produção de alimentos no Brasil. Plataforma Brasileira de Biodiversidade e Serviços Ecossistêmicos (BPBES) & Rede Brasileira de Interações Planta-Polinizador (REBIPP), São Paulo.

Boff, S., Melo-de-Pinna, G.A.F., Pott, A., Araujo, A.C., 2018. High visitation rate of oil bees may increase pollination efficiency of *Couepia uiti* in Pantanal wetland. Apidologie. 49, 747–758. https://doi.org/10.1007/s13592-018-0598-7

Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia. 169, 1025–1032. https://doi.org/10.1007/s00442-012-2271-6

Brittain, C.A., Vighi, M., Bommarco, R., Settele, J., Potts, S.G., 2010. Impacts of a pesticide on pollinator species richness at different spatial scales. Basic and Applied Ecology. 11(2), 106–115. https://doi.org/10.1016/j.baae.2009.11.007

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Camillo, E., 2005. Nesting biology of four *Tetrapedia* species in trap-nests (Hymenoptera: Apidae: Tetrapediini). Revista de Biología Tropical. 5(1-2)

Campbell, A., Lichtenberg, E.M., Carvalheiro, L.G., Menezes, C., Borges, R.C., Coelho, B.W.T. *et al.*, 2021. High bee functional diversity buffers crop pollination services against Amazon deforestation. Agriculture, Ecosystems & Environment. 326, 107777. https://doi.org/10.1016/j.agee.2021.107777

Carvalheiro, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R. *et al.*, 2013. Species richness declines and biotic homogenization have slowed down for NW-European pollinators and plants. Ecology Letters. 16, 870–878. https://doi.org/10.1111/ele.12121

Centeno-Alvarado, D., Lopes, A.V., Arnan, X., 2023. Fostering pollination through agroforestry: A global review. Agriculture, Ecosystems & Environment. 351, 108578. https://doi.org/10.1016/j.agee.2023.108478

Cerqueira, M.A., Limas, A.M., Teixeira, J.A., Moreira, Vicente, A.A. (2009). Suitability of novel galactomannans as edible coatings for tropical fruits. Journal of Food Engineering. 49, 3-4, 372–378. https://doi.org/10.1016/j.jfoodeng.2009.04.003

Chase, M.H., Fraterrigo, J.M., Harmon-Threatt, A., 2023. Bee functional traits and their relationship to pollination services depend on many factors: A meta-regression analysis. Insect Conservation and Diversity. 16(3), 313–323. https://doi.org/10.1111/icad.12635

Chautá-Mellizo, A., Campbell, S.A., Bonilla, M.A., 2012. Effects of natural and artificial pollination on fruit and offspring quality. Basic and Applied Ecology. 13(6), 524–532. https://doi.org/10.1016/j.baae.2012.08.013

Coutinho, J.G.E., Hipólito, J., Santos, R.L.S., Moreira, E.F., Boscolo, D., Viana, B.F., 2021. Frontiers in Ecology and Evolution Sec. Biogeography and Macroecology. 9. https://doi.org/10.3389/fevo.2021.624835

Cook, R.D., 1977. Detection of influential observation in linear regression. Technometrics. 19(1), 15–18. https://doi.org/10.2307/1268249

Decourtye, A., Mader, E., Desneux, N., 2010. Landscape enhancement of floral resources for honey bees in agro-ecosystems. Apidologie. 41(3), 264–277. https://doi.org/10.1051/apido/2010024

Dias, A.S., Lima, G.S., Sá, F.V.S., Gheyi, H.R., Soares, L.A.A., Fernandes, P.D., 2018. Gas exchanges and photochemical efficiency of West Indian cherry cultivated with saline water and potassium fertilization. Revista Brasileira de Engenharia Agrícola e Ambiental. 22(9), 628–633. https://doi.org/10.1590/1807-1929/agriambi.v22n9p628-633

do Rêgo, E.R., do Rêgo, M.M., Finger, F.L., Cruz, C.D., Casali, V.W.D., 2009. A diallel study of yield components and fruit quality in chilli pepper (*Capsicum baccatum*). Euphytica. 168, 275–287. https://doi.org/10.1007/s10681-009-9947-y

Dray, S., Dufour, A.B., Thioulouse, J., 2023. Ade4: Analysis of ecological data: exploratory and Euclidean methods in environmental sciences (v. 1.7-22). Available from: https://cran.r-project.org/web/packages/ade4

Eckerter, T., Buse, J., Bauhus, J., Förschler, M.I., Klein, A.M., 2021. Wild bees benefit from structural complexity enhancement in a forest restoration experiment. Forest Ecology and Management. 496, 119412. https://doi.org/10.1016/j.foreco.2021.119412

EMBRAPA, 2012. A cultura da acerola. Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Brasília.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J. *et al.*, 2010. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters. 14(2), 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Faith, D.P., 1989. Homoplasy as pattern: multivariate analysis of morphological convergence in Anseriformes. Cladistics. 5, 235–258. https://doi.org/10.1111/j.1096-0031.1989.tb00488.x

Faith, D.P., 2015. The unimodal relationship between species' functional traits and habitat gradients provides a family of indices supporting the conservation of functional trait diversity. Plant Ecology. 216, 725–740. https://doi.org/10.1007/s11258-015-0454-z

FAO, 2017. Sustainable woodfuel for food security – A smart choice: green renewable and affordable. Food and Agriculture Organization of the United Nations (FAO), Rome.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. *et al.*, 2005. Global consequences of land use. Science. 309(5734), 570–574. https://doi.org/10.1126/science.1111772

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M. (2005). Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. PLoS Biology. 4, e1. https://doi.org/10.1371/journal.pbio.0040001

Fornoff, F., Klein, A.M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M. *et al.*, 2017. Functional flower traits and their diversity drive pollinator visitation. Oikos. 126, 1020–1030. https://doi.org/10.1111/oik.03869

Fox, J., 2003. Effect displays in R for generalised linear models. Journal of Statistical Software. 8(15). https://doi.org/10.18637/jss.v008.i15

Fox, J., Weisberg, S., Price, B., Friendly, M., Hong, J., Andersen, R. *et al.*, 2022. effects: Effect displays for linear, generalized linear, and other models (v. 4.2-1). Available from: https://cran.r-project.org/web/packages/effects/

Freitas, B.M., Alves, J.E., Brandão, G.F., Araujo, Z.B., 1999. Pollination requirements of West Indian cherry (*Malpighia ermarginata*) and its putative pollinators, *Centris* bees, in NE Brazil. Journal of Agricultural Science. 133(3), 303–311. https://doi.org/10.1017/s0021859699006930

Fründ, J., Dormann, C.F., Holzschuh, Tscharntke, T., 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology. 94(9). 2042–2054. https://doi.org/10.1890/12-1620.1

Fründ, J., Linsenmair, K.E., Blüthgen, N., 2010. Pollinator diversity and specialization in relation to flower diversity. Oikos. 119(1), 1581–1590. https://doi.org/10.1111/j.1600-0706.2010.18450.x

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C. *et al.*, 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society B. 282(1801), 20142620. https://doi.org/10.1098/rspb.2014.2620

Gajc-Wolska, J., Kowalczyk, K., Mikas, J., Drajski, R., 2011. Efficiency of cucumber (*Cucumis sativus* L.) pollination by bumblebees (*Bombus terrestris*). Acta Scientiarum Polonorum. 10, 159–169.

Ganuza, C., Redlich, S., Uhler, J., Tobish, C., Rojas-Botero, S., Peters, M.K. et al., 2022. Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. Science Advances. 8(18), eabm9359. https://doi.org/10.1126/sciadv.abm9359

Gardein, H., Fabian, Y., Westphal, C., Tscharntke, T., Hass, A., 2022. Ground-nesting bees prefer bare ground areas on calcareous grasslands. Global Ecology and Conservation. 39, e02289. https://doi.org/10.1016/j.gecco.2022.e02289

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A. e*t al.*, 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters. 14, 1062–1072. https://doi.org/10.1111/j.1461- 0248.2011.01669.x

Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M. *et al.*, 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology. 85, 2630–2637. https://doi.org/10.1890/03-0799

Garratt, M.P.D., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C., Potts, S.G., 2014. Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. Agriculture, Ecosystems & Environment. 184, 34–40. https://doi.org/10.1016/j.agee.2013.10.032

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. Journal of Animal Ecology. 71, 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Gomes, J.E., Pavani, M.C.M.D., Perecin, D., Martins, A.B.G., 2001. Morfologia floral e biologia reprodutiva de genótipos de aceroleira. Scientia Agricola. 58(3), 519–523. https://doi.org/10.1590/S0103-90162001000300013

Griffin, S.R., Haddad, N.M., 2021. Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape. Ecography. 44(6), 919–927. https://doi.org/10.1111/ecog.05299

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Baillod, A.B., Sirami, C. *et al.*, 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proceedings of the Royal Society B. 285, 20172242. https://doi.org/10.1098/rspb.2017.2242

Hevia, V., Carmona, C.P., Azcárate, F.M., Heredia, R., González, J.A., 2021. Role of floral strips and semi-natural habitats as enhancers of wild bee functional diversity in intensive agricultural landscapes. Agriculture, Ecosystems & Environment. 319, 107544. https://doi.org/10.1016/j.agee.2021.107544

Hooper, D.U., Solan, M., Symstad, A., Díaz, S., Gessner, M.O., Buchmann, N. *et al.* 2002. Species diversity, functional diversity, and ecosystem functioning, in: Loreau, M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and Ecosystem Functioning. Oxford University Press, Oxford, pp. 195–208.

IBGE, 2017. Censo Agropecuário 2017. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro.

IPBES, 2017. The assessment report on pollinators, pollination and food production. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), Bonn.

Jung, M., 2016. LecoS – A python plugin for automated landscape ecology analysis. Ecological Informatics. 31, 18–21. https://doi.org/10.1016/j.ecoinf.2015.11.006

Kadmon, R., Allouche, O., 2007. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. The American Naturalist. 170, 443–454. https://doi.org/10.1086/519853

Kevan, P.G., Baker, H.G., 1983. Insects as flower visitors and pollinators. Annual Review of Entomology. 28, 407–453. https://doi.org/10.1146/annurev.en.28.010183.002203

Klatt, B.K., Holzchuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. et al., 2014. Bee pollination improves crop quality, shelf life and commercial value. Proceedings of the Royal Society B. 128(1175). https://doi.org/10.1098/rspb.2013.2440

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. *et al.*, 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B. 274(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Kumar, M., Rawat, V., Rawat, J.M.S., Tomar, Y.K., 2010. Effect of pruning intensity on peach yield and fruit quality. Scientia Horticulturae. 125(3), 218–221. https://doi.org/10.1016/j.scienta.2010.03.027

Kuussaari, M., Heliölä, J., Luoto, M., Pöyry, J., 2007. Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. Agriculture, Ecosystems & Environment. 122, 366–376. https://doi.org/10.1016/j.agee.2007.02.008

Lacher, T.E., Davidson, A.D., Fleming, T.H., Gómez-Ruíz, E.P., McCracken, G.F., Owen-Smith, N. *et al.*, 2019. The functional roles of mammals in ecosystems. Journal of Mammalogy. 100(3), 942–964. https://doi.org/10.1093/jmammal/gyy183

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology. 91(1), 299–305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P., Shipley, B., 2022. FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology (v.1.0-12.1). The R Project for Statistical Computing, CRAN Repository. Available from: https://cran.r-project.org/web/packages/FD/

Larsson, M., 2005. Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized Knauita arvensis (Dipsacaceae). Oecologia. 146, 394–403. https://doi.org/10.1007/s00442-005-0217-y

Lázaro, A., Hegland, S.J., Totland, Ø., 2008. The relationships between floral traits and specificity of pollination systems in three Scandinavian plant communities. Oecologia. 157, 249–257. https://doi.org/10.1007/s00442-008-1066-2

Lima, G.S., Pinheiro, F.W.A., Dias, A.S., Gheyi, H.R., Soares, L.A.A., Silva, S.S., 2019. Growth and production components of West Indian cherry cultivated with saline waters and potassium fertilization. Revista Brasileira de Engenharia Agrícola e Ambiental. 23(4), 250–256. https://doi.org/10.1590/1807-1929/agriambi.v23n4p250-256

Machado, I.C., 2004. Oil-collecting bees and related plants: a review of the studies in the last twenty years and case histories of plants occurring in NE Brazil, in: Freitas, B.M., Pereira, J.O.P. (Eds.), Solitary bees: Conservation, rearing and management for pollination. Imprensa Universitária da Universidade Federal do Ceará, Fortaleza, pp. 255–280.

MacInnis, G., Forrest, J.R.K., 2020. Field design can affect cross-pollination and crop yield in strawberry (*Fragaria* × *ananassa* D.). Agriculture, Ecosystems & Environment. 285, 106738. https://doi.org/10.1016/j.agee.2019.106738

Magalhães, C.B., Freitas, B.M., 2013. Introducing nests of the oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini) for pollination of acerola (*Malpighia emarginata*) increases yield. Apidologie. 44, 234–239. https://doi.org/10.1007/s13592-012-0175-4

MapBiomas Project, 2021. MapBiomas Project Collection (v.7.1.) of the Annual Series of Land Use and Land Cover Maps of Brazil. MapBiomas Project, São Paulo. Available from: https://plataforma.brasil.mapbiomas.org/

Martinelli, G.C., Schlindwein, M.M., Padovan, M.P., Gimenes, R.M.T., 2019. Decreasing uncertainties and reversing paradigms on the economic performance of agroforestry systems in Brazil. Land Use Policy. 80, 274–286. https://doi.org/10.1016/j.landusepol.2018.09.019

Martínez-Núñez, C., Kleijn, D., Ganuza, C., Heupink, D., Raemakers, I., Vertommen, W. *et al.*, 2022. Temporal and spatial heterogeneity of semi-natural habitat, but not crop diversity is correlated with landscape pollinator richness. Journal of Applied Ecology. 59(5), 1258–1267. https://doi.org/10.1111/1365-2664.14137

Martins, K.T., Gonzales, A., Lechowicz, M.J., 2015. Pollination services are mediated by bee functional diversity and landscape context. Agriculture, Ecosystems & Environment. 200, 12–20. https://doi.org/10.1016/j.agee.2014.10.018

Mello, M.A.R., Bezerra, E.L.S., Machado, I.C., 2013. Functional roles of Centridini oil bees and Malpighiaceae oil flowers in biome-wide pollinator networks. Biotropica. 45(1), 45–53. https://doi-org/10.1111/j.1744-7429.2012.00899.x

Ministério de Agricultura, Pecuária e Abastecimento, 2021. Plano Setorial para Adaptação à Mudança do Clima e Baixa Emissão de Carbono na Agropecuária 2020-2030. Ministério de Agricultura, Pecuária e Abastecimento, Brasília.

Montagnana, P.C., Alves, R.S.C., Garófalo, C.A., Ribeiro, M.C., 2021. Landscape heterogeneity and forest cover shape cavity-nesting hymenopteran communities in a multi-scale perspective. Basic and Applied Ecology. 56, 239-249. https://doi.org/10.1016/j.baae.2021.08.004

Moser, B., Jaefer, J.A.G., Tappeiner, U., Tasser, E., Eiselt, B., 2007. Modification of the effective mesh size for measuring landscape fragmentation to solve the boundary problem. Landscape Ecology. 22, 447–459. https://doi.org/10.1007/s10980-006-9023-0

Mountcastle, A.M., Alexander, T.M., Switzer, C.M., Combes, S.A., 2016. Wing wear reduces bumblebee flight performance in a dynamic obstacle course. Biology Letters. 12, 1060294. https://doi.org/10.1098/rsbl.2016.0294

Moura, C.F.H., Oliveira, L.S., Souza, K.O., Franca, L.G., Ribeiro, L.B., Souza, P.A. et al., 2018. Acerola – *Malpighia emarginata*. Exotic Fruits. Reference Guide, 7–14. https://doi.org/10.1016/B978-0-12-803138-4.00003-4

Murphy, J.T., Breeze, T.D., Willcox, B., Kavanagh, S., Stout, J.C., 2022. Globalisation and pollinators: pollinator declines are an economic threat to global food systems. People and Nature. 4(3), 773 - 785. https://doi.org/10.1002/pan3.10314

Murúa, M.M., Grez, A.A., Simonetti, J.A., 2011. Changes in wing length in the pollinator Bombus dahlbomii occuring with the fragmentation of the Maulino forest, Chile. Ciencia e Investigación Agraria. 38(3), 391-396. https://doi.org/10.4067/S0718-16202011000300008

Oliveira, R., Schlindwein, C., 2009. Searching for a manageable pollinator for acerola orchards: the solitary oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini). Horticultural Entomology. 102(1), 265–273. https://doi.org/0022-0493/09/0265-0273$04.00/0

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos. 120(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Pacheco-Filho, A.J.S., Verola, C.F., Verde, L.W.L., Freitas, B.M., 2015. Bee-flower association in the Neotropics: implications to bee conservation and plant pollination. Apidologie. 46, 530–541. https://doi.org/10.1007/s13592-014-0344-8

Perfectti, F., Gómez, J.M., Bosch, J., 2009. The functional consequences of diversity in plant–pollinator interactions. Oikos. 118, 1430–1440. https://doi.org/10.1111/j.1600-0706.2009.17491.x

Peters, M.K., Peisker, J., Steffan-Dewenter, I., Hoiss, B., 2016. Morphological traits are linked to the cold performance and distribution of bees along elevational gradients. Journal of Biogeography. 43(1), 2040–2049, https://doi.org/10.1111/jbi.12768

Phillips, B.B., Williams, A., Osborne, J.L., Shaw, R.F., 2018. Shared traits make flies and bees effective pollinators of oilseed rape (*Brassica napus* L.). Basic and Applied Ecology. 32, 66–76. https://doi.org/10.1016/j.baae.2018.06.0

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., EISPACK, Heisterkamp, S. *et al.*, 2023. nlme: Linear and nonlinear mixed effect models (v. 3.1-162). Available from: https://cran.r-project.org/web/packages/nlme/

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution. 25(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Prado, S.G., Collazo, J.A., Marand, M.H., Irwin, R.E., The influence of floral resources and microclimate on pollinator visitation in an agro-ecosystem. Agriculture, Ecosystems & Environment. 307, 107196. https://doi.org/10.1016/j.agee.2020.107196

Prakash, A., Baskaran, R., 2018. Acerola, an untapped functional superfruit: a review on lastest frontiers. Journal of Food Science and Technology. 55(9), 3373–3384. https://doi.org/10.1007/s13197-018-3309-5

R Core Team, 2022. The R ‘stats’ package (v.4.4.0). The R Project for Statistical Computing. Available from: https://stat.ethz.ch/R-manual/R-devel/library/stats

R Core Team, 2022. The R Project for Statistical Computing (v. 4.1.3). The R Project for Statistical Computing. Available from: https://www.r-project.org/

Rabelo, L.S., Vilhena, A.M., Bastos, E.M., Aguiar, C.M., Augusto, S.C., 2015. Oil-collecting bee–flower interaction network: do bee size and anther type influence the use of pollen sources? Apidologie. 46, 465–477. https://doi.org/10.1007/s13592-014-0336-8

Ranta, P., Blom, T., Niemelã, J., Joensuu, E., Siitonen, M., 1998. The fragmented Atlantic rain forest of Brazil: size, shape, and distribution of forest fragments. Biodiversity and Conservation. 7, 385–403. https://doi.org/10.1023/A:1008885813543

Renner, S.S., Schaefer, H., 2010. The evolution and loss of oil-offering flowers: New insights from dated phylogenies for angiosperms and bees. Philosophical Transaction of the Royal Society B. 365, 423–435. https://doi.org/10.1098/rstb.2009.0229

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A. et al. 2008. Landscape effects on crop pollination services: are there general patterns? Ecology Letters. 11(5) 499 - 515. https://doi.org/10.1111/j.1461-0248.2008.01157.x

Ricotta, C., Moretti, M., 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia. 167, 181–188. https://doi.org/10.1007/s00442-011-1965-5

Roquer-Beni, L., Alins, G., Arnan, X., Boreux, V., García, D., Hambäck, P.A. *et al*., 2021. Management-dependent effects of pollinator functional diversity on apple pollination services: A response-effect trait approach. Journal of Applied Ecology. 58(12), 2843-2853. https://doi.org/10.1111/1365-2664.14022

Roquer-Beni, L., Rodrigo, A., Arnan, X., Klein, A., Fornoff, F., Boreux, V. *et al.*, 2020. A novel method to measure hairiness in bees and other insect pollinators. Ecology and Evolution. 10(6), 2979– 2990. https://doi.org/10.1002/ece3.6112

Samnegård,U., Hambäck, P.A., Smith, H.G., 2019. Pollination treatment affects fruit set and modifies marketable and storable fruit quality of commercial apples. Royal Society Open Science. 6(12), 190326. https://doi.org/10.1098/rsos.190326

Schlindwein, C. 2004. Are oligolectic bees always the most effective pollinators?, in: Freitas, B.M., Pereira, J.O.P. (Eds.), Conservation, rearing and management for pollination. Imprensa Universitária, Fortaleza, pp. 231–240.

Santos, C.S.M., Freitas, M.A.V., Silva, N.F., Deus, L.A.B., Prodanoff, J.H.A., 2023. The role of rural credit policies in agricultural income generation in family farms in Pernambuco State, northeastern Brazil -

spatial trend and future scenarios. Ciencia Rural. 53(10). https://doi.org/10.1590/0103-8478cr20220261

Sawe, T., Eldegard, K., Totland, Ø., Macrice, S., Nielsen, A., 2020. Enhancing pollination is more effective than increased conventional agriculture inputs for improving watermelon yields. Ecology and Evolution. 10(12) 5343-5353. https://doi.org/10.1002/ece3.6278

Sazan, M.S., Queiroz, E.P., Caliman, L.J.F., Parra-Hinijosa, A., Silca, C.I., Fonseca, V.L.I. *et al.*, 2014. Manejo de polinizadores da aceroleira. Holos, Ribeirão Preto.

Schäffler, I., Dötterl, S., 2011. A day in the life of an oil bee: phenology, nesting, and foraging behavior. Apidologie. 42, 409–424. https://doi.org/10.1007/s13592-011-0010-3

Schembergue, A., Cunha, D.A., Carlos, S.M., Pires, M.V., Faria, R.M., 2017. Sistemas agroflorestais como estratégia de adaptação aos desafios das mudanças climáticas no Brasil. Revista Economia e Sociologia Rural. 55(1). https://doi.org/10.1590/1234-56781806-94790550101

Schneider, D., Goldway, M., Rotman, N., Adato, I., Stern, R.A., 2009. Cross pollination improves 'Orri' mandarin fruit yield. Scientia Horticulturae. 122(3), 380–384. https://doi.org/10.1016/j.scienta.2009.06.009

Sciligo, A.R., M'Gonigle, L.K., Kremen, C., 2022. Local diversification enhances pollinator visitation to strawberry and may improve pollination and marketability. Frontiers in Sustainable Food Systems. 6. https://doi.org/10.3389/fsufs.2022.941840

Shinozaki, Y., Beauvoit, B.P., Takahara, M., Hao, S., Ezure, K., Andrieu, M.H. e*t al.*, 2020. Fruit setting rewires central metabolism via gibberellin cascades. Proceedings of the National Academy of Sciences USA. 117(38), 23970–23981. https://doi.org/10.1073/pnas.2011859117

Silva, M.A.C., Silva, Z.E., Mariani, V.C., Darche, S., 2012. Mass transfer during the osmotic dehydration of West Indian cherry. LWT - Food Science and Technology. 45(2), 246–252. https://doi.org/10.1016/j.lwt.2011.07.032

Siqueira Filho, J.A., Santos, A.M.M., Leme, E.M.C., Cabral, J.S., 2007. Atlantic Forest fragments and bromeliads in Pernambuco and Alagoas: Distribution, composition, richness and conservation, in: Siqueira Filho, J.A., Leme, E.M.C. (Eds.), Fragments of the Atlantic Forest of Northeast Brazil: Biodiversity, conservation and the bromeliads. Bromeliad Society International, Texas, pp. 101–131.

Sluijs, J.P., Vaage, N.S., 2016. Pollinators and global food security: the need for holistic global stewardship. Food Ethics. 1, 75–91. https://doi.org/10.1007/s41055-016-0003-z

Sollern-Norrlin, M., Ghaley, B.B., Rintoul, N.L.J., 2020. Agroforestry benefits and challenges for adoption in Europe and beyond. Sustainability. 12(7). https://doi.org/10.3390/su12177001

Stavert, J.R., Liñán-Cembrano, G., Beggs, J.R., Howlett, B.G., Pattemore, D.E., Bartomeus, I., 2016. Hairiness: The missing link between pollinators and pollination. PeerJ. 4, e2779. https://doi.org/10.7717/peerj.2779

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002, Scale-dependent effects of landscape context on three pollinator guilds. Ecology. 83, 1421–1432. https://doi.org/10.2307/3071954

Steffan-Dewenter, I., Westphal, C., 2008. The interplay of pollinator diversity, pollination services and landscape change. Journal of Applied Ecology. 45(3), 737–741. https://doi.org/10.1111/j.1365-2664.2008.01483.x

Stein, K., Coulibaly, D., Stenchly, K., Goetze, D., Porembski, S., Lindner, A. *et al.*, 2017. Bee pollination increases yield quality and quality of cash crops in Burkina Faso, West Africa. Scientific Reports. 7(1), 17691. https://doi.org/10.1038/s41598-017-17970-2

Tilman, D., 2001. Functional diversity, in: Levin, S.A., (Ed.), Encyclopedia of Biodiversity. Academic Press, New York, pp. 109–120.

Ulyshen, M., Urban-Mead, K.R., Dorey, J.B., Rivers, J.W., 2023. Forests are critically important to global pollinator diversity and enhance pollination in adjacent crops. Biological Reviews. https://doi.org/10.1111/brv.12947

USDA, 2019. Agroforestry Strategic Framework: Fiscal Years 2019–2024. United States Department of Agriculture (USDA), Washington DC.

Vanbergen, A.J., the Insect Pollinators Initiative, 2013. Threats to an ecosystem service: pressures on pollinators. Frontiers in Ecology and the Environment. 11(5), 251–259. https://doi.org/10.1890/120126

Vaudo, A.D., Tooker, J.F., Grozinger, C.M., Patch, H.M., 2015. Bee nutrition and floral resource restoration. Current Opinion in Insect Science. 10, 133–141. https://doi.org/10.1016/j.cois.2015.05.008

Vogel, S. 1990. History of the Malpighiaceae in the light of the pollination ecology. Memoirs of the New York Botanical Garden. 55, 130–142.

Wessinger, C.A., 2021. From pollen dispersal to plant diversification: genetic consequences of pollination mode. New Phytologist. 229(6), 3125–3132. https://doi.org/10.1111/nph.17073

Whelan, C.J., Wenny, D.G., Marquis, R.J., 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences. 1134(1), 25–60. https://doi.org/10.1196/annals.1439.003

Winfree, R., Bartomeus, I., Cariveau, D.P., 2011. Native pollinators in anthropogenic habitats. Annual Review of Ecology, Evolution, and Systematics. 42, 1–22. https://doi.org/10.1146/annurev-ecolsys-102710-145042

Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J. *et al*. 2019. Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. Nature Communications. 10, 1481. https://doi.org/10.1038/s41467-019-09393-6

Wright S., 1946. Isolation by distance under diverse systems of mating. Genetics. 31(1), 39–59. https://doi.org/10.1093/genetics/31.1.39

Xu, X., Ren, Z.X., Trunschke, J., Kuppler, J., Zhao, Y.H., Knop, E. et al., 2021. Bimodal activity of diurnal flower visitation at high elevation. Ecology and Evolution. 11, 13487–13500. https://doi.org/10.1002/ece3.8074

Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. One Earth. 4(1), 114–123. https://doi.org/10.1016/j.oneear.2020.12.005

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation. 143, 669–676. https://doi.org/10.1016/j.biocon.2009.12.003

Table 1. Summary of the best-supported models examining the associations between (1) management-related variables and pollinator functional diversity and (2) pollinator functional diversity and acerola (*Malpighia emarginata* DC.) fruit traits. The data were collected in smallholder agroforestry systems in the humid coastal areas of Pernambuco, northeastern Brazil. Indicated below are the names for the full models (*model ID* – response variable), the structure of the full models, the explanatory variables retained in the best-supported models (see Table S12 – Supplementary Materials for details about the model comparisons). Abbreviation: E: effect traits.

Full model	**Best-supported models**	**Explanatory variables retained**
CWM (forewing aspect ratio)		
CWM (forewing aspect ratio) = floral cover + light intensity + light intensity^2 + regional forest cover	1	light intensity^2 + regional forest cover
Fruit set – trait diversity		
Fruit set = FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate	1	pollinator visitation rate
Fruit set – trait identity		
Fruit set = CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate	1	CWM (oligolectic) + CWM (oligolectic)^2 + pollinator visitation rate
Log (maximum fruit length + 1) – trait diversity		

Log (maximum fruit length + 1) = FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate	1	FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate
Log (maximum fruit length + 1) – trait identity		
Log (maximum fruit length + 1) = CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate	1, 2	CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors)
Log (maximum fruit width + 1) – trait diversity		
Log (maximum fruit width + 1) = FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate	1, 2	FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate
Log (maximum fruit width + 1) – trait identity		
Log (maximum fruit width + 1) = CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate	1	CWM (oligolectic)^2 + CWM (oil collectors)
Log (fruit fresh mass + 1) – trait diversity		

Log (fruit fresh mass + 1) = FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate	1	FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2
Log (fruit fresh mass + 1) – trait identity		
Log (fruit fresh mass + 1) = CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate	1	(oligolectic)^2 + CWM (oil collectors)
Log (fruit firmness + 1) – trait diversity		
Log (fruit firmness + 1) = FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate	1, 2, 3	FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate
Log (fruit firmness + 1) – trait identity		
Log (fruit firmness + 1) = CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate	1	CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate
Log (fruit sugar content + 1) – trait diversity		

Log (fruit sugar content + 1) = FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate	1, 2	FDis (E) + FDis (E)^2 + FDis (dietary specialization) + FDis (dietary specialization)^2 + pollinator visitation rate
Log (fruit sugar content + 1) – trait identity		
Log (fruit sugar content + 1) = CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate	1	CWM (oligolectic) + CWM (oligolectic)^2 + CWM (oil collectors) + pollinator visitation rate

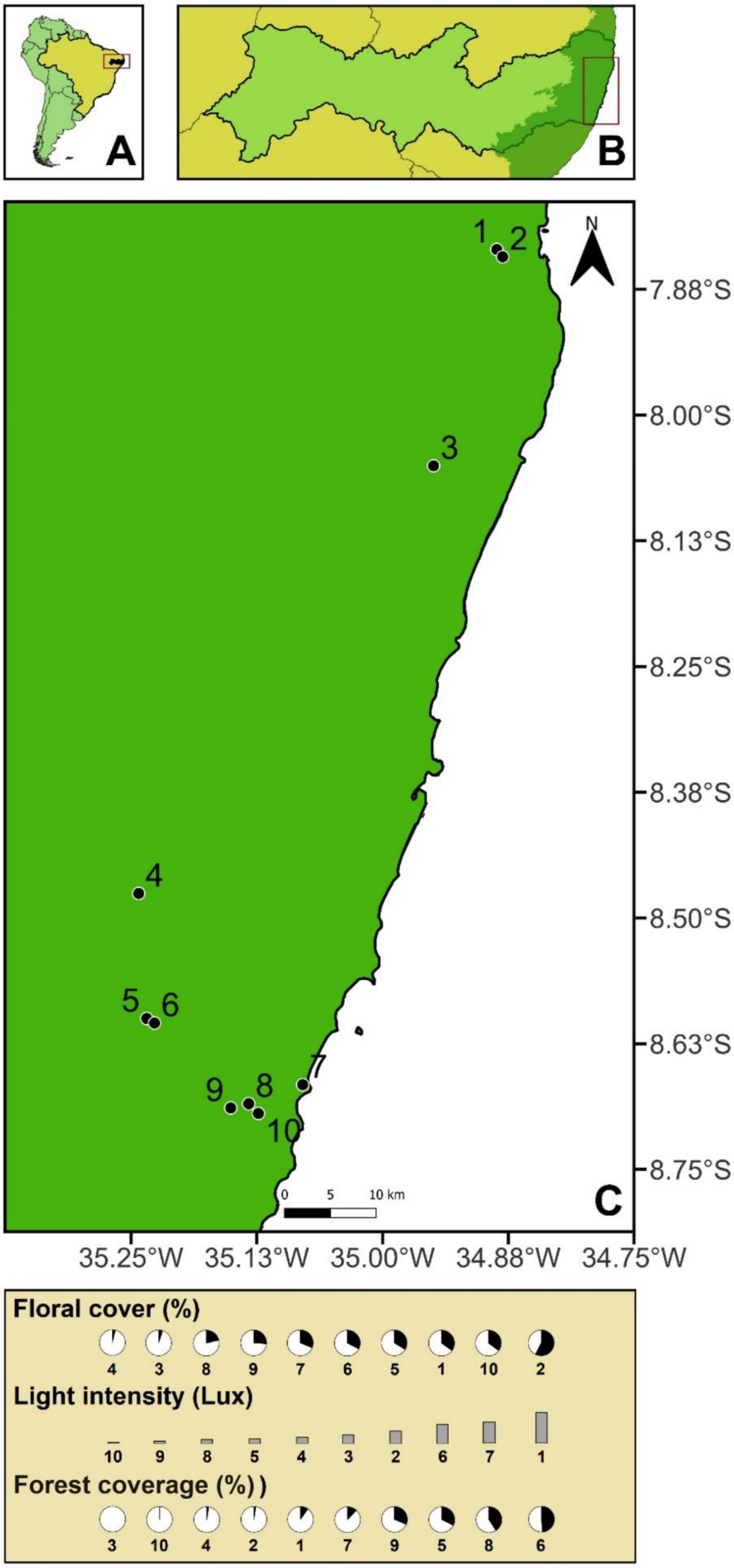
FIGURE LEGENDS

Figure 1. (A) Map of Brazil with the state of Pernambuco shown in black. (B) Study zone within Pernambuco indicated by a red rectangle. (C) The 10 study plots (20 m^2) numbered 1 to 10. They experienced different management practices, which affected floral cover, light intensity, and forest coverage. The lower panel shows the relative values of these variables for each of the plots (plot number beneath the pie and bar graphs).

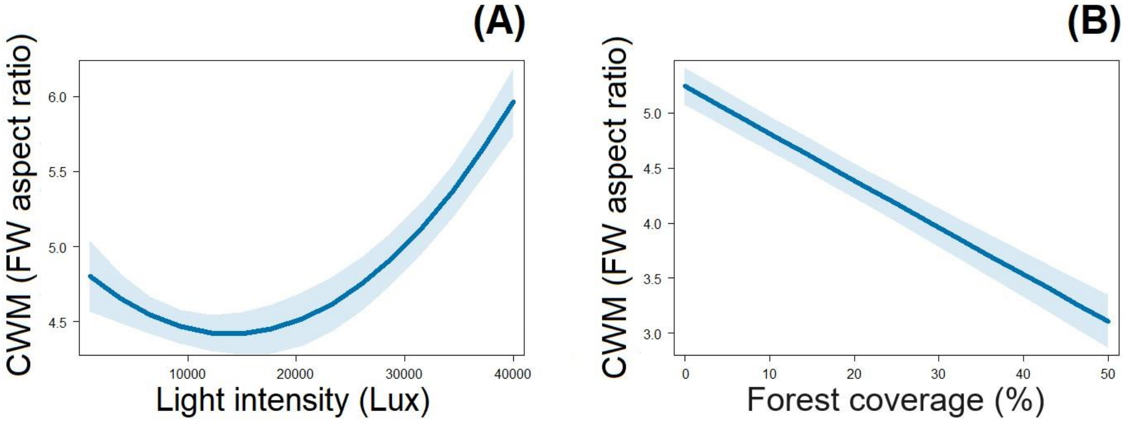
Figure 2. Associations between management-related variables and pollinator functional diversity (i.e., response traits) for acerola (*Malpighia emarginata* DC.) grown in smallholder agroforestry systems in the humid coastal areas of Pernambuco, northeastern Brazil. These results came from the best-supported models; the blue lines indicate the model-fitted values. Abbreviations: FDis: functional dispersion; CWM: community-weighted mean; FW: forewing.

Figure 3. Associations between pollinator functional diversity (effect traits) and acerola (*Malpighia emarginata* DC.) yield and quality for smallholder agroforestry systems in the humid coastal areas of Pernambuco, northeastern Brazil. These results came from the best-supported models; the blue lines indicate the model-fitted values. Abbreviations: FDis: functional dispersion; CWM: community-weighted mean; lecty: dietary specialization; m: maximum; c: content.

Figure 1.

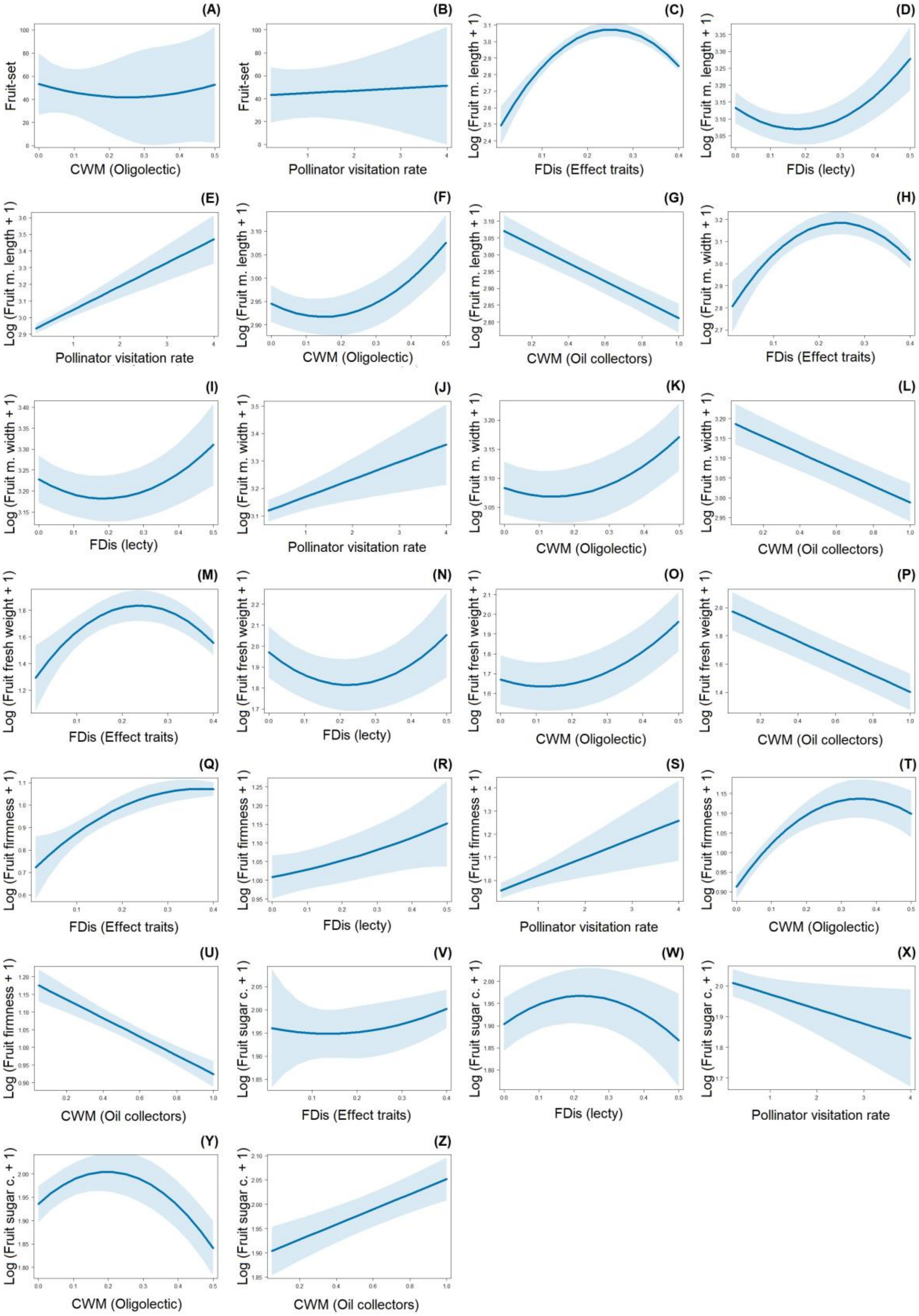

A
B
N
1
2
3
4
5
6
7
8
9
10
7.88°S
8.00°S
8.13°S
8.25°S
8.38°S
8.50°S
8.63°S
8.75°S
0
5
10 km
C
35.25°W
35.13°W
35.00°W
34.88°W
34.75°W
Floral cover (%)
4 3 8 9 7 6 5 1 10 2
Light intensity (Lux)
10 9 8 5 4 3 2 6 7 1
Forest coverage (%))
3 10 4 2 1 7 9 5 8 6

957 **Figure 2.**



958

Figure 3.


(A)
Fruit-set
CWM (Oligolectic)
(B)
Fruit-set
Pollinator visitation rate
(C)
Log (Fruit m. length + 1)
FDis (Effect traits)
(D)
Log (Fruit m. length + 1)
FDis (lecty)
(E)
Log (Fruit m. length + 1)
Pollinator visitation rate
(F)
Log (Fruit m. length + 1)
CWM (Oligolectic)
(G)
Log (Fruit m. length + 1)
CWM (Oil collectors)
(H)
Log (Fruit m. width + 1)
FDis (Effect traits)
(I)
Log (Fruit m. width + 1)
FDis (lecty)
(J)
Log (Fruit m. width + 1)
Pollinator visitation rate
(K)
Log (Fruit m. width + 1)
CWM (Oligolectic)
(L)
Log (Fruit m. width + 1)
CWM (Oil collectors)
(M)
Log (Fruit fresh weight + 1)
FDis (Effect traits)
(N)
Log (Fruit fresh weight + 1)
FDis (lecty)
(O)
Log (Fruit fresh weight + 1)
CWM (Oligolectic)
(P)
Log (Fruit fresh weight + 1)
CWM (Oil collectors)
(Q)
Log (Fruit firmness + 1)
FDis (Effect traits)
(R)
Log (Fruit firmness + 1)
FDis (lecty)
(S)
Log (Fruit firmness + 1)
Pollinator visitation rate
(T)
Log (Fruit firmness + 1)
CWM (Oligolectic)
(U)
Log (Fruit firmness + 1)
CWM (Oil collectors)
(V)
Log (Fruit sugar c. + 1)
FDis (Effect traits)
(W)
Log (Fruit sugar c. + 1)
FDis (lecty)
(X)
Log (Fruit sugar c. + 1)
Pollinator visitation rate
(Y)
Log (Fruit sugar c. + 1)
CWM (Oligolectic)
(Z)
Log (Fruit sugar c. + 1)
CWM (Oil collectors)

Supplementary Material

Using a response-effect framework to identify agroforestry practices for increasing pollinator functional diversity and improving acerola fruit yield and quality

This document contains 13 tables and 5 figures.

Table S1. Local and regional characteristics of smallholder agroforestry systems in humid coastal areas of Pernambuco, northeastern Brazil.

Plot	Area (ha)	Forest connectivity (effective mesh size; m^2)			Forest land cover (%)			Floral cover (%)			Light intensity (Lux)
		0.5 km buffer radius	1 km buffer radius	2 km buffer radius	0.5 km buffer radius	1 km buffer radius	2 km buffer radius	Total	Trees and bushes	Herbaceous ground cover	
1	0.5	5138.78	3638.26	11964.39	9.75	9.49	12.33	40	5	35	58115
2	0.5	135.63	14774.22	21168.72	2.69	16.26	17.72	57.5	0	57.5	23245
3	0.2	0	0	30.53	0	0	0.28	8.75	3.75	5	1405
4	1	244.98	282.10	2710.51	2.45	2.20	5.11	3.75	0.00	3.75	15505
5	1	75597.91	147630.14	1997093.35	32.25	30.72	45.24	35.00	1.25	33.75	8850
6	1	169284.51	894060.47	1859014.58	48.83	55.42	42.39	36.25	3.75	32.50	35465
7	0.3	1678.85	10874.85	9270.17	11.92	15.50	11.74	41.25	10.00	31.25	40110
8	1	104871.82	148215.27	135177.26	40.88	28.76	26.91	22.50	1.25	21.25	7805
9	1	29124.42	31057.33	89542.92	31.40	22.06	24.10	33.75	7.50	26.25	3975
10	0.5	0.85	2335.08	78563.85	0.09	6.34	20.46	37.50	2.50	35.00	11315

Table S2. Results of Spearman rank correlation (ρ) tests for stratum-specific floral cover. Significant associations are in bold ($P < 0.05$).

Variable 1	Variable 2	ρ	n	*P*
Total floral cover	**Floral cover from herbaceous ground cover**	**0.86**	**10**	**0.001**
	Floral cover from trees and bushes	0.23	10	0.52
Floral cover from trees and bushes	Floral cover from herbaceous ground cover	-0.03	10	0.93

Table S3. Results of Spearman rank correlation (ρ) tests for landscape metrics across spatial scales. Significant associations are in bold (*P* < 0.05).

Variable 1	Variable 2	ρ	n	*P*
Forest effective mesh size within a 0.5 km buffer radius	**Forest effective mesh size within a 1 km buffer radius**	**0.89**	**10**	**0.001**
	Forest effective mesh size within a 2 km buffer radius	**0.77**	**10**	**0.014**
	Forest land cover percentage within a 0.5 km buffer radius	**0.98**	**10**	**<0.001**
	Forest land cover percentage within a 1 km buffer radius	**0.88**	**10**	**0.002**
	Forest land cover percentage within a 2 km radius	**0.77**	**10**	**0.01**
Forest effective mesh size within a 1 km buffer radius	**Forest effective mesh size within a 2 km buffer radius**	**0.88**	**10**	**0.002**
	Forest land cover percentage within a 0.5 km buffer radius	**0.95**	**10**	**<0.001**
	Forest land cover percentage within a 1 km buffer radius	**0.99**	**10**	**<0.001**
	Forest land cover percentage within a 2 km radius	**0.87**	**10**	**0.002**
Forest effective mesh size within a 2 km buffer radius	**Forest land cover percentage within a 0.5 km buffer radius**	**0.79**	**10**	**0.01**
	Forest land cover percentage within a 1 km buffer radius	**0.90**	**10**	**0.001**
	Forest land cover percentage within a 2 km radius	**1**	**10**	**<0.001**

Forest land cover percentage within a 0.5 km buffer radius	**Forest land cover percentage within a 1 km buffer radius**	**0.94**	**10**	**<0.001**
	Forest land cover percentage within a 2 km buffer radius	**0.79**	**10**	**0.010**
Forest land cover percentage within a 1 km buffer radius	**Forest land cover percentage within a 2 km buffer radius**	**0.90**	**10**	**<0.001**

Table S4. Description of the pollinator community associated with acerola (*Malpighia emarginata* DC.) based on flower visitation surveys conducted in smallholder agroforestry systems in humid coastal areas of Pernambuco, northeastern Brazil.

	Plots									
Species	1	2	3	4	5	6	7	8	9	10
Apis mellifera L. 1758	0	7	0	9	0	0	0	7	2	8
Centris (Heterocentris) analis (Fabricius, 1804)	93	32	64	37	17	38	134	0	16	27
Centris (Centris) flavifrons (Fabricius, 1775)	15	0	0	0	0	0	2	0	0	0
Centris (Hemisiella) tarsata Smith, 1874	0	0	0	18	0	13	0	6	32	5
Frieseomelitta doederleini (Friese, 1900)	0	3	0	0	0	4	0	0	0	0
Paratetrapedia sp.	0	0	0	0	0	0	6	20	10	0
Plebeia flavocincta (Cockerell, 1912)	15	0	39	0	0	0	0	0	0	0
Tetragonisca angustula (Latreille, 1811)	0	0	0	43	105	0	0	0	0	0
Trigona spinipes (Fabricius, 1793)	16	2	9	0	237	112	0	16	0	4

Table S5. Description of the focal functional traits of pollinators associated with acerola (*Malpighia emarginata* DC.). Abbreviation: SE: standard error.

No.	Trait	Trait type (Q: quantitative, C: categorical; R: response, E: effect)		Units / Categories (n species)	Trait function	Procedure / Source
1	Body length	Q	R – E	mm	Bee body size, such as length, responds to environmental changes and effects pollination through foraging behavior. On the one hand, bees with larger bodies might be less susceptible to habitat fragmentation due to the disconnection between nesting and foraging sites (Gathmann & Tscharntke, 2002, Greenleaf et al., 2007, Wright et al., 2015). On the other hand, body size has been linked to the foraging range of bees and their capacity to carry pollen loads (Ramalho et al., 1998; Goulson et al., 2002; Alcock et al., 2005; Greenleaf et al., 2007; Kerr et al., 2019). Research has documented a higher prevalence of smaller-sized bees in areas characterized by limited resources, whereas the opposite trend has been observed in sites with increased floral resources (Persson & Smith, 2011). This finding suggests that an increase in floral resources could lead to elevated demand for foraging loads (Persson & Smith, 2011).	We measured the distance from the tip of the head to the tip of the abdomen, excluding appendages. For bees with a body length > 5 mm, a digital caliper was utilized for measurements. On the other hand, bees with a body length < 5 mm were measured using a stereomicroscope with a micrometer at 35X.
2	Inter-tegular span	Q	R – E	mm	The inter-tegular span is considered a proxy for bee dry mass (Cane, 1987). It can be influenced by environmental conditions and can affect pollination effectiveness. The availability of resources can influence the bees' ability to accumulate dry mass (e.g., Peterson	We measured the distance between the two tegulae using a

					& Roitberg, 2006). Furthermore, dry mass can impact plant reproductive success, as bees with higher dry mass may have higher absolute metabolic rates, enhancing their foraging activity (e.g., Brodschneider et al., 2009).	stereomicroscope with a micrometer at 35X.
3	Forewing aspect ratio	Q	R	index	Forewing aspect ratio, which is the ratio of maximum wing length to maximum wing width, is closely linked to flight performance in bees (Polidori & Nieves-Aldrey, 2015). In addition, insects living in different habitats and climates may exhibit variations in wings as an adaptation to their specific environmental conditions (e.g., Tommasi et al., 2022). For instance, wing morphology have been shown to be altered in response to pollutants and climatic variation (e.g., Klingenberg et al., 2001; Hoffmann et al., 2002).	We measured the maximum length and width of the forewing using a stereomicroscope with a micrometer at 35X.
4	Dietary specialization (lecty)	C	R – E	Polylectic or generalist (8), oligolectic (2)	Dietary specialization (lecty) is both responsive and influencing of the environment and pollination effectiveness, respectively. On the one hand, it reflects the adaptive foraging behaviors and preferences of bees in response to floral resources available in their environment (Ogilvie & Forrest, 2017). On the other hand, it influences key ecological processes such as pollination effectiveness, and thus community structure and ecosystem functioning. Their dietary preferences can significantly impact the reproductive success (e.g., Bogush et al., 2020).	Michener, 2000; Neto et al., 2007; Oliveira et al., 2008; Dórea et al., 2010; Gonçalves et al., 2012; Aguiar et al., 2013; Dórea et al., 2017; Barbosa et al., 2020; Malerbo-Souza et al., 2023; Urquizo et al., 2022
5	Nesting location / substrate	C	R	Above-ground (7), below-ground (1), mixed (2)	The availability and suitability of nesting locations and substrates directly impact the composition and diversity of bee communities within an ecosystem (e.g., Potts et al., 2005). This is due to the varying habitat requirements of different bee species. For example, bee	Jesus & Garófalo et al., 2000; Michener, 2000; Alves-dos-Santos et al., 2002; Aguiar & Garófalo, 2004; Velez-Ruiz et

					species that rely on tree cavities for nesting have been shown to be correlated to areas with larger fragments and lower edge (e.g., Brosi et al., 2007).	al., 2013; Martins et al., 2014b; Coutinho et al., 2021; Vaz et al., 2021; Maia et al., 2022
6	Sociality	C	R	Social (6), solitary (4)	Social and solitary bees often exhibit differences in resource utilization and foraging behavior. Social bees may have larger foraging ranges and more efficient foraging strategies due to division of labor and communication within the colony (Visscher & Seeley, 1982; Grüter & Hayes, 2022). Solitary bees, as individual foragers, may have narrower foraging ranges and rely on different floral resources (Grüter & Hayes, 2022). Thus, solitary bees might be more susceptible to habitat intensification (Klein et al., 2008; De Palma et al., 2015).	Michener, 2000; Dórea et al., 2010; Gouw & Gimenes, 2013; Martins & Melo, 2015; Cavalcante et al., 2019; Coutinho et al., 2021; Paixão et al., 2021
7	Hairiness	C	R – E	Sparse (6), dense (4)	Bee hairiness is responsive to changes in the surroundings through thermoregulation and affects pollination effectiveness. On the one hand, in cooler temperatures, bees tend to have denser and longer hair to provide better insulation, reducing heat loss from their bodies (Jarimi et al., 2020). Conversely, in warmer temperatures, bees may have sparser and shorter hair, allowing for increased airflow and heat dissipation (Jarimi et al., 2020). On the other hand, bee hairiness plays a crucial role in the collection and distribution of pollen (Stavert et al., 2016). For instance, bees with hairier bodies have more surface area for pollen attachment (e.g., Layek et al., 2022.), enhancing their ability to gather pollen from flowers. This promotes effective pollination by transferring pollen between flowers.	Michener, 2000; Capellari et al., 2012; Coutinho et al., 2021

8	Pollen transportation structure	C	E	Corbicula (6), leg scopa (4)	Pollen transportation structures have evolved as adaptations to collect, transport, and deposit pollen (Parker et al., 2015; Portmand et al., 2019), thereby influencing plant reproductive success.	Alves-dos-Santos et al., 2002; Martins et al., 2014a; Engel & Rasmussen, 2020; Coutinho et al., 2021
9	Specialization in obtaining some resource	C	E	Resin collector (5), oil collector (4), no specialist (1)	Specialization in resource collection can influence ecological interactions and mutualistic relationships between bees and the plant species they rely on for specific resources. For instance, bees that are specialized in collecting oils may have coevolved with certain plant species, forming specialized plant-pollinator mutualisms (e.g., Simpson et al., 1990). These interactions may have cascading effects on the reproductive success of plants and the foraging efficiency for specialized bee species.	Michener, 2000; Alves-dos-Santos et al., 2002; Gaustauer et al., 2011; Martins & Melo, 2015; Coutinho et al., 2021
10	Voltinism	C	R	Multivoltine (10)	The voltinism of bees is often influenced by environmental cues, such as temperature (e.g., Forrest et al., 2019). Different insect species have adapted their life cycles to optimize reproduction and survival based on specific environmental conditions (Altermatt, 2010; Buckley et al., 2015; Neff & Simpson, 1992). For example, bees in temperate regions may become broodless in periods of cold temperatures, while bees in tropical regions may exhibit continuous or opportunistic breeding patterns (e.g., Feliciano-Cardona et al., 2020).	Michener, 2000; Silva et al., 2001; Steiner et al., 2010; Magalhães & Freitas, 2013; Rocha-Filho & Garófalo, 2016; Coutinho et al., 2021

References

Aguiar, C.M.L., Garófalo, C.A., 2004. Nesting biology of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera, Apidae, Centridini). Revista Brasileira de Zoologia. 21(3), 477–486. https://doi.org/10.1590/S0101-81752004000300009

Aguiar, C.M.L., Santos, G.M.M., Martins, C.F., Presley, S.J., 2013. Trophic niche breadth and niche overlap in a guild of flower-visiting bees in a Brazilian dry forest. Apidologie. 44 (2), 153–162. https://doi.org/10.1007/s13592-012-0167-4

Alcock, J., Simmons, L.W., Beveridge, M., 2005. Seasonal change in offspring sex and size in Dawson's burrowing bees (*Amegilla dawsoni*) (Hymenoptera: Anthophorini). Ecological Entomology. 30, 247–254. https://doi.org/10.1111/j.0307-6946.2005.00695.x

Altermatt, F., 2010. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society B. 277, 1281–1287. https://doi.org/10.1098/rspb.2009.1910

Alves-dos-Santos, I., Melo, G.A.R., Rozen Jr., J.G., 2002. Biology and immature stages of the bee tribe Tetrapediini (Hymenoptera: Apidae). American Museum Novitates. 2002 (3377), 1–45. https://doi.org/10.1206/0003-0082(2002)377%3C0001:BAISOT%3E2.0.CO;2

Barbosa, A.B.S., Meneses, H.M., Rosa, F.L., Freitas, B.M., 2020. Flight activity of the stingless bee *Plebeia* aff. *flavocincta* in tropical conditions as indicator of the general health of the colony. Sociobiology. 67(4), 545–553. https://doi.org/10.13102/sociobiology.v67i4.4926

Bogusch, P., Bláhová, E., Horák, J., 2020. Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. Arthropod-Plant Interactions. 14(6), 3. https://doi.org/10.1007/s11829-020-09789-y

Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F., Durán, G., 2007. The effects of forest fragmentation on bee communities in tropical countryside. Journal of Applied Ecology. 45(3), 773–783. https://doi.org/10.1111/j.1365-2664.2007.01412.x

Brodschneider, R., Riessberger-Gallé, U., Crailsheim, K., 2009. Flight performance of artificially reared honeybees (*Apis mellifera*). Apidologie. 40(4), 441–449. https://doi.org/10.1051/apido/2009006

Buckley, L.B., Nufio, C.R., Kirk, E.M., Kingsolver, J.G., 2015. Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming. Proceedings of the Royal Society B. 282, 20150441. https://doi.org/10.1098/rspb.2015.0441

Cane, J.H., 1987. Estimation of bee size using intertegular span (Apoidea). Journal of the Kansas Entomological Society. 60, 145–147.

Capellari, S.C., Melo, G.A.R., Aguiar, A.J.C., Neff, J.L., 2012. Floral oil collection by male *Tetrapedia* bees (Hymenoptera: Apidae: Tetrapediini). Apidologie. 43, 39–50. https://doi.org/10.1007/s13592-011-0072-2

Coutinho, J.G.E., Hipólito, J., Santos, R.L.S., Moreira, E.F., Boscolo, D., Viana, B.F., 2021. Frontiers in Ecology and Evolution Sec. Biogeography and Macroecology. 9. https://doi.org/10.3389/fevo.2021.624835

De Palma, A., Kuhlmann, M., Roberts, S.P.M., Potts, S.G., Börger, L., Hudson, L.N. *et al.*, 2015. Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. Journal of Applied Ecology. 52, 1567–1577. https://doi.org/10.1111/1365-2664.12524

Dórea, M.C., Aguiar, C.M.L., Figueroa, L.E.R., Lima, L.C.L., Santos, F.A.R., 2010. Residual pollen in nests of *Centris analis* (Hymenoptera, Apidae, Centridini) in an area of Caatinga vegetation from Brazil. Oecologia Australis. 14(1), 232–237. https://doi.org/10.4257/oeco.2010.1401.13

Dorea, M.C., Santos, F.A.R., Aguiar, C.M.L., Martins, C.F., 2017. Bee life in the city: an analysis of the pollen provisions of *Centris* (*Centris*) *flavifrons* (Centridini) in an urban area. Sociobiology. 64(2), 166–173. https://doi.org/10.13102/sociobiology.v64i2.1277

Engel, M.S., Rasmussen, C., 2020. Corbiculate bees, in: Starr, C.K., (Ed.), Encyclopedia of Social Insects. Springer, Cham, pp 1–9.

Forrest, J.R.K., Cross, R., CaraDonna, P.J., 2019. Two-year bee, or not two-year bee? How voltinism is affected by temperature and season length in a high-elevation solitary bee. The American Naturalist. 194(3), 560–574. https://doi.org/10.5061/dryad.r2dm56s

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. Journal of Animal Ecology. 71, 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Gaustauer, M., Campos, L.A.O., Wittmann, D., 2011. Handling sticky resin by stingless bees (Hymenoptera, Apidae). Revista Brasileira de Entomologia. 55(2), 234–240. https://doi.org/10.1590/S0085-56262011005000018

Gonçalves, L., Silva, C.I., Buschini, M.L.T., 2012. Collection of pollen grains by *Centris* (*Hemisiella*) *tarsata* Smith (Apidae: Centridini): Is *C. tarsata* an oligolectic of polylactic species? Zoological Studies. 51(2), 195–203.

Goulson, D., Peat, J., Stout, J.C., Tucker, J., Darvill, B., Derwent, L.C. *et al.*, 2002. Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? Animal Behaviour. 64, 123–130. https://doi.org/10.1006/anbe.2002.3041

Gouw, M.S., Gimenes, M., 2013. Differences of the daily flight activity rhythm in two neotropical stingless bees (Hymenoptera, Apidae). Sociobiology. 60(2), 183–189. https://doi.org/10.13102/sociobiology.v60i2.183-189

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia. 153, 598–596. https://doi.org/10.1007/s00442-007-0752-9

Grüter, C., Hayes, L., 2022. Sociality is a key driver of foraging ranges in bees. Current Biology. 32, 5390–5397. https://doi.org/10.1016/j.cub.2022.10.064

Hoffmann, A.A., Collins, E., Woods, R., 2002 Wing shape and wing size changes as indicators of environmental stress in *Helicoverpa punctigera* (Lepidoptera: Noctuidae) Moths: comparing shifts in means, variances, and asymmetries. Environmental Entomolology. 31(6), 965–971. https://doi.org/10.1603/0046-225X-31.6.965

Jarimi, H., Tapia-Brito, E., Riffat, S., 2020. A review on thermoregulation techniques in honey bee's (*Apis mellifera*) beehive microclimate and its similarities to the heating and cooling management in buildings. Future Cities and Environment. 6, 7. https://doi.org/10.5334/fce.81

Jesus, B.M.V., Garófalo, C.A., 2000. Nesting behaviour of *Centris* (*Heterocentris*) *analis* (Fabricius) in southeastern Brazil (Hymenoptera, Apidae, Centridini). Apidologie. 21, 503-515. https://doi.org/10.1051/apido:2000142

Kerr, N.Z., Crone, E.E., Williams, N.M., 2019. Integrating vital rates explains optimal worker size for resource return by bumblebee workers. Functional Ecology. 33, 467–478. https://doi.org/10.1111/1365-2435.13251

Klingenberg, C.P., Badyaev, A.V., Sowry, S.M., Beckwith, N.J., 2001. Inferring developmental modularity from morphological integration: analysis of individual variation and asymmetry in bumble bee wings. The American Naturalist. 157(1), 11–23. https://doi.org/10.1086/317002

Klein, A.M., Cunningham, S.A., Bos, M., Steffan-Dewenter, I., 2008. Advances in pollination ecology from tropical plantation crops. Ecology. 89, 935–943. https://doi.org/10.1890/07-0088.1

Layek, U., Das, A., Karmakar, P., 2022. Supplemental stingless bee pollination in fennel (*Foeniculum vulgare* Mill.): An assessment of impacts on native pollinators and crop yield. Frontiers in Sustainable Food Systems. 6. https://doi.org/10.3389/fsufs.2022.820264

Magalhães, C.B., Freitas, B.M., 2013. Introducing nests of the oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini) for pollination of acerola (*Malpighia emarginata*) increases yield. Apidologie. 44, 234–239. https://doi.org/10.1007/s13592-012-0175-4

Maia, U.M., Borges, R.C., Santos-Júnior, J.E., Dias, V.H.P., Carvalho, A.T., Imperatriz-Fonseca, V.L. et al., 2022. Species redescription and nest architecture of *Plebeia flavocincta* (Hymenoptera: Apidae: Meliponini). Apidologie. 53, 63. https://doi.org/10.1007/s13592-022-00968-9

Malerbo-Souza, D., Costa, C.F.S., Pimentel, A.C.S., Andrade, M.O., Siqueira, R.A., Silva, R.C.B. et al., 2023. Stingless bee *Trigona spinipes* (Hymenoptera: Apidae) behavior on chayote flowers (*Sechium edule*). Acta Scientiarum. 45, e56760. https://doi.org/10.4025/actasianimsci.v45i1.56760

Martins, A.C., Melo, A.R., Renner, S.S., 2014a. The corbiculate bees arose from New World oil-collecting bees: Implications for the origin of pollen baskets. Molecular Phylogenetics and Evolution. 80, 88–94.

Martins, A.C., Melo, G.A.R., 2015. The New World oil-collecting bees *Centris* and *Epicharis* (Hymenoptera, Apidae): molecular phylogeny and biogeographic history. Zoologica Scripta. 45(1), 22–33. https://doi.org/10.1111/zsc.12133

Martins, C.F., Peixoto, M.P., Aguiar, C.M.L., 2014b. Plastic nesting behavior of *Centris* (*Centris*) *flavifrons* (Hymenoptera: Apidae: Centridini) in an urban area. Apidologie. 45, 156–171. https://doi.org/10.1007/s13592-013-0235-4

Michener, C.D., 2000. The bees of the world. Johns Hopkins University Press, Maryland.

Neff, J.L., Simpson, B.B., 1992. Partial bivoltinism in a ground-nesting bee: the biology of *Diadasia rinconis* (Hymenoptera, Anthophoridae) in Texas. Journal of the Kansas Entomological Society. 65, 377–392.

Neto, H.S., Oliveira, R., Schlindwein, 2007. Polilectia em *Tetrapedia* (Apidae, Tetrapediini): Fêmeas buscam pólen de numerosas espécies na floresta Atlântica de Pernambuco. Anais do VIII Congresso de Ecologia do Brasil, Minas Gerais.

Ogilvie, J.E., Forrest, J.R.K., 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. Current Opinion in Insect Science. 21, 75–82. https://doi.org/10.1016/j.cois.2017.05.015

Oliveira, M.E.C., Poderoso, J.C.M., Ferreira, A.F., Lessa, A.C.V., Dantas, P.C., Ribeiro, G.T. et al., 2008. Análise melissopalinológica e estrutura de ninho de abelhas *Trigona spinipes* (Fabricius, 1793) (Hymenoptera: Apidae) encontradas no Campus da Universidade Federal de Sergipe, São Cristovão, SE. EntomoBrasilis. 1, 17–22. https://doi.org/10.12741/ebrasilis.v1i2.14

Paixão, M.V.S., Ferreira, E.A., Paixão, P.P., Cremonini, G.M., Grobério, R.B.C., 2021. Social behavior between *Apis mellifera* and *Tetragonisca angustula* bees. Acta Apicola Brasilica. 9, e7983. https://doi.org/10.18378/aab.9.7983

Parker, A.J., Tran, J.L., Ison, J.L., Bai, J.D.K., Weis, A.E., Thomson, J.D., 2015. Pollen packing affects the function of pollen on corbiculate bees but not non-corbiculate bees. Arthropod-Plant Interactions. 9, 197–203. https://doi.org/10.1007/s11829-015-9358-z

Persson, A.S., Smith, H.G., 2011. Bumblebee colonies produce larger foragers in complex landscapes. Basic and Applied Ecology. 12, 695–702. https://doi.org/10.1016/j.baae.2011.10.002

Peterson, J.H., Roitberg, B.D., 2006. Impact of resource levels on sex ratio and resource allocation in the solitary bee, *Megachile rotundata*. Environmental Entomology. 35, 1404–1410. https://doi.org/10.1093/ee/35.5.1404

Polidori, C., Nieves-Aldrey, J.L., 2015. Comparative flight morphology in queens of invasive and native Patagonian bumblebees (Hymenoptera: *Bombus*). Comptes Rendus Biologies. 338(2), 126-133. https://doi.org/10.1016/j.crvi.2014.11.001

Portman, Z.M., Orr, M.C., Griswold, T., 2019. A review and updated classification of pollen gathering behavior in bees (Hymenoptera, Apoidea). Journal of Hymenoptera Research. 71, 171–209. https://doi.org/10.3897/jhr.71.32671

Potts, S.G., Vulliamy, B., Roberts, S., O’Toole, C., Dafni, A., Ne’Eman, G. *et al*., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology. 30, 78–85. https://doi.org/10.1111/j.0307-6946.2005.00662.x

Ramalho, M., Imperatriz-Fonseca, V.L., Giannini, T.C., 1998. Within-colony size variation of foragers and pollen load capacity in the stingless bee *Melipona quadrifasciata anthidioides* Lepeletier (Apidae, Hymenoptera). Apidologie. 29, 221–228. https://doi.org/10.1051/apido:19980302

Rocha-Filho, L.C., Garófalo, C.A., 2016. Natural history of *Tetrapedia diversipes* (Hymenoptera: Apidae) in an Atlantic semideciduous forest remnant surrounded by coffee crops, *Coffea arabica* (Rubiaceae).

Annals of the Entomological Society of America. 109(2), 183–197, https://doi.org/10.1093/aesa/sav153

Silva, F.O., Viana, B.F., Neves, E.L., 2001. Biologia e arquitetura de ninhos de *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera: Apidae: Centridini). Neotropical Entomology. 30(4), 541-545. https://doi.org/10.1590/S1519-566X2001000400005

Simpson, B.B., Neff, J.L., Dieringer, G., 1990. The production of floral oils by *Monttea* (Scrophulariaceae) and the function of tarsal pads in *Centris* bees. Plant Systematics and Evolution. 173(3), 209–222. https://doi.org/10.1007/BF00940864

Stavert, J.R., Liñán-Cembrano, G., Beggs, J.R., Howlett, B.G., Pattemore, D.E., Bartomeus, I., 2016. Hairiness: the missing link between pollinators and pollination. PeerJ. 4, e2779. https://doi.org/10.7717/peerj.2779

Steiner, J., Zillikens, A., Kamke, R., Feja, E.P., Falkenberg, D.B., 2010. Bees and melittophilous plants of secondary Atlantic Forest habitats at Santa Catarina Island, southern Brazil. Oecologia Australis. 14(1), 16–39. https://doi.org/10.4257/oeco.2010.1401.01

Tommasi, N., Pioltelli, E., Biella, P., Labra, M., Casiraghi, M., Galimberti, A., 2022. Effect of urbanization and it environmental stressors on the intraspecific variation of flight functional traits in two bumblebee species. Oecologia. 199, 289–299. https://doi.org/10.1007/s00442-022-05184-x

Urquizo, O.N., Cardozo-Alarcón, F., Adler, M., Lozano, R., Calcina-Mamani, S., Collao-Alvarado, K., 2022. Pollen preference patterns by *Tetragonisca angustula* (Apidae: Meliponini) in a Boliviano-Tucumano Forest. Neotropical Entomology. 51(5), 649–659. https://doi.org/10.1007/s13744-022-00986-3

Vaz, M.A., Aquino, I.S., Cruz, G.R.B., Barbosa, A.S., Medeiros, G.R., Borges, P.F., 2021. Nesting behavior of *Melipona subnitida* (Ducke, 1910) and *Frieseomelitta* sp. in the eastern Seridó of Rio Grande do Norte, Brazil. Research, Society and Development. 10(8), e55610817725. https://doi.org/10.33448/rsd-v10i8.17725

Velez-Ruiz, R.I., Gonzales, V.H., Engel, M.S., 2013. Observations on the urban ecology of the Neotropical stingless bee *Tetragonisca angustula*. Journal of Melittology. 15, 1–8. https://doi.org/10.17161/jom.v0i15.4528

WrightI. R., Roberts, S.P.M., Collins, B.E., 2015. Evidence of forage distance limitations for small bees (Hymenoptera: Apidae). European Journal of Entomology. 112, 303–310. https://doi.org/10.14411/eje.2015.028

Table S6. Functional traits of pollinators associated with acerola (*Malpighia emarginata* DC.). Abbreviations: SE: standard error; Q: quantitative trait; C: categorical trait; R: response trait; E: effect trait.

No.	Species	Body length (mm; mean ± SE)	Inter-tegular span (mm; mean ± SE)	Forewing maximum length (mm; mean ± SE)	Forewing maximum width (mm; mean ± SE)	Forewing aspect ratio; mean ± SE)	Dietary specialization (lecty)*	Nesting location / substrate*	Sociality*	Hairiness*	Pollen transportation structure*	Specialization in obtaining some resource*	Voltinism*
		Q	Q	Q	Q	Q	C	C	C	C	C	C	C
		R – E	R – E	-	-	R	R – E	R	R	R – E	E	E	R
1	*Apis mellifera**	11.28	3.34	8.71	3.01	2.89	Polylectic	Above-ground	Social	Dense	Corbicula	No specialist	Multivoltine
2	*Centris (Heterocentris) analis*	11.24 ± 0.06	2.98 ± 0.10	7.24 ± 0.17	2.05 ± 0.31	6.51 ± 0.75	Polylectic	Mixed	Solitary	Dense	Leg scopa	Oil collector	Multivoltine
3	*Centris (Centris) flavifrons*	21.19 ± 0	6.19 ± 0	15.54 ± 0	4.21 ± 0	3.69 ± 0	Oligolectic	Below-ground	Solitary	Dense	Leg scopa	Oil collector	Multivoltine
4	*Centris (Hemisiella) tarsata**	12.10	4.48	10.10	3.08	3.28	Oligolectic	Mixed	Solitary	Dense	Leg scopa	Oil collector	Multivoltine
5	*Frieseomelitta doederleini*	5.45 ± 0.01	1.35 ± 0.03	5.43 ± 0.29	1.46 ± 0.13	3.73 ± 0.15	Polylectic	Above-ground	Social	Sparse	Corbicula	Resin collector	Multivoltine
6	*Paratetrapedia* sp.	6.55 ± 0.83	1.72 ± 0.34	6.39 ± 0.47	1.80 ± 0.21	3.62 ± 0.34	Polylectic	Above-ground	Solitary	Dense	Leg scopa	Oil collector	Multivoltine
7	*Plebeia flavocincta*	4.07 ± 0.16	1.09 ± 0.04	3.14 ± 0.17	0.88 ± 0.10	3.84 ± 0.35	Polylectic	Above-ground	Social	Sparse	Corbicula	Resin collector	Multivoltine
8	*Tetragonisca angustula*	4.47 ± 0.27	0.90 ± 0.05	3.53 ± 0.21	0.79 ± 0.16	4.80 ± 0.88	Polylectic	Above-ground	Social	Sparse	Corbicula	Resin collector	Multivoltine
9	*Trigona spinipes*	5.71 ± 0.11	1.38 ± 00.03	5.51 ± 0.09	1.61 ± 0.07	3.53 ± 0.15	Polylectic	Above-ground	Social	Sparse	Corbicula	Resin collector	Multivoltine

*Trait information from these species was taken from specialized literature (sources listed below).

References

Aguiar, C.M.L., Garófalo, C.A., 2004. Nesting biology of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera, Apidae, Centridini). Revista Brasileira de Zoologia. 21(3), 477–486. https://doi.org/10.1590/S0101-81752004000300009

Aguiar, C.M.L., Santos, G.M.M., Martins, C.F., Presley, S.J., 2013. Trophic niche breadth and niche overlap in a guild of flower-visiting bees in a Brazilian dry forest. Apidologie. 44 (2), 153–162. https://doi.org/10.1007/s13592-012-0167-4

Alcock, J., Simmons, L.W., Beveridge, M., 2005. Seasonal change in offspring sex and size in Dawson’s burrowing bees (*Amegilla dawsoni*) (Hymenoptera: Anthophorini). Ecological Entomology. 30, 247–254. https://doi.org/10.1111/j.0307-6946.2005.00695.x

Altermatt, F., 2010. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society B. 277, 1281–1287. https://doi.org/10.1098/rspb.2009.1910

Alves-dos-Santos, I., Melo, G.A.R., Rozen Jr., J.G., 2002. Biology and immature stages of the bee tribe Tetrapediini (Hymenoptera: Apidae). American Museum Novitates. 2002 (3377), 1–45. https://doi.org/10.1206/0003-0082(2002)377%3C0001:BAISOT%3E2.0.CO;2

Barbosa, A.B.S., Meneses, H.M., Rosa, F.L., Freitas, B.M., 2020. Flight activity of the stingless bee *Plebeia* aff. *flavocincta* in tropical conditions as indicator of the general health of the colony. Sociobiology. 67(4), 545–553. https://doi.org/10.13102/sociobiology.v67i4.4926

Bogusch, P., Bláhová, E., Horák, J., 2020. Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. Arthropod-Plant Interactions. 14(6), 3. https://doi.org/10.1007/s11829-020-09789-y

Brodschneider, R., Riessberger-Gallé, U., Crailsheim, K., 2009. Flight performance of artificially reared honeybees (*Apis mellifera*). Apidologie. 40(4), 441–449. https://doi.org/10.1051/apido/2009006

Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F., Durán, G., 2007. The effects of forest fragmentation on bee communities in tropical countryside. Journal of Applied Ecology. 45(3), 773–783. https://doi.org/10.1111/j.1365-2664.2007.01412.x

Buckley, L.B., Nufio, C.R., Kirk, E.M., Kingsolver, J.G., 2015. Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming. Proceedings of the Royal Society B. 282, 20150441. https://doi.org/10.1098/rspb.2015.0441

Cane, J.H., 1987. Estimation of bee size using intertegular span (Apoidea). Journal of the Kansas Entomological Society. 60, 145–147.

Capellari, S.C., Melo, G.A.R., Aguiar, A.J.C., Neff, J.L., 2012. Floral oil collection by male *Tetrapedia* bees (Hymenoptera: Apidae: Tetrapediini). Apidologie. 43, 39–50. https://doi.org/10.1007/s13592-011-0072-2

Coutinho, J.G.E., Hipólito, J., Santos, R.L.S., Moreira, E.F., Boscolo, D., Viana, B.F., 2021. Frontiers in Ecology and Evolution Sec. Biogeography and Macroecology. 9. https://doi.org/10.3389/fevo.2021.624835

De Palma, A., Kuhlmann, M., Roberts, S.P.M., Potts, S.G., Börger, L., Hudson, L.N. *et al.*, 2015. Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. Journal of Applied Ecology. 52, 1567–1577. https://doi.org/10.1111/1365-2664.12524

Dórea, M.C., Aguiar, C.M.L., Figueroa, L.E.R., Lima, L.C.L., Santos, F.A.R., 2010. Residual pollen in nests of *Centris analis* (Hymenoptera, Apidae, Centridini) in an area of Caatinga vegetation from Brazil. Oecologia Australis. 14(1), 232–237. https://doi.org/10.4257/oeco.2010.1401.13

Dorea, M.C., Santos, F.A.R., Aguiar, C.M.L., Martins, C.F., 2017. Bee life in the city: an analysis of the pollen provisions of *Centris* (*Centris*) *flavifrons* (Centridini) in an urban area. Sociobiology. 64(2), 166–173. https://doi.org/10.13102/sociobiology.v64i2.1277

Engel, M.S., Rasmussen, C., 2020. Corbiculate bees, in: Starr, C.K., (Ed.), Encyclopedia of Social Insects. Springer, Cham, pp 1–9.

Forrest, J.R.K., Cross, R., CaraDonna, P.J., 2019. Two-year bee, or not two-year bee? How voltinism is affected by temperature and season length in a high-elevation solitary bee. The American Naturalist. 194(3), 560–574. https://doi.org/10.5061/dryad.r2dm56s

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. Journal of Animal Ecology. 71, 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Gaustauer, M., Campos, L.A.O., Wittmann, D., 2011. Handling sticky resin by stingless bees (Hymenoptera, Apidae). Revista Brasileira de Entomologia. 55(2), 234–240. https://doi.org/10.1590/S0085-56262011005000018

Gonçalves, L., Silva, C.I., Buschini, M.L.T., 2012. Collection of pollen grains by *Centris* (*Hemisiella*) *tarsata* Smith (Apidae: Centridini): Is *C. tarsata* an oligolectic of polylactic species? Zoological Studies. 51(2), 195–203.

Goulson, D., Peat, J., Stout, J.C., Tucker, J., Darvill, B., Derwent, L.C. *et al.*, 2002. Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? Animal Behaviour. 64, 123–130. https://doi.org/10.1006/anbe.2002.3041

Gouw, M.S., Gimenes, M., 2013. Differences of the daily flight activity rhythm in two neotropical stingless bees (Hymenoptera, Apidae). Sociobiology. 60(2), 183–189. https://doi.org/10.13102/sociobiology.v60i2.183-189

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia. 153, 598–596. https://doi.org/10.1007/s00442-007-0752-9

Grüter, C., Hayes, L., 2022. Sociality is a key driver of foraging ranges in bees. Current Biology. 32, 5390–5397. https://doi.org/10.1016/j.cub.2022.10.064

Hoffmann, A.A., Collins, E., Woods, R., 2002 Wing shape and wing size changes as indicators of environmental stress in *Helicoverpa punctigera* (Lepidoptera: Noctuidae) Moths: comparing shifts in means, variances, and asymmetries. Environmental Entomolology. 31(6), 965–971. https://doi.org/10.1603/0046-225X-31.6.965

Jarimi, H., Tapia-Brito, E., Riffat, S., 2020. A review on thermoregulation techniques in honey bee's (*Apis mellifera*) beehive microclimate and its similarities to the heating and cooling management in buildings. Future Cities and Environment. 6, 7. https://doi.org/10.5334/fce.81

Jesus, B.M.V., Garófalo, C.A., 2000. Nesting behaviour of *Centris* (*Heterocentris*) *analis* (Fabricius) in southeastern Brazil (Hymenoptera, Apidae, Centridini). Apidologie. 21, 503-515. https://doi.org/10.1051/apido:2000142

Kerr, N.Z., Crone, E.E., Williams, N.M., 2019. Integrating vital rates explains optimal worker size for resource return by bumblebee workers. Functional Ecology. 33, 467–478. https://doi.org/10.1111/1365-2435.13251

Klein, A.M., Cunningham, S.A., Bos, M., Steffan-Dewenter, I., 2008. Advances in pollination ecology from tropical plantation crops. Ecology. 89, 935–943. https://doi.org/10.1890/07-0088.1

Klingenberg, C.P., Badyaev, A.V., Sowry, S.M., Beckwith, N.J., 2001. Inferring developmental modularity from morphological integration: analysis of individual variation and asymmetry in bumble bee wings. The American Naturalist. 157(1), 11–23. https://doi.org/10.1086/317002

Layek, U., Das, A., Karmakar, P., 2022. Supplemental stingless bee pollination in fennel (*Foeniculum vulgare* Mill.): An assessment of impacts on native pollinators and crop yield. Frontiers in Sustainable Food Systems. 6. https://doi.org/10.3389/fsufs.2022.820264

Magalhães, C.B., Freitas, B.M., 2013. Introducing nests of the oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini) for pollination of acerola (*Malpighia emarginata*) increases yield. Apidologie. 44, 234–239. https://doi.org/10.1007/s13592-012-0175-4

Maia, U.M., Borges, R.C., Santos-Júnior, J.E., Dias, V.H.P., Carvalho, A.T., Imperatriz-Fonseca, V.L. et al., 2022. Species redescription and nest architecture of *Plebeia flavocincta* (Hymenoptera: Apidae: Meliponini). Apidologie. 53, 63. https://doi.org/10.1007/s13592-022-00968-9

Malerbo-Souza, D., Costa, C.F.S., Pimentel, A.C.S., Andrade, M.O., Siqueira, R.A., Silva, R.C.B. et al., 2023. Stingless bee *Trigona spinipes* (Hymenoptera: Apidae) behavior on chayote flowers (*Sechium edule*). Acta Scientiarum. 45, e56760. https://doi.org/10.4025/actasianimsci.v45i1.56760

Martins, A.C., Melo, A.R., Renner, S.S., 2014a. The corbiculate bees arose from New World oil-collecting bees: Implications for the origin of pollen baskets. Molecular Phylogenetics and Evolution. 80, 88–94.

Martins, A.C., Melo, G.A.R., 2015. The New World oil-collecting bees *Centris* and *Epicharis* (Hymenoptera, Apidae): molecular phylogeny and biogeographic history. Zoologica Scripta. 45(1), 22–33. https://doi.org/10.1111/zsc.12133

Martins, C.F., Peixoto, M.P., Aguiar, C.M.L., 2014b. Plastic nesting behavior of *Centris* (*Centris*) *flavifrons* (Hymenoptera: Apidae: Centridini) in an urban area. Apidologie. 45, 156–171. https://doi.org/10.1007/s13592-013-0235-4

Michener, C.D., 2000. The bees of the world. Johns Hopkins University Press, Maryland.

Neff, J.L., Simpson, B.B., 1992. Partial bivoltinism in a ground-nesting bee: the biology of *Diadasia rinconis* (Hymenoptera, Anthophoridae) in Texas. Journal of the Kansas Entomological Society. 65, 377–392.

Neto, H.S., Oliveira, R., Schlindwein, 2007. Polilectia em *Tetrapedia* (Apidae, Tetrapediini): Fêmeas buscam pólen de numerosas espécies na floresta Atlântica de Pernambuco. Anais do VIII Congresso de Ecologia do Brasil, Minas Gerais.

Ogilvie, J.E., Forrest, J.R.K., 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. Current Opinion in Insect Science. 21, 75–82. https://doi.org/10.1016/j.cois.2017.05.015

Oliveira Jr., W.P., Brandeburgo, M.A.M., Marcolino, M.T., 2000. Morphometrics and adaptatives aspects in africanized honeybees (*Apis mellifera*). Revista Brasileira de Biologia. 60(2), 307–314. https://doi.org/10.1590/S0034-71082000000200015

Oliveira, M.E.C., Poderoso, J.C.M., Ferreira, A.F., Lessa, A.C.V., Dantas, P.C., Ribeiro, G.T. et al., 2008. Análise melissopalinológica e estrutura de ninho de abelhas *Trigona spinipes* (Fabricius, 1793) (Hymenoptera: Apidae) encontradas no Campus da Universidade Federal de Sergipe, São Cristovão, SE. EntomoBrasilis. 1, 17–22. https://doi.org/10.12741/ebrasilis.v1i2.14

Paixão, M.V.S., Ferreira, E.A., Paixão, P.P., Cremonini, G.M., Grobério, R.B.C., 2021. Social behavior between *Apis mellifera* and *Tetragonisca angustula* bees. Acta Apicola Brasilica. 9, e7983. https://doi.org/10.18378/aab.9.7983

Parker, A.J., Tran, J.L., Ison, J.L., Bai, J.D.K., Weis, A.E., Thomson, J.D., 2015. Pollen packing affects the function of pollen on corbiculate bees but not non-corbiculate bees. Arthropod-Plant Interactions. 9, 197–203. https://doi.org/10.1007/s11829-015-9358-z

Persson, A.S., Smith, H.G., 2011. Bumblebee colonies produce larger foragers in complex landscapes. Basic and Applied Ecology. 12, 695–702. https://doi.org/10.1016/j.baae.2011.10.002

Peterson, J.H., Roitberg, B.D., 2006. Impact of resource levels on sex ratio and resource allocation in the solitary bee, *Megachile rotundata*. Environmental Entomology. 35, 1404–1410. https://doi.org/10.1093/ee/35.5.1404

Polidori, C., Nieves-Aldrey, J.L., 2015. Comparative flight morphology in queens of invasive and native Patagonian bumblebees (Hymenoptera: *Bombus*). Comptes Rendus Biologies. 338(2), 126-133. https://doi.org/10.1016/j.crvi.2014.11.001

Portman, Z.M., Orr, M.C., Griswold, T., 2019. A review and updated classification of pollen gathering behavior in bees (Hymenoptera, Apoidea). Journal of Hymenoptera Research. 71, 171–209. https://doi.org/10.3897/jhr.71.32671

Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G. *et al*., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology. 30, 78–85. https://doi.org/10.1111/j.0307-6946.2005.00662.x

Ramalho, M., Imperatriz-Fonseca, V.L., Giannini, T.C., 1998. Within-colony size variation of foragers and pollen load capacity in the stingless bee *Melipona quadrifasciata anthidioides* Lepeletier (Apidae, Hymenoptera). Apidologie. 29, 221–228. https://doi.org/10.1051/apido:19980302

Rocha-Filho, L.C., Garófalo, C.A., 2016. Natural history of *Tetrapedia diversipes* (Hymenoptera: Apidae) in an Atlantic semideciduous forest remnant surrounded by coffee crops, *Coffea arabica* (Rubiaceae). Annals of the Entomological Society of America. 109(2), 183–197, https://doi.org/10.1093/aesa/sav153

Silva, F.O., Viana, B.F., Neves, E.L., 2001. Biologia e arquitetura de ninhos de *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera: Apidae: Centridini). Neotropical Entomology. 30(4), 541-545. https://doi.org/10.1590/S1519-566X2001000400005

Simpson, B.B., Neff, J.L., Dieringer, G., 1990. The production of floral oils by *Monttea* (Scrophulariaceae) and the function of tarsal pads in *Centris* bees. Plant Systematics and Evolution. 173(3), 209–222. https://doi.org/10.1007/BF00940864

Stavert, J.R., Liñán-Cembrano, G., Beggs, J.R., Howlett, B.G., Pattemore, D.E., Bartomeus, I., 2016. Hairiness: the missing link between pollinators and pollination. PeerJ. 4, e2779. https://doi.org/10.7717/peerj.2779

Steiner, J., Zillikens, A., Kamke, R., Feja, E.P., Falkenberg, D.B., 2010. Bees and melittophilous plants of secondary Atlantic Forest habitats at Santa Catarina Island, southern Brazil. Oecologia Australis. 14(1), 16–39. https://doi.org/10.4257/oeco.2010.1401.01

Tommasi, N., Pioltelli, E., Biella, P., Labra, M., Casiraghi, M., Galimberti, A., 2022. Effect of urbanization and it environmental stressors on the intraspecific variation of flight functional traits in two bumblebee species. Oecologia. 199, 289–299. https://doi.org/10.1007/s00442-022-05184-x

Urquizo, O.N., Cardozo-Alarcón, F., Adler, M., Lozano, R., Calcina-Mamani, S., Collao-Alvarado, K., 2022. Pollen preference patterns by *Tetragonisca angustula* (Apidae: Meliponini) in a Boliviano-Tucumano Forest. Neotropical Entomology. 51(5), 649–659. https://doi.org/10.1007/s13744-022-00986-3

Vaz, M.A., Aquino, I.S., Cruz, G.R.B., Barbosa, A.S., Medeiros, G.R., Borges, P.F., 2021. Nesting behavior of *Melipona subnitida* (Ducke, 1910) and *Frieseomelitta* sp. in the eastern Seridó of Rio Grande do Norte, Brazil. Research, Society and Development. 10(8), e55610817725. https://doi.org/10.33448/rsd-v10i8.17725

Velez-Ruiz, R.I., Gonzales, V.H., Engel, M.S., 2013. Observations on the urban ecology of the Neotropical stingless bee *Tetragonisca angustula*. Journal of Melittology. 15, 1–8. https://doi.org/10.17161/jom.v0i15.4528

Vivallo, F., Vélez, D., 2016, A synopsis of the subgenus *Centris* (*Hemisiella*) Moure, 1945 (Hymenoptera: Apidae: Centridini) in Colombia, with description of a new species. Zootaxa. 4162, 107–133. https://doi.org/10.11646/zootaxa.4162.1

WrightI. R., Roberts, S.P.M., Collins, B.E., 2015. Evidence of forage distance limitations for small bees (Hymenoptera: Apidae). European Journal of Entomology. 112, 303–310. https://doi.org/10.14411/eje.2015.028

Table S7. Functional trait diversity metrics of pollinators associated with acerola (*Malpighia emarginata* DC.). Abbreviations: FDis: functional dispersion; R: response traits; E: effect traits; R-E: response-effect traits.

Plot	FDis (R)	FDis (E)	FDis (R-E)	FDis (Body length)	FDis (Inter-tegular span)	FDis (Forewing aspect ratio)	FDis (Dietary specialization)	FDis (Nesting location)	FDis (Sociality)	FDis (Hairiness)	FDis (Pollen transportation structure)	FDis (Specialization in obtaining some resource)
				R-E	R-E	R	R-E	R	R	R-E	E	E
1	0.32	0.3	0.25	0.16	0.14	0.35	0.19	0.44	0.35	0.35	0.35	0.35
2	0.27	0.28	0.11	0.07	0.06	0.36	0	0.4	0.4	0.2	0.4	0.39
3	0.36	0.4	0.28	0.2	0.17	0.37	0	0.49	0.49	0.49	0.49	0.49
4	0.4	0.42	0.33	0.2	0.23	0.29	0.28	0.5	0.5	0.48	0.5	0.52
5	0.1	0.08	0.06	0.04	0.05	0.19	0	0.09	0.09	0.09	0.09	0.09
6	0.32	0.34	0.26	0.14	0.16	0.29	0.14	0.42	0.42	0.42	0.42	0.42
7	0.05	0.01	0.02	0.02	0.02	0.09	0.03	0.1	0	0	0	0
8	0.31	0.4	0.29	0.12	0.17	0.05	0.21	0.21	0.5	0.44	0.5	0.53
9	0.29	0.11	0.27	0.09	0.18	0.34	0.5	0.32	0.06	0	0.06	0.06
10	0.31	0.27	0.16	0.05	0.07	0.44	0.2	0.4	0.4	0.17	0.4	0.4

Table S8. Functional trait identity metrics of pollinators associated with acerola (*Malpighia emarginata* DC.). Abbreviations: FDis: functional dispersion; R: response traits; E: effect traits; R-E: response-effect traits.

	CWM																
Plot	Body length	Inter-tegular span	Fore-wing aspect ratio	Dietary specialization		Nesting location			Sociality		Hairiness		Pollen transportation structure		Specialization in obtaining some resource		
				Poly-lectic	Oligo-lectic	Above-ground	Below-ground	Mixed	Social	Solitary	Dense	Sparse	Corbicula	Leg scopa	Resin	Oil	None
	R-E	R-E	R	R-E	R-E	R	R	R	R	R	R-E	R-E	E	E	E	E	E
1	10.9	2.94	5.57	0.89	0.11	0.22	0.11	0.67	0.22	0.78	0.78	0.22	0.22	0.78	0.22	0.78	0
2	10.60	2.85	5.61	1	0	0.27	0	0.73	0.27	0.73	0.89	0.11	0.27	0.73	0.11	0.73	0.16
3	8.3	2.19	5.34	1	0	0.43	0	0.57	0.43	0.57	0.57	0.43	0.43	0.57	0.43	0.57	0
4	8.67	2.43	4.97	0.83	0.17	0.49	0	0.51	0.49	0.51	0.6	0.4	0.49	0.51	0.4	0.51	0.08
5	5.61	1.32	4.04	1	0	0.95	0	0.05	0.95	0.05	0.05	0.95	0.95	0.05	0.95	0.05	0
6	7.46	1.98	4.19	0.92	0.08	0.69	0	0.31	0.69	0.31	0.31	0.69	0.69	0.31	0.69	0.31	0
7	11.18	2.97	6.35	0.99	0.01	0.04	0.01	0.94	0	1	1	0	0	1	0	1	0
8	7.63	2.18	3.44	0.88	0.12	0.88	0	0.12	0.47	0.53	0.67	0.33	0.47	0.53	0.33	0.53	0.14
9	10.92	3.58	4.19	0.47	0.53	0.2	0	0.8	0.03	0.97	1	0	0.03	0.97	0	0.97	0.03
10	10.84	3.07	5.21	0.89	0.11	0.27	0	0.73	0.27	0.73	0.91	0.09	0.27	0.73	0.09	0.73	0.18

Table S9. Pollinator visitation rate and acerola (*Malpighia emarginata* DC.) fruit yield and quality in smallholder agroforestry systems in humid coastal areas of Pernambuco, northeastern Brazil. Abbreviation: SE: standard error.

Plot	Pollinator visitation rate	Fruit formed	Fruit not formed	Fruit-set	Maximum length (mm; mean ± SE)	Maximum width (mm; mean ± SE)	Fresh weight (g; mean ± SE)	Firmness (kg/cm^2; mean ± SE)	Sugar content (Brix; mean ± SE)
1	0.64	48	22	68.57	20.00 ± 0.26	23.59 ± 0.33	6.25 ± 0.25	1.53 ± 0.05	6.21 ± 0.19
2	0.21	23	47	32.86	16.49 ± 0.31	19.29 ± 0.47	3.76 ± 0.24	1.26 ± 0.04	6.25 ± 0.17
3	1.70	52	18	74.29	19.53 ± 0.28	22.12 ± 0.32	5.35 ± 0.21	2.08 ± 0.07	6.10 ± 0.17
4	1.37	20	50	28.57	17.60 ± 0.32	19.40 ± 0.43	4.00 ± 0.26	2.40 ± 0.07	6.60 ± 0.13
5	1.58	37	33	52.86	21.00 ± 0.29	23.50 ± 0.23	6.70 ± 0.20	1.70 ± 0.05	5.00 ± 0.17
6	1.09	38	32	54.29	20.70 ± 0.43	23.80 ± 0.50	6.90 ± 0.39	2.20 ± 0.07	5.70 ± 0.17
7	4.38	36	34	51.43	15.50 ± 0.39	18.60 ± 0.35	3.10 ± 0.19	1.40 ± 0.05	5.10 ± 0.20
8	0.56	32	38	45.71	13.36 ± 0.45	16.95 ± 0.59	2.55 ± 0.23	1.07 ± 0.09	6.58 ± 0.30
9	0.57	37	33	52.86	19.80 ± 0.46	22.80 ± 0.49	5.90 ± 0.35	1.70 ± 0.09	5.50 ± 0.17
10	0.17	22	48	31.43	16.56 ± 0.28	19.90 ± 0.31	3.87 ± 0.16	1.89 ± 0.10	8.42 ± 0.31

Table S10. Results of Spearman rank correlation (ρ) tests for pairs of functional trait diversity metrics. Significant associations are in bold (*P* < 0.05). Abbreviations: FDis: functional dispersion; E: effect traits; R-E: response-effect traits.

Variable 1	Variable 2	ρ	n	*P*
Pollinator visitation rate	FDis (E)	-0.08	10	0.83
	FDis (R-E)	-0.1	10	0.79
	FDis (Body length)	0.08	10	0.83
	FDis (Inter-tegular span)	-0.12	10	0.75
	FDis (Forewing aspect ratio)	-0.37	10	0.28
	FDis (Dietary specialization)	-0.37	10	0.29
	FDis (Nesting location)	0.54	10	0.11
	FDis (Sociality)	0.04	10	0.91
	FDis (Hairiness)	0.07	10	0.85
	FDis (Pollen transportation structure)	-0.18	10	0.61
	FDis (Specialization in obtaining some resource)	-0.21	10	0.56
FDis (E)	**FDis (R-E)**	**0.86**	**10**	**0.001**
	FDis (Body length)	**0.89**	**10**	**0.001**
	FDis (Inter-tegular span)	**0.73**	**10**	**0.02**
	FDis (Forewing aspect ratio)	0.08	10	0.81
	FDis (Dietary specialization)	0.24	10	0.5
	FDis (Nesting location)	**0.76**	**10**	**0.01**
	FDis (Sociality)	**0.94**	**10**	**<0.001**
	FDis (Hairiness)	**0.96**	**10**	**<0.001**
	FDis (Pollen transportation structure)	**0.94**	**10**	**<0.001**
	FDis (Specialization in obtaining some resource)	**0.92**	**10**	**<0.001**

FDis (R-E)	**FDis (Body length)**	**0.83**	**10**	**0.01**
	FDis (Inter-tegular span)	**0.96**	**10**	**<0.001**
	FDis (Forewing aspect ratio)	-0.01	10	0.99
	FDis (Dietary specialization)	0.58	10	0.08
	FDis (Nesting location)	0.6	10	0.07
	FDis (Sociality)	0.58	10	0.08
	FDis (Hairiness)	**0.74**	**10**	**0.02**
	FDis (Pollen transportation structure)	**0.77**	**10**	**0.01**
	FDis (Specialization in obtaining some resource)	**0.77**	**10**	**0.01**
FDis (Body length)	**FDis (Inter-tegular span)**	**0.79**	**10**	**0.01**
	FDis (Forewing aspect ratio)	0.23	10	0.51
	FDis (Dietary specialization)	0.25	10	0.49
	FDis (Nesting location)	**0.87**	**10**	**0.001**
	FDis (Sociality)	**0.7**	**10**	**0.001**
	FDis (Hairiness)	**0.85**	**10**	**0.002**
	FDis (Pollen transportation structure)	**0.7**	**10**	**0.02**
	FDis (Specialization in obtaining some resource)	**0.7**	**10**	**0.03**
FDis (Inter-tegular span)	FDis (Forewing aspect ratio)	0.07	10	0.85
	FDis (Dietary specialization)	**0.7**	**10**	**0.03**
	FDis (Nesting location)	0.59	10	0.08
	FDis (Sociality)	0.6	10	0.07
	FDis (Hairiness)	0.57	10	0.09
	FDis (Pollen transportation structure)	0.6	10	0.07

	FDis (Specialization in obtaining some resource)	0.59	10	0.07
FDis (Forewing aspect ratio)	FDis (Dietary specialization)	-0.14	10	0.7
	FDis (Nesting location)	0.54	10	0.11
	FDis (Sociality)	0.04	10	0.91
	FDis (Hairiness)	0.13	10	0.72
	FDis (Pollen transportation structure)	0.04	10	0.91
	FDis (Specialization in obtaining some resource)	0.03	10	0.93
FDis (Dietary specialization)	FDis (Nesting location)	0.14	10	0.68
	FDis (Sociality)	0.17	10	0.65
	FDis (Hairiness)	-0.02	10	0.96
	FDis (Pollen transportation structure)	0.17	10	0.65
	FDis (Specialization in obtaining some resource)	0.19	10	0.6
FDis (Nesting location)	FDis (Sociality)	0.58	10	0.08
	FDis (Hairiness)	**0.73**	**10**	**0.02**
	FDis (Pollen transportation structure)	0.58	10	0.08
	FDis (Specialization in obtaining some resource)	0.53	10	0.11
FDis (Sociality)	**FDis (Hairiness)**	**0.91**	**10**	**<0.001**
	FDis (Pollen transportation structure)	**1**	**10**	**<0.001**
	FDis (Specialization in obtaining some resource)	**0.99**	**10**	**<0.001**

FDis (Hairiness)	**FDis (Pollen transportation structure)**	**0.92**	**10**	**<0.001**
	FDis (Specialization in obtaining some resource)	**0.9**	**10**	**<0.001**
FDis (Pollen transportation structure)	**FDis (Specialization in obtaining some resource)**	**0.99**	**10**	**<0.001**

Table S11. Results of Spearman rank correlation (ρ) tests for pairs of functional trait identity metrics. Significant associations are in bold (*P* < 0.05). Abbreviation: CWM: community weighted mean.

Variable 1	Variable 2	ρ	n	*P*
Pollinator visitation rate	CWM (Body length)	-0.09	10	0.81
	CWM (Inter-tegular span)	-0.32	10	0.37
	CWM (Forewing aspect ratio)	0.16	10	0.65
	CWM (Polylectic bees)	0.35	10	0.32
	CWM (Oligolectic bees)	-0.35	10	0.32
	CWM (Above-ground nesters)	0.02	10	0.95
	CWM (Mixed nesters)	-0.11	10	0.76
	CWM (Social bees)	0.11	10	0.76
	CWM (Solitary bees)	-0.11	10	0.76
	CWM (Hairiness - Dense)	-0.33	10	0.35
	CWM (Hairiness - Sparse)	0.33	10	0.35
	CWM (Pollen transportation structure – Corbicula)	0.11	10	0.76
	CWM (Pollen transportation structure – Leg scopa)	-0.11	10	0.76
	CWM (Resin collectors)	0.33	10	0.35
	CWM (Oil collectors)	-0.11	10	0.76
	CWM (No specialist in resource collection)	**-0.82**	**10**	**0.004**
CWM (Body length)	**CWM (Inter-tegular span)**	**0.94**	**10**	**<0.001**
	CWM (Forewing aspect ratio)	**0.7**	**10**	**0.04**
	CWM (Polylectic bees)	-0.32	10	0.37
	CWM (Oligolectic bees)	0.32	10	0.37
	CWM (Above-ground nesters)	**-0.97**	**10**	**<0.001**
	CWM (Mixed nesters)	**0.94**	**10**	**<0.001**
	CWM (Social bees)	**-0.96**	**10**	**<0.001**

	CWM (Solitary bees)	**0.96**	**10**	**<0.001**
	CWM (Hairiness - Dense)	**0.92**	**10**	**<0.001**
	CWM (Hairiness - Sparse)	**-0.92**	**10**	**<0.001**
	CWM (Pollen transportation structure – Corbicula)	**-0.96**	**10**	**<0.001**
	CWM (Pollen transportation structure – Leg scopa)	**0.96**	**10**	**<0.001**
	CWM (Resin collectors)	**-0.92**	**10**	**<0.001**
	CWM (Oil collectors)	**0.96**	**10**	**<0.001**
	CWM (No specialist in resource collection)	0.12	10	0.74
CWM (Inter-tegular span)	CWM (Forewing aspect ratio)	0.50	10	0.14
	CWM (Polylectic bees)	-0.42	10	0.22
	CWM (Oligolectic bees)	0.42	10	0.22
	CWM (Above-ground nesters)	**-0.9**	**10**	**<0.001**
	CWM (Mixed nesters)	**0.91**	**10**	**<0.001**
	CWM (Social bees)	**-0.89**	**10**	**0.001**
	CWM (Solitary bees)	**0.89**	**10**	**<0.001**
	CWM (Hairiness - Dense)	**0.93**	**10**	**<0.001**
	CWM (Hairiness - Sparse)	**-0.93**	**10**	**<0.001**
	CWM (Pollen transportation structure – Corbicula)	**-0.89**	**10**	**0.001**
	CWM (Pollen transportation structure – Leg scopa)	**0.89**	**10**	**0.001**
	CWM (Resin collectors)	**-0.93**	**10**	**<0.001**
	CWM (Oil collectors)	**0.89**	**10**	**0.001**
	CWM (No specialist in resource collection)	0.34	10	0.33

CWM (Forewing aspect ratio)	CWM (Polylectic bees)	0.37	10	0.29
	CWM (Oligolectic bees)	-0.37	10	0.29
	CWM (Above-ground nesters)	**-0.73**	**10**	**0.02**
	CWM (Mixed nesters)	**0.72**	**10**	**0.02**
	CWM (Social bees)	**-0.7**	**10**	**0.04**
	CWM (Solitary bees)	**0.7**	**10**	**0.04**
	CWM (Hairiness - Dense)	0.48	10	0.16
	CWM (Hairiness - Sparse)	-0.48	10	0.16
	CWM (Pollen transportation structure – Corbicula)	**-0.7**	**10**	**0.04**
	CWM (Pollen transportation structure – Leg scopa)	**0.7**	**10**	**0.04**
	CWM (Resin collectors)	-0.48	10	0.16
	CWM (Oil collectors)	**0.7**	**10**	**0.04**
	CWM (No specialist in resource collection)	-0.08	10	0.83
CWM (Polylectic bees)	**CWM (Oligolectic bees)**	**-1**	**10**	**<0.001**
	CWM (Above-ground nesters)	0.16	10	0.64
	CWM (Mixed nesters)	-0.11	10	0.75
	CWM (Social bees)	0.19	10	0.59
	CWM (Solitary bees)	-0.19	10	0.59
	CWM (Hairiness - Dense)	-0.36	10	0.3
	CWM (Hairiness - Sparse)	0.36	10	0.3
	CWM (Pollen transportation structure – Corbicula)	0.19	10	0.59
	CWM (Pollen transportation structure – Leg scopa)	-0.19	10	0.59
	CWM (Resin collectors)	0.36	10	0.3

	CWM (Oil collectors)	-0.19	10	0.59
	CWM (No specialist in resource collection)	-0.34	10	0.33
CWM (Oligolectic bees)	CWM (Above-ground nesters)	-0.17	10	0.63
	CWM (Mixed nesters)	0.11	10	0.75
	CWM (Social bees)	-0.19	10	0.59
	CWM (Solitary bees)	0.19	10	0.59
	CWM (Hairiness - Dense)	0.36	10	0.3
	CWM (Hairiness - Sparse)	-0.36	10	0.3
	CWM (Pollen transportation structure – Corbicula)	-0.19	10	0.59
	CWM (Pollen transportation structure – Leg scopa)	0.19	10	0.59
	CWM (Resin collectors)	-0.36	10	0.3
	CWM (Oil collectors)	0.19	10	0.59
	CWM (No specialist in resource collection)	0.34	10	0.33
CWM (Above-ground nesters)	**CWM (Mixed nesters)**	**-0.96**	**10**	**<0.001**
	CWM (Social bees)	**0.96**	**10**	**<0.001**
	CWM (Solitary bees)	**-0.96**	**10**	**<0.001**
	CWM (Hairiness - Dense)	**-0.87**	**10**	**0.001**
	CWM (Hairiness - Sparse)	**0.87**	**10**	**0.001**
	CWM (Pollen transportation structure – Corbicula)	**0.96**	**10**	**<0.001**
	CWM (Pollen transportation structure – Leg scopa)	**-0.96**	**10**	**<0.001**
	CWM (Resin collectors)	**0.87**	**10**	**0.001**
	CWM (Oil collectors)	**-0.96**	**10**	**<0.001**

	CWM (No specialist in resource collection)	0	10	1
CWM (Mixed nesters)	**CWM (Social bees)**	**-0.93**	**10**	**<0.001**
	CWM (Solitary bees)	**0.93**	**10**	**<0.001**
	CWM (Hairiness - Dense)	**0.91**	**10**	**<0.001**
	CWM (Hairiness - Sparse)	**-0.91**	**10**	**<0.001**
	CWM (Pollen transportation structure – Corbicula)	**-0.93**	**10**	**<0.001**
	CWM (Pollen transportation structure – Leg scopa)	**0.93**	**10**	**<0.001**
	CWM (Resin collectors)	**-0.91**	**10**	**<0.001**
	CWM (Oil collectors)	**0.93**	**10**	**<0.001**
	CWM (No specialist in resource collection)	0.17	10	0.64
CWM (Social bees)	**CWM (Solitary bees)**	**-1**	**10**	**<0.001**
	CWM (Hairiness - Dense)	**-0.92**	**10**	**<0.001**
	CWM (Hairiness - Sparse)	**0.92**	**10**	**<0.001**
	CWM (Pollen transportation structure – Corbicula)	**1**	**10**	**<0.001**
	CWM (Pollen transportation structure – Leg scopa)	**-1**	**10**	**<0.001**
	CWM (Resin collectors)	**0.92**	**10**	**<0.001**
	CWM (Oil collectors)	**-1**	**10**	**<0.001**
	CWM (No specialist in resource collection)	-0.08	10	0.83
CWM (Solitary bees)	**CWM (Hairiness - Dense)**	**0.92**	**10**	**<0.001**
	CWM (Hairiness - Sparse)	**-0.92**	**10**	**<0.001**
	CWM (Pollen transportation structure – Corbicula)	**-1**	**10**	**<0.001**

	CWM (Pollen transportation structure – Leg scopa)	**1**	**10**	**<0.001**
	CWM (Resin collectors)	**-0.92**	**10**	**<0.001**
	CWM (Oil collectors)	**1**	**10**	**<0.001**
	CWM (No specialist in resource collection)	0.08	10	0.83
CWM (Hairiness - Dense)	**CWM (Hairiness - Sparse)**	**-1**	**10**	**<0.001**
	CWM (Pollen transportation structure – Corbicula)	**-0.92**	**10**	**<0.001**
	CWM (Pollen transportation structure – Leg scopa)	**0.92**	**10**	**<0.001**
	CWM (Resin collectors)	**-0.1**	**10**	**<0.001**
	CWM (Oil collectors)	**0.92**	**10**	**<0.001**
	CWM (No specialist in resource collection)	0.39	10	0.27
CWM (Hairiness - Sparse)	**CWM (Pollen transportation structure – Corbicula)**	**0.92**	**10**	**<0.001**
	CWM (Pollen transportation structure – Leg scopa)	**-0.92**	**10**	**<0.001**
	CWM (Resin collectors)	**1**	**10**	**<0.001**
	CWM (Oil collectors)	**-0.93**	**10**	**<0.001**
	CWM (No specialist in resource collection)	-0.39	10	0.27
CWM (Pollen transportation structure – Corbicula)	**CWM (Pollen transportation structure – Leg scopa)**	**-1**	**10**	**<0.001**
	CWM (Resin collectors)	**0.92**	**10**	**<0.001**
	CWM (Oil collectors)	**-1**	**10**	**<0.001**
	CWM (No specialist in resource collection)	-0.08	10	0.83

CWM (Pollen transportation structure – Leg scopa)	**CWM (Resin collectors)**	**-0.92**	**10**	**<0.001**
	CWM (Oil collectors)	**1**	**10**	**<0.001**
	CWM (No specialist in resource collection)	0.08	10	0.83
CWM (Resin collectors)	**CWM (Oil collectors)**	**-0.92**	**10**	**<0.001**
	CWM (No specialist in resource collection)	-0.39	10	0.27
CWM (Oil collectors)	CWM (No specialist in resource collection)	0.08	10	0.83

Table S12. Comparisons of the models analyzing (1) the influence of management-related variables on pollinator functional diversity and (2) the influence of pollinator functional diversity on acerola (*Malpighia emarginata* DC.) fruit yield and quality in smallholder agroforestry systems in humid coastal areas of Pernambuco, northeastern Brazil. The best-supported models (in bold) were identified using Akaike's information criterion with small-sample correction (ΔAICc < 2). Abbreviations: df: degrees of freedom; R: response traits; E: effect traits; R-E: response-effect traits.

Model ID (Response variable)	Sites	Model No.	Explanatory variables selected	df	AICc	ΔAICc	Weight	R^2
FDis (R)	10	1	Null	2	-10.9	0	0.57	0
		2	Floral cover	3	-8.5	2.46	0.17	-0.04
		3	Light intensity	3	-7	3.96	0.08	-0.01
		4	Forest land cover	3	-6.9	3.99	0.07	-0.01
		5	Light intensity^2	3	-6.8	4.17	0.01	-0.003
		6	Floral cover + Forest land cover	4	-2.7	8.22	0.01	-0.04
		7	Floral cover + Light intensity	4	-2.5	8.46	0.01	-0.04
		8	Floral cover + Light intensity^2	4	-2.5	8.46	0.01	-0.04
		9	Light intensity + Light intensity^2	4	-1.5	9.4	0.01	-0.02

		10	Light intensity + Forest land cover	4	-1.3	9.64	0.004	-0.01
		11	Light intensity^2 + Forest land cover	4	-1.1	9.85	0	-0.01
		12	Floral cover + Light intensity + Forest land cover	5	6.3	17.21	0	-0.04
		13	Floral cover + Light intensity^2 + Forest land cover	5	6.3	17.22	0	-0.04
		14	Floral cover + Light intensity + Light intensity^2	5	6.4	17.31	0	-0.04
		15	Light intensity + Light intensity^2 + Forest land cover	5	7.2	18.14	0	-0.03
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	21.2	32.04	0	-0.05
FDis (R-E)	9	1	Floral cover	3	-9.2	0	0.41	-0.11
		2	Null	2	-8.8	0.42	0.34	0
		3	Light intensity	3	-5.9	3.29	0.08	-0.05
		4	Light intensity^2	3	-5.9	3.35	0.08	-0.04

5	Forest land cover	3	-4.2	5.02	0.02	-0.01
6	Floral cover + Light intensity^2	4	-3	6.25	0.02	-0.12
7	Floral cover + Forest land cover	4	-2.8	6.44	0.02	-0.12
8	Floral cover + Light intensity	4	-2.6	6.63	0.02	-0.11
9	Light intensity^2 + Forest land cover	4	0.8	10.02	0.003	-0.06
10	Light intensity + Forest land cover	4	0.8	10.03	0.003	-0.06
11	Light intensity + Light intensity^2	4	1.2	10.48	0.002	-0.05
12	Floral cover + Light intensity^2 + Forest land cover	5	7.9	17.11	0	-0.13
13	Floral cover + Light intensity + Light intensity^2	5	8.2	17.44	0	-0.13
14	Floral cover + Light intensity + Forest land cover	5	8.4	17.68	0	-0.13

		15	Light intensity + Light intensity^2 + Forest land cover	5	12.8	21.99	0	-0.06
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	30.4	39.69	0	-0.15
FDis (Body length)	9	1	Floral cover	3	-19.7	0	0.5	-0.04
		2	Null	2	-18	1.67	0.22	0
		3	Floral cover + Light intensity^2	4	-17.1	2.61	0.14	-0.05
		4	Floral cover + Light intensity	4	-15.8	3.9	0.07	-0.05
		5	Forest land cover	3	-13.5	6.12	0.02	-0.002
		6	Light intensity^2	3	-13.3	6.41	0.02	-4.48×10^{-4}
		7	Light intensity	3	-13.2	6.47	0.01	-4.72×10^{-7}
		8	Floral cover + Forest land cover	4	-12.6	7.11	0.001	-0.04
		9	Light intensity + Light intensity^2	4	-7	12.66	0.001	-0.01
		10	Floral cover + Light intensity^2 + Forest land cover	5	-6.5	13.17	0.001	-0.1

		11	Light intensity^2 + Forest land cover	4	-6.4	13.28	0.001	-0.003
		12	Light intensity + Forest land cover	4	-6.4	13.32	0	-0.003
		13	Floral cover + Light intensity + Light intensity^2	5	-5.7	14.01	0	-0.1
		14	Floral cover + Light intensity + Forest land cover	5	-4.5	15.12	0	-0.1
		15	Light intensity + Light intensity^2 + Forest land cover	5	4.9	24.52	0	-0.01
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	16.3	36.01	0	-0.1
FDis (Inter-tegular span)	9	1	Floral cover	3	-18.1	0	0.48	-0.04
		2	Null	2	-17.5	0.66	0.34	0
		3	Light intensity	3	-13.2	4.99	0.04	-0.004
		4	Floral cover + Forest land cover	4	-13.1	5.09	0.04	-0.05
		5	Light intensity^2	3	-12.9	5.2	0.03	-0.002

6	Forest land cover	3	-12.7	5.41	0.02	-3.78×10^{-4}
7	Floral cover + Light intensity^2	4	-11.3	6.83	0.01	-0.04
8	Floral cover + Light intensity	4	-11.2	6.99	0.001	-0.04
9	Light intensity + Light intensity^2	4	-6.3	11.8	0.001	-0.01
10	Light intensity + Forest land cover	4	-6	12.15	0.001	-0.004
11	Light intensity^2 + Forest land cover	4	-5.8	12.37	0	-0.002
12	Floral cover + Light intensity^2 + Forest land cover	5	-2.5	15.61	0	-0.05
13	Floral cover + Light intensity + Forest land cover	5	-1.9	16.24	0	-0.04
14	Floral cover + Light intensity + Light intensity^2	5	0.5	18.63	0	-0.04
15	Light intensity + Light intensity^2 + Forest land cover	5	5.5	23.65	0	-0.01

		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	20.7	38.81	0	-0.05
FDis (Forewing aspect ratio)	9	1	Forest land cover	3	-5.7	0	0.43	-0.16
		2	Null	2	-5.6	0.13	0.41	0
		3	Floral cover	3	-0.9	4.83	0.04	-0.005
		4	Light intensity	3	-0.8	4.9	0.04	-0.001
		5	Light intensity^2	3	-0.8	4.93	0.02	-3.71×10^{-6}
		6	Light intensity^2 + Forest land cover	4	0.6	6.32	0.01	-0.18
		7	Light intensity + Forest land cover	4	1.2	6.94	0.01	-0.17
		8	Floral cover + Forest land cover	4	1.3	6.98	0.01	-0.17
		9	Light intensity + Light intensity^2	4	5.9	11.57	0.001	-0.02
		10	Floral cover + Light intensity	4	6.2	11.92	0.001	-0.01

		11	Floral cover + Light intensity^2	4	6.3	12.02	0.001	-0.01
		12	Light intensity + Light intensity^2 + Forest land cover	5	9.6	15.3	0	-0.24
		13	Floral cover + Light intensity + Forest land cover	5	11.6	17.35	0	-0.2
		14	Floral cover + Light intensity^2 + Forest land cover	5	12.8	18.5	0	-0.18
		15	Floral cover + Light intensity + Light intensity^2	5	17.2	22.92	0	-0.05
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	27.4	33.1	0	-0.31
FDis (Dietary specialization)	9	1	Null	2	-2.6	0	0.53	0
		2	Floral cover	3	-1	1.64	0.24	-0.18
		3	Light intensity	3	1.1	3.73	0.08	-0.07
		4	Light intensity^2	3	1.8	4.45	0.06	-0.02
		5	Forest land cover	3	2	4.65	0.05	-0.01

6	Light intensity + Light intensity^2	4	5	7.66	0.01	-0.24
7	Floral cover + Light intensity	4	5.7	8.3	0.01	-0.21
8	Floral cover + Light intensity^2	4	6.1	8.74	0.01	-0.19
9	Floral cover + Forest land cover	4	6.2	8.8	0.01	-0.19
10	Light intensity + Forest land cover	4	8.3	10.89	0.002	-0.07
11	Light intensity^2 + Forest land cover	4	8.9	11.56	0.002	-0.03
12	Floral cover + Light intensity + Light intensity^2	5	14.5	17.15	0	-0.33
13	Light intensity + Light intensity^2 + Forest land cover	5	17	19.66	0	-0.24
14	Floral cover + Light intensity + Forest land cover	5	17.7	20.29	0	-0.21
15	Floral cover + Light intensity^2 + Forest land cover	5	18.1	20.72	0	-0.19

		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	38.5	41.15	0	-0.33
FDis (Nesting location)	9	1	Forest land cover	3	-3.4	0	0.5	-0.29
		2	Null	2	-2.7	0.77	0.34	0
		3	Floral cover	3	1.4	4.85	0.04	-0.05
		4	Light intensity^2	3	2.1	5.54	0.03	-0.002
		5	Light intensity	3	2.1	5.57	0.03	-8.19×10^{-5}
		6	Floral cover + Forest land cover	4	2.5	5.92	0.03	-0.33
		7	Forest land cover + Light intensity	4	3.1	6.57	0.02	-0.31
		8	Forest land cover + Light intensity^2	4	3.7	7.08	0.01	-0.29
		9	Floral cover + Light intensity^2	4	8.4	11.87	0.001	-0.06
		10	Floral cover + Light intensity	4	8.5	11.95	0.001	-0.05
		11	Light intensity + Light intensity^2	4	8.7	12.15	0.001	-0.04

		12	Light intensity + Light intensity^2 + Forest land cover	5	11.6	14.98	0	-0.41
		13	Floral cover + Light intensity + Forest land cover	5	14.3	17.76	0	-0.33
		14	Floral cover + Light intensity^2 + Forest land cover	5	14.5	17.92	0	-0.33
		15	Floral cover + Light intensity + Light intensity^2	5	20.3	23.71	0	-0.07
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	35.5	38.93	0	-0.41
FDis (Sociality)	9	1	Null	2	1.9	0	0.59	0
		2	Floral cover	3	3.9	2.07	0.21	-0.45
		3	Forest land cover	3	6.4	4.55	0.06	-0.05
		4	Light intensity	3	6.5	4.67	0.06	-0.03
		5	Light intensity^2	3	6.6	4.7	0.06	-0.02
		6	Floral cover + Light intensity	4	10.9	9.02	0.01	-0.49
		7	Floral cover + Light intensity^2	4	10.9	9.03	0.01	-0.48

8	Floral cover + Forest land cover	4	11.1	9.26	0.01	-0.45
9	Light intensity + Forest land cover	4	13.5	11.61	0.002	-0.07
10	Light intensity^2 + Forest land cover	4	13.5	11.63	0.002	-0.07
11	Light intensity + Light intensity^2	4	13.7	11.84	0.002	-0.03
12	Floral cover + Light intensity^2 + Forest land cover	5	22.9	20.97	0	-0.49
13	Floral cover + Light intensity + Forest land cover	5	22.9	20.98	0	-0.49
14	Floral cover + Light intensity + Light intensity^2	5	22.9	21.02	0	-0.49
15	Light intensity + Light intensity^2 + Forest land cover	5	25.5	23.61	0	-0.07
16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	46.8	44.97	0	-0.49

FDis (Hairiness)	9	1	Null	2	2	0	0.49	0
		2	Floral cover	3	2.9	1.09	0.32	-0.63
		3	Forest land cover	3	6.8	5.68	0.05	-0.01
		4	Light intensity^2	3	6.8	5.79	0.05	-0.001
		5	Light intensity	3	6.8	5.86	0.05	-1.63×10^{-6}
		6	Floral cover + Light intensity	4	8.5	5.87	0.02	-0.82
		7	Floral cover + Light intensity^2	4	8.5	5.96	0.02	-0.82
		8	Floral cover + Forest land cover	4	9.7	6.28	0.01	-0.68
		9	Light intensity + Light intensity^2	4	13.9	12.64	0.001	-0.-2
		10	Light intensity^2 + Forest land cover	4	14	12.97	0.001	-0.01
		11	Light intensity + Forest land cover	4	14	13.04	0.001	-0.01
		12	Floral cover + Light intensity^2 + Forest land cover	5	19.3	15.27	0	-0.95

		13	Floral cover + Light intensity + Forest land cover	5	19.5	16.05	0	-0.93
		14	Floral cover + Light intensity + Light intensity^2	5	20.5	17.62	0	-0.83
		15	Light intensity + Light intensity^2 + Forest land cover	5	25.9	24.64	0	-0.02
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	43.3	38.95	0	-0.95
CWM (Body length)	10	1	Null	2	46.3	0	0.39	0
		2	Forest land cover	3	47.3	1.04	0.23	0.28
		3	Light intensity^2	3	49.1	2.75	0.1	0.14
		4	Light intensity	3	49.1	2.83	0.1	0.14
		5	Floral cover	3	49.6	3.3	0.08	0.1
		6	Light intensity + Forest land cover	4	51.5	5.18	0.03	0.41
		7	Light intensity^2 + Forest land cover	4	51.5	5.23	0.03	0.4
		8	Floral cover + Forest land cover	4	51.6	5.25	0.03	0.4

		9	Floral cover + Light intensity^2	4	54.5	8.25	0.01	0.19
		10	Floral cover + Light intensity	4	54.8	8.46	0.01	0.17
		11	Light intensity + Light intensity^2	4	55	8.75	0.01	0.14
		12	Floral cover + Light intensity^2 + Forest land cover	5	59.4	13.11	0.001	0.47
		13	Floral cover + Light intensity + Forest land cover	5	59.6	13.31	0.001	0.46
		14	Light intensity + Light intensity^2 + Forest land cover	5	60.5	14.16	0	0.41
		15	Floral cover + Light intensity + Light intensity^2	5	63.5	17.17	0	0.19
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	74.4	28.06	0	0.47
CWM (Inter-tegular span)	10	1	Null	2	24.6	0	0.57	0
		2	Forest land cover	3	27.4	2.76	0.14	0.17

3	Light intensity^2	3	28.4	3.82	0.08	0.05
4	Floral cover	3	28.5	3.86	0.08	0.05
5	Light intensity	3	28.5	3.95	0.08	0.04
6	Floral cover + Forest land cover	4	32.7	8.12	0.08	0.23
7	Light intensity^2 + Forest land cover	4	32.9	8.32	0.01	0.21
8	Light intensity + Forest land cover	4	33	8.42	0.01	0.2
9	Floral cover + Light intensity^2	4	34.2	9.59	0.01	0.08
10	Floral cover + Light intensity	4	34.3	9.73	0.01	0.06
11	Light intensity + Light intensity^2	4	34.3	9.75	0.004	0.06
12	Floral cover + Light intensity^2 + Forest land cover	5	41.5	16.91	0.004	0.25
13	Floral cover + Light intensity + Forest land cover	5	41.6	17.03	0	0.24

		14	Light intensity + Light intensity^2 + Forest land cover	5	41.9	17.29	0	0.21
		15	Floral cover + Light intensity + Light intensity^2	5	42.9	18.29	0	0.11
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	56.2	31.65	0	0.27
CWM (Forewing aspect ratio)	9	**1**	**Light intensity^2 + Forest land cover**	**4**	**13**	**0**	**0.93**	**1.04**
		2	Light intensity + Light intensity^2 + Forest land cover	5	19.6	6.58	0.04	1.06
		3	Light intensity + Forest land cover	4	20.2	7.19	0.03	0.98
		4	Floral cover + Light intensity^2 + Forest land cover	5	24.4	11.43	0.003	1.04
		5	Forest land cover	3	25.3	12.35	0.002	0.66
		6	Null	2	28.9	15.92	0	0
		7	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	30.2	17.26	0	1.08

		8	Floral cover + Forest land cover	4	31.2	18.26	0	0.71
		9	Light intensity^2	3	31.5	18.48	0	0.24
		10	Light intensity	3	31.7	18.68	0	0.22
		11	Floral cover + Light intensity + Forest land cover	5	32.2	19.18	0	0.98
		12	Floral cover	3	33.5	20.5	0	0.03
		13	Light intensity + Light intensity^2	4	38.7	25.67	0	0.24
		14	Floral cover + Light intensity^2	4	38.7	25.68	0	0.24
		15	Floral cover + Light intensity	4	38.9	25.87	0	0.22
		16	Floral cover + Light intensity + Light intensity^2	5	50.7	37.67	0	0.24
CWM (Polylectic)	9	1	Null	2	-18.7	0	0.67	0
		2	Floral cover	3	-15.2	3.47	0.12	-0.01
		3	Light intensity^2	3	-14	4.69	0.06	-0.001
		4	Light intensity	3	-14	4.71	0.06	-0.001

5	Forest land cover	3	-13.9	4.78	0.06	-0.0002
6	Floral cover + Light intensity	4	-8.8	9.86	0.005	-0.01
7	Floral cover + Light intensity^2	4	-8.6	10.12	0.004	-0.01
8	Floral cover + Forest land cover	4	-8.1	10.6	0.003	-0.01
9	Light intensity^2 + Forest land cover	4	-6.8	11.87	0.002	-0.001
10	Light intensity + Forest land cover	4	-6.8	11.89	0.002	-0.001
11	Light intensity + Light intensity^2	4	-6.8	11.89	0.002	-0.001
12	Floral cover + Light intensity + Light intensity^2	5	2.9	21.62	0	-0.02
13	Floral cover + Light intensity + Light intensity^2	5	3.1	21.79	0	-0.02
14	Floral cover + Light intensity + Forest land cover	5	3.4	22.03	0	-0.01

		15	Light intensity + Light intensity^2 + Forest land cover	5	5.2	23.86	0	-0.001
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	26.9	45.58	0	-0.02
CWM (Oligolectic)	9	1	Null	2	-18.7	0	0.67	0
		2	Floral cover	3	-15.2	3.47	0.12	-0.01
		3	Light intensity^2	3	-14	4.69	0.06	-0.001
		4	Light intensity	3	-14	4.71	0.06	-0.001
		5	Forest land cover	3	-13.9	4.78	0.06	-0.0002
		6	Floral cover + Light intensity	4	-8.8	9.86	0.005	-0.01
		7	Floral cover + Light intensity^2	4	-8.6	10.12	0.004	-0.01
		8	Floral cover + Forest land cover	4	-8.1	10.6	0.003	-0.01
		9	Light intensity^2 + Forest land cover	4	-6.8	11.87	0.002	-0.001
		10	Light intensity + Forest land cover	4	-6.8	11.89	0.002	-0.001

		11	Light intensity + Light intensity^2	4	-6.8	11.89	0.002	-0.001
		12	Floral cover + Light intensity + Light intensity^2	5	2.9	21.62	0	-0.02
		13	Floral cover + Light intensity + Forest land cover	5	3.1	21.79	0	-0.02
		14	Floral cover + Light intensity^2 + Forest land cover	5	3.4	22.03	0	-0.01
		15	Light intensity + Light intensity^2 + Forest land cover	5	5.2	23.86	0	-0.001
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	26.9	45.58	0	-0.02
CWM (Nesting location - Above-ground)	10	1	Forest land cover	3	9	0	0.36	1.22
		2	Null	2	9.4	0.38	0.3	0
		3	Light intensity^2	3	12.1	3.1	0.08	0.48
		4	Light intensity	3	12.2	3.18	0.07	0.45
		5	Light intensity + Forest land cover	4	12.8	3.81	0.05	1.63

6	Light intensity^2 + Forest land cover	4	12.9	3.88	0.05	1.62
7	Floral cover	3	13.2	4.27	0.04	0.13
8	Floral cover + Forest land cover	4	14	5.03	0.03	1.41
9	Floral cover + Light intensity^2	4	18	9	0.004	0.5
10	Light intensity + Light intensity^2	4	18.1	9.09	0.004	0.48
11	Floral cover + Light intensity	4	18.1	9.14	0.004	0.46
12	Floral cover + Light intensity^2 + Forest land cover	5	21.4	12.46	0.001	1.68
13	Floral cover + Light intensity + Forest land cover	5	21.5	12.56	0.001	1.67
14	Light intensity + Light intensity^2 + Forest land cover	5	21.8	12.79	0.001	1.63
15	Floral cover + Light intensity + Light intensity^2	5	27	17.99	0	0.51

		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	36.4	27.46	0	1.68
CWM (Nesting location - Mixed)	10	1	Forest land cover	3	8.3	0	0.4	1.45
		2	Null	2	8.7	0.38	0.33	0
		3	Light intensity	3	12.1	3.77	0.06	0.33
		4	Light intensity^2	3	12.1	3.8	0.06	0.32
		5	Floral cover	3	12.6	4.32	0.05	0.13
		6	Light intensity + Forest land cover	4	13	4.74	0.04	1.74
		7	Light intensity^2 + Forest land cover	4	13.2	4.93	0.03	1.7
		8	Floral cover + Forest land cover	4	13.4	5.14	0.03	1.65
		9	Floral cover + Light intensity^2	4	18	9.68	0.003	0.37
		10	Floral cover + Light intensity	4	18	9.71	0.003	0.36

		11	Light intensity + Light intensity^2	4	18.1	9.77	0.003	0.33
		12	Floral cover + Light intensity + Forest land cover	5	21.7	13.43	0	1.81
		13	Floral cover + Light intensity^2 + Forest land cover	5	21.8	13.47	0	1.8
		14	Light intensity + Light intensity^2 + Forest land cover	5	22	13.72	0	1.75
		15	Floral cover + Light intensity + Light intensity^2	5	27	18.68	0	0.37
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	36.7	28.43	0	1.81
CWM (Social)	10	1	Null	2	8.3	0	0.55	0
		2	Forest land cover	3	10.8	2.47	0.16	0.72
		3	Light intensity^2	3	11.8	3.5	0.09	0.33
		4	Light intensity	3	12	3.69	0.09	0.25
		5	Floral cover	3	12.4	4.1	0.07	0.08

6	Light intensity^2 + Forest land cover	4	16	7.69	0.01	0.99
7	Light intensity + Forest land cover	4	16.2	7.83	0.01	0.95
8	Floral cover + Forest land cover	4	16.5	8.15	0.01	0.84
9	Light intensity + Light intensity^2	4	17.7	9.42	0.01	0.36
10	Floral cover + Light intensity^2	4	17.8	9.47	0.01	0.34
11	Floral cover + Light intensity	4	18	9.67	0.004	0.26
12	Floral cover + Light intensity^2 + Forest land cover	5	24.9	16.58	0	1.03
13	Floral cover + Light intensity + Forest land cover	5	25	16.65	0	1.01
14	Light intensity + Light intensity^2 + Forest land cover	5	25.1	16.75	0	0.97
15	Floral cover + Light intensity + Light intensity^2	5	26.6	18.3	0	0.41

		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	39.8	31.44	0	1.08
CWM (Solitary)	10	1	Null	2	8.3	0	0.55	0
		2	Forest land cover	3	10.8	2.47	0.16	0.72
		3	Light intensity^2	3	11.8	3.5	0.09	0.33
		4	Light intensity	3	12	3.69	0.09	0.25
		5	Floral cover	3	12.4	4.1	0.07	0.08
		6	Light intensity^2 + Forest land cover	4	16	7.69	0.01	0.99
		7	Light intensity + Forest land cover	4	16.2	7.83	0.01	0.95
		8	Floral cover + Forest land cover	4	16.5	8.15	0.01	0.84
		9	Light intensity + Light intensity^2	4	17.7	9.42	0.01	0.36
		10	Floral cover + Light intensity^2	4	17.8	9.47	0.01	0.34
		11	Floral cover + Light intensity	4	18	9.67	0.004	0.26

		12	Floral cover + Light intensity^2 + Forest land cover	5	24.9	16.58	0	1.03
		13	Floral cover + Light intensity + Forest land cover	5	25	16.65	0	1.01
		14	Light intensity + Light intensity^2 + Forest land cover	5	25.1	16.75	0	0.97
		15	Floral cover + Light intensity + Light intensity^2	5	26.6	18.3	0	0.41
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	39.8	31.44	0	1.08
CWM (Hairiness - Dense)	10	1	Null	2	9.6	0	0.54	0
		2	Forest land cover	3	11.6	2.03	0.2	0.63
		3	Floral cover	4	13.5	3.92	0.08	0.11
		4	Light intensity^2	4	13.6	4.03	0.07	0.08
		5	Light intensity	3	13.7	4.06	0.07	0.07
		6	Floral cover + Forest land cover	3	17	7.4	0.01	0.78
		7	Light intensity + Forest land cover	3	17.4	7.8	0.01	0.68

8	Light intensity^2 + Forest land cover	4	17.4	7.81	0.01	0.68
9	Floral cover + Light intensity^2	4	19.4	9.8	0.01	0.15
10	Floral cover + Light intensity	4	19.5	9.85	0.004	0.13
11	Light intensity + Light intensity^2	4	19.6	10.03	0.004	0.08
12	Floral cover + Light intensity^2 + Forest land cover	5	25.9	16.33	0.004	0.79
13	Floral cover + Light intensity + Forest land cover	5	26	16.36	0	0.79
14	Light intensity + Light intensity^2 + Forest land cover	5	26.4	16.8	0	0.68
15	Floral cover + Light intensity + Light intensity^2	5	28.3	18.72	0	0.17
16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	40.9	31.28	0	0.81

CWM (Hairiness - Sparse)	10	1	Null	2	9.6	0	0.54	0
		2	Forest land cover	3	11.6	2.03	0.2	0.63
		3	Floral cover	4	13.5	3.92	0.08	0.11
		4	Light intensity^2	4	13.6	4.03	0.07	0.08
		5	Light intensity	3	13.7	4.06	0.07	0.07
		6	Floral cover + Forest land cover	3	17	7.4	0.01	0.78
		7	Light intensity + Forest land cover	3	17.4	7.8	0.01	0.68
		8	Light intensity^2 + Forest land cover	4	17.4	7.81	0.01	0.68
		9	Floral cover + Light intensity^2	4	19.4	9.8	0.01	0.15
		10	Floral cover + Light intensity	4	19.5	9.85	0.004	0.13
		11	Light intensity + Light intensity^2	4	19.6	10.03	0.004	0.08
		12	Floral cover + Light intensity^2 + Forest land cover	5	25.9	16.33	0.004	0.79

		13	Floral cover + Light intensity + Forest land cover	5	26	16.36	0	0.79
		14	Light intensity + Light intensity^2 + Forest land cover	5	26.4	16.8	0	0.68
		15	Floral cover + Light intensity + Light intensity^2	5	28.3	18.72	0	0.17
		16	Floral cover + Light intensity + Light intensity^2 + Forest land cover	6	40.9	31.28	0	0.81
Fruit-set – Trait diversity	7	**1**	**Pollinator visitation rate**	**2**	**61**	**0**	**0.44**	**0.97**
		2	FDis (E) + Pollinator visitation rate	3	62	2.06	0.26	0.99
		3	FDis (E)^2 + Pollinator visitation rate	3	63.2	2.28	0.14	0.98
		4	FDis (Dietary specialization) + Pollinator visitation rate	3	64.2	3.21	0.09	0.98
		5	FDis (Dietary specialization)^2 + Pollinator visitation rate	3	64.3	3.38	0.08	0.98
		6	FDis (E) + FDis (E)^2 + Pollinator visitation rate	4	73.4	12.44	0.001	0.99

7	FDis (E) + FDis (Dietary specialization) + Pollinator visitation rate	4	74.7	13.72	0	0.99
8	FDis (E) + FDis (Dietary specialization)^2 + Pollinator visitation rate	4	74.7	13.76	0	0.99
9	FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	4	75.7	14.74	0	0.99
10	FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	4	75.9	14.89	0	0.99
11	FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	4	78.2	17.21	0	0.98
12	FDis (E)^2	2	80.8	19.85	0	0.49
13	Null	1	81.3	20.36	0	0
14	FDis (E) + FDis (E)^2	3	81.4	20.45	0	0.8
15	FDis (E)	2	83.1	22.13	0	0.29
16	FDis (E)^2 + FDis (Dietary specialization)^2	3	83.9	22.91	0	0.71
17	FDis (Dietary specialization)^2	2	83.9	22.93	0	0.21

18	FDis (Dietary specialization)	2	84.4	23.48	0	0.14
19	FDis (E)^2 + FDis (Dietary specialization)	3	84.8	23.84	0	0.67
20	FDis (E) + FDis (Dietary specialization)^2	3	86.3	25.32	0	0.59
21	FDis (E) + FDis (Dietary specialization)	3	87.1	26.16	0	0.54
22	FDis (Dietary specialization) + FDis (Dietary specialization)^2	3	89.2	28.2	0	0.38
23	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2	4	94	33.05	0	0.83
24	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)	4	94.8	33.82	0	0.81
25	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	4	96.3	35.34	0	0.77
26	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2	4	99.1	38.09	0	0.66
27	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	5	112.7	51.79	0	0.99

		28	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	5	113.6	52.63	0	0.99
		29	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	5	116.7	55.71	0	0.99
		30	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	5	117.7	56.72	0	0.99
		31	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	5	131.7	70.74	0	0.91
		32	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	Inf.	Inf.	0	1
Fruit-set – Trait identity	8	**1**	**CWM (Oligolectic) + CWM (Oligolectic)^2 + Pollinator visitation rate**	**4**	**80.3**	**0**	**0.7**	**0.99**
		2	CWM (Oligolectic)^2 + Pollinator visitation rate	3	84.7	4.42	0.22	0.99

3	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	5	84.7	4.43	0.03	0.99
4	CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	4	85.3	4.96	0.03	0.96
5	Pollinator visitation rate	2	89.7	9.36	0.01	0.95
6	CWM (Oligolectic)^2	2	90.4	10.08	0.01	0.87
7	CWM (Oligolectic) + Pollinator visitation rate	3	90.8	10.52	0.001	0.8
8	CWM (Oil collectors) + Pollinator visitation rate	3	91	10.72	0.001	0.9
9	CWM (Oligolectic) + CWM (Oligolectic)^2	3	93.5	13.24	0.001	0.89
10	CWM (Oligolectic) + CWM (Oil collectors) + Pollinator visitation rate	4	94	13.69	0	0.87
11	CWM (Oligolectic)	2	94.5	14.19	0	0.72
12	CWM (Oligolectic)^2 + CWM (Oil collectors)	3	96	15.66	0	0.95
13	Null	1	98.9	18.63	0	0.95

		14	CWM (Oligolectic) + CWM (Oil collectors) + Pollinator visitation rate	3	100.1	19.78	0	0.72
		15	CWM (Oil collectors)	2	101.9	21.57	0	0
		16	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors)	4	102.7	22.39	0	0.18
Log (Fruit maximum length + 1) – Trait diversity	10	**1**	**FDis (E) + FDis (E)^2 + + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate**	**8**	**-322.2**	**0**	**1**	**-0.22**
		2	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-306.9	15.31	0	-0.18
		3	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	6	-298.6	23.57	0	-0.15
		4	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	7	-295.2	26.95	0	-0.15
		5	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	7	-281	41.17	0	-0.1

6	FDis (E) + FDis (E)^2	5	-274.9	47.25	0	-0.07
7	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)	6	-272.4	49.74	0	-0.07
8	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-271.9	50.26	0	-0.07
9	FDis (Dietary specialization) + FDis (Dietary specialization)^2	5	-271.7	50.49	0	-0.06
10	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2	6	-271	51.21	0	-0.07
11	FDis (E)^2	4	-270.4	51.78	0	-0.05
12	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-267.3	54.88	0	-0.06
13	FDis (E)^2 + FDis (Dietary specialization)^2	5	-266.9	55.29	0	-0.05
14	FDis (E)^2 + FDis (Dietary specialization)^2	5	-266.3	55.84	0	-0.05
15	FDis (E)	4	-263.2	58.96	0	-0.03
16	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-262.3	59.9	0	-0.07

17	FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-261.8	60.32	0	-0.06
18	FDis (E)^2 + Pollinator visitation rate	5	-260.5	61.62	0	-0.05
19	FDis (E) + FDis (Dietary specialization)	5	-259.5	62.64	0	-0.04
20	FDis (E) + FDis (Dietary specialization)^2	5	-259	63.19	0	-0.03
21	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-257.9	64.28	0	-0.06
22	Null	3	-257.4	64.77	0	-0.0001
23	FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	6	-257.2	64.96	0	-0.05
24	FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation	6	-256.5	65.63	0	-0.05
25	FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation	4	-254.5	67.7	0	-0.01
26	FDis (E) + Pollinator visitation rate	5	-253.5	68.63	0	-0.03
27	FDis (Dietary specialization)^2	4	-250.6	69.14	0	-0.0001

		28	FDis (E) + FDis (Dietary specialization) + Pollinator visitation rate	6	-249.6	71.52	0	-0.04
		29	FDis (E) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-249.4	72.59	0	-0.03
		30	Pollinator visitation rate	4	-249.5	72.74	0	-0.01
		31	FDis (Dietary specialization)^2 + Pollinator visitation rate	5	-245.4	76.8	0	-0.01
		32	FDis (Dietary specialization)^2 + Pollinator visitation rate	5	-245.4	76.81	0	-0.01
Log (Fruit maximum length + 1) – Trait identity	10	**1**	**CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors)**	**6**	**-373.4**	**0**	**0.56**	**-0.19**
		2	**CWM (Oligolectic)^2 + CWM (Oil collectors)**	**5**	**-372.9**	**0.49**	**0.44**	**-0.18**
		3	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	7	-363.7	9.61	0.01	-0.19
		4	CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	6	-362.7	10.62	0.003	-0.18
		5	CWM (Oligolectic) + CWM (Oil collectors)	5	-360.1	13.29	0.001	-0.16

		6	CWM (Oligolectic) + CWM (Oil collectors) + Pollinator visitation rate	6	-350.2	23.18	0	-0.16
		7	CWM (Oil collectors)	4	-345.6	27.77	0	-0.12
		8	CWM (Oil collectors) + Pollinator visitation rate	5	-336.6	36.79	0	-0.12
		9	CWM (Oligolectic) + CWM (Oligolectic)^2	5	-299.3	74.03	0	-0.02
		10	Null	3	-298.7	74.69	0	-0.003
		11	CWM (Oligolectic)^2	4	-297.4	76	0	-0.01
		12	CWM (Oligolectic) + CWM (Oligolectic)^2 + Pollinator visitation rate	6	-294.3	79.05	0	-0.03
		13	CWM (Oligolectic)	4	-293.7	79.67	0	-0.01
		14	Pollinator visitation rate	4	-291	82.34	0	-0.01
		15	CWM (Oligolectic)^2 + Pollinator visitation rate	5	-289	84.4	0	-0.01
		16	CWM (Oligolectic) + Pollinator visitation rate	5	-285.5	87.82	0	-0.01
Log (Fruit maximum width + 1) – Trait diversity	10	1	**FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate**	**8**	**-358.5**	**0**	**0.51**	**-0.12**

2	**FDis (E) + FDis (E)^2**	**5**	**-357**	**1.54**	**0.24**	**-0.08**
3	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	7	-356.3	2.26	0.16	-0.1
4	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-352.7	5.81	0.03	-0.1
5	FDis (E) + FDis (E)^2 + Pollinator visitation rate	6	-352.5	5.99	0.03	-0.09
6	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2	6	-352.5	6.02	0.03	-0.08
7	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)	6	-351.1	7.44	0.01	-0.08
8	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	7	-347.2	11.27	0.002	-0.09
9	FDis (E)^2 + Pollinator visitation rate	5	-334.7	23.83	0	-0.05
10	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-331.1	27.41	0	-0.06

11	FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-330.7	27.83	0	-0.05
12	FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	6	-330.6	27.92	0	-0.06
13	FDis (E) + Pollinator visitation rate	5	-329.4	29.15	0	-0.05
14	FDis (E)^2	4	-329.3	29.19	0	-0.02
15	FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-328.6	29.91	0	-0.05
16	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-326.9	31.62	0	-0.06
17	Null	3	-325.7	32.8	0	-0.01
18	FDis (E) + FDis (Dietary specialization) + Pollinator visitation rate	6	-325.7	32.85	0	-0.05
19	FDis (E) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-325.5	33.02	0	-0.05
20	FDis (E)^2 + FDis (Dietary specialization)^2	5	-325.1	33.39	0	-0.03
21	Pollinator visitation rate	4	-324.5	34.05	0	-0.03

		22	FDis (Dietary specialization) + FDis (Dietary specialization)^2	5	-324.4	34.13	0	-0.02
		23	FDis (E)^2 + FDis (Dietary specialization)	5	-323.2	35.28	0	-0.02
		24	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-323	35.51	0	-0.03
		25	FDis (Dietary specialization)^2	4	-322.4	36.07	0	-0.01
		26	FDis (E)	4	-322.1	36.45	0	-0.01
		27	FDis (Dietary specialization)^2 + Pollinator visitation rate	5	-320.1	38.41	0	-0.03
		28	FDis (Dietary specialization)	4	-319.7	38.86	0	-0.01
		29	FDis (Dietary specialization) + Pollinator visitation rate	5	-319.5	39.04	0	-0.03
		30	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-318.8	39.69	0	-0.02
		31	FDis (E) + FDis (Dietary specialization)^2	5	-318.3	40.23	0	-0.01
		32	FDis (E) + FDis (Dietary specialization)	5	-316	42.51	0	-0.01
Log (Fruit maximum width + 1) – Trait identity	10	**1**	**CWM (Oligolectic)^2 + CWM (Oil collectors)**	**5**	**-534.8**	**0**	**0.8**	**-0.1**

2	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors)	6	-531	3.87	0.12	-0.1
3	CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	6	-528.8	6.09	0.04	-0.1
4	CWM (Oligolectic) + CWM (Oil collectors)	5	-528.5	6.39	0.03	-0.09
5	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	7	-526.8	8.01	0.02	-0.1
6	CWM (Oligolectic) + CWM (Oil collectors) + Pollinator visitation rate	6	-521.1	13.79	0.001	-0.09
7	CWM (Oil collectors) + Pollinator visitation rate	5	-512.5	22.36	0	-0.08
8	CWM (Oil collectors)	4	-512.1	22.72	0	-0.07
9	Pollinator visitation rate	4	-472.4	62.44	0	-0.03
10	CWM (Oligolectic) + CWM (Oligolectic)^2 + Pollinator visitation rate	6	-469.8	65	0	-0.03
11	CWM (Oligolectic)$^{2\ +}$ Pollinator visitation rate	5	-468	66.87	0	-0.01
12	Null	3	-467.8	67.05	0	-0.03

		13	CWM (Oligolectic) + Pollinator visitation rate	5	-466.1	68.71	0	-0.01
		14	CWM (Oligolectic)^2	4	-464.9	69.95	0	-0.01
		15	CWM (Oligolectic)	4	-462.7	72.1	0	-0.01
		16	CWM (Oligolectic) + CWM (Oligolectic)^2	5	-461.7	73.12	0	-0.01
Log (Fruit fresh weight + 1) – Trait diversity	10	**1**	**FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2**	**7**	**244.5**	**0**	**0.9**	**0.31**
		2	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	8	249	4.49	0.1	0.31
		3	FDis (E) + FDis (E)^2	5	257.5	12.95	0.001	0.23
		4	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)	6	260.5	15.96	0	0.24
		5	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2	6	260.6	16.13	0	0.23
		6	FDis (E) + FDis (E)^2 + Pollinator visitation rate	6	264	19.47	0	0.23

7	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	264.7	20.22	0	0.25
8	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	266.2	21.7	0	0.23
9	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	7	267.2	22.71	0	0.24
10	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	268.7	24.22	0	0.21
11	FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	271.2	26.67	0	0.21
12	FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	6	273.2	28.69	0	0.19
13	FDis (E)^2 + Pollinator visitation rate	5	274.5	30.01	0	0.19
14	FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	276.2	31.67	0	0.2

15	FDis (E) + FDis (Dietary specialization) + Pollinator visitation rate	6	277.5	32.98	0	0.17
16	FDis (E) + Pollinator visitation rate	5	279.2	35.43	0	0.18
17	FDis (E) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	277.5	36.55	0	0.13
18	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	279.9	39.62	0	0.12
19	FDis (Dietary specialization) + FDis (Dietary specialization)^2	5	281.1	40.46	0	0.1
20	FDis (E)^2	4	284.1	41.5	0	0.1
21	FDis (E)^2 + FDis (Dietary specialization)^2	5	285	44.52	0	0.12
22	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	286	44.6	0	0.1
23	FDis (E)^2 + FDis (Dietary specialization)	5	289	45.77	0	0.08
24	Pollinator visitation rate	4	289.1	51.1	0	0.06
25	FDis (E)	4	290.3	51.32	0	0.06
26	FDis (Dietary specialization) + Pollinator visitation rate	5	295.6	51.81	0	0.1

		27	Null	3	296.3	52.73	0	0.04
		28	FDis (E) + FDis (Dietary specialization)^2	5	297.2	54.08	0	0.07
		29	FDis (Dietary specialization)^2 + Pollinator visitation rate	5	298.7	54.13	0	0.08
		30	FDis (Dietary specialization)^2	4	299.4	54.88	0	0.04
		31	FDis (E) + FDis (Dietary specialization)	5	300.1	55.62	0	0.07
		32	FDis (Dietary specialization)	4	301.4	56.88	0	0.04
Log (Fruit fresh weight + 1) – Trait identity	10	1	**CWM (Oligolectic)^2 + CWM (Oil collectors)**	**5**	**189.8**	**0**	**0.58**	**0.53**
		2	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors)	6	191.8	2.02	0.21	0.53
		3	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	7	193.1	3.29	0.11	0.56
		4	CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	6	193.5	3.71	0.09	0.55
		5	CWM (Oligolectic) + CWM (Oil collectors)	5	200.7	10.84	0.003	0.5

		6	CWM (Oligolectic) + CWM (Oil collectors) + Pollinator visitation rate	6	206.4	16.55	0	0.51
		7	CWM (Oil collectors) + Pollinator visitation rate	5	230.3	40.47	0	0.41
		8	CWM (Oil collectors)	4	235.3	45.52	0	0.36
		9	CWM (Oligolectic) + CWM (Oligolectic)^2 + Pollinator visitation rate	6	288.5	98.69	0	0.19
		10	Pollinator visitation rate	4	293.2	103.43	0	0.14
		11	CWM (Oligolectic)^2 + Pollinator visitation rate	5	293.9	104.06	0	0.16
		12	CWM (Oligolectic) + Pollinator visitation rate	5	297.3	107.45	0	0.09
		13	CWM (Oligolectic)^2	4	301	111.15	0	0.1
		14	CWM (Oligolectic) + CWM (Oligolectic)^2	5	301.9	112.09	0	0.1
		15	Null	3	303	113.22	0	0.07
		16	CWM (Oligolectic)	4	304.2	114.44	0	0.08
Log (Fruit firmness + 1) – Trait diversity	10	**1**	**FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate**	**7**	**-180.3**	**0**	**0.27**	**-0.39**

2	**FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate**	**7**	**-179.2**	**1.08**	**0.16**	**-0.39**
3	**FDis (E)^2**	**4**	**-179**	**1.27**	**0.15**	**-0.31**
4	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	8	-177.6	2.72	0.07	-0.4
5	FDis (E) + FDis (E)^2	5	-177.4	2.94	0.06	-0.31
6	FDis (E)^2 + FDis (Dietary specialization)^2	5	-177.3	3.04	0.04	-0.32
7	FDis (E)^2 + FDis (Dietary specialization)	5	-176.6	3.69	0.03	-0.32
8	FDis (E)^2 + FDis (Dietary specialization) + FDis (E) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-176	4.29	0.03	-0.37
9	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2	6	-175.8	4.54	0.03	-0.33
10	FDis (E) + FDis (Dietary specialization) + Pollinator visitation rate	6	-175.7	4.55	0.02	-0.38

11	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)	6	-175.4	4.87	0.02	-0.33
12	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-174.8	5.48	0.01	-0.32
13	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	7	-173.9	6.39	0.01	-0.34
14	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-173.7	6.55	0.01	-0.38
15	FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	6	-173.3	6.98	0.01	-0.36
16	FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-173.2	7.14	0.004	-0.35
17	FDis (E)^2 + Pollinator visitation rate	5	-172	8.27	0.004	-0.32
18	FDis (E) + FDis (E)^2 + Pollinator visitation rate	6	-172	8.34	0.004	-0.33
19	FDis (E) + Pollinator visitation rate	5	-171.7	8.59	0.003	-0.33

20	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-171.5	8.78	0.003	-0.36
21	FDis (E)	4	-171.1	9.21	0.003	-0.27
22	FDis (E) + FDis (Dietary specialization)^2	5	-168.8	11.48	0.001	-0.28
23	FDis (E) + FDis (Dietary specialization)	5	-168.2	12.09	0	-0.28
24	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-166.6	13.68	0	-0.29
25	FDis (Dietary specialization) + FDis (Dietary specialization)^2	5	-142.8	37.5	0	-0.13
26	FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-133.7	46.64	0	-0.13
27	Null	3	-129.2	51.13	0	1.89×10^{-15}
28	FDis (Dietary specialization)	4	-127.5	52.84	0	-0.02
29	FDis (Dietary specialization)^2	4	-125.1	55.22	0	-4.54×10^{-4}
30	Pollinator visitation rate	4	-119.9	60.41	0	-0.003
31	FDis (Dietary specialization) + Pollinator visitation rate	5	-117.8	62.5	0	-0.02

		32	FDis (Dietary specialization)^2 + Pollinator visitation rate	5	-115.8	64.48	0	-0.003
Log (Fruit firmness + 1) – Trait identity	10	**1**	**CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate**	**7**	**-188.8**	**0**	**0.75**	**-0.38**
		2	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors)	6	-186.5	2.24	0.25	-0.32
		3	CWM (Oligolectic) + CWM (Oil collectors)	5	-174	14.82	0	-0.25
		4	CWM (Oligolectic) + CWM (Oil collectors) + Pollinator visitation rate	6	-169.4	19.34	0	-0.28
		5	CWM (Oligolectic)^2 + CWM (Oil collectors)	5	-166.4	22.4	0	-0.21
		6	CWM (Oil collectors)	4	-165.6	23.15	0	-0.18
		7	CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	6	-158.2	30.54	0	-0.21
		8	CWM (Oil collectors) + Pollinator visitation rate	5	-156	32.74	0	-0.18
		9	CWM (Oligolectic) + CWM (Oligolectic)^2	5	-152.7	36.07	0	-0.12

		10	CWM (Oligolectic) + CWM (Oligolectic)^2 + Pollinator visitation rate	6	-144.8	43.94	0	-0.12
		11	Null	3	-139	49.77	0	-3.46×10^{-15}
		12	CWM (Oligolectic)^2	4	-134.7	54.09	0	-4.61×10^{-4}
		13	CWM (Oligolectic)	4	-134.7	54.11	0	-0.01
		13	Pollinator visitation rate	4	-129.4	59.43	0	-0.01
		15	CWM (Oligolectic)^2 + Pollinator visitation rate	5	-125.1	63.64	0	-0.01
		16	CWM (Oligolectic) + Pollinator visitation rate	5	-125	63.83	0	-0.01
Log (Fruit sugar content + 1) – Trait diversity	10	**1**	**FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2**	**7**	**-287.1**	**0**	**0.4**	**-0.24**
		2	**FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate**	**7**	**-285.2**	**1.90**	**0.15**	**-0.25**
		3	FDis (E) + FDis (E)^2	5	-284.5	2.6	0.11	-0.21

4	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	8	-284.5	2.85	0.1	-0.25
5	FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-284.3	3.37	0.07	-0.24
6	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-283.7	3.48	0.03	-0.25
7	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-283.6	5.53	0.02	-0.22
8	FDis (E)^2 + Pollinator visitation rate	5	-281.6	5.87	0.02	-0.22
9	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2	6	-281.2	6.48	0.01	-0.21
10	FDis (E) + Pollinator visitation rate	5	-280.6	6.86	0.01	-0.22
11	FDis (E) + FDis (E)^2 + Pollinator visitation rate	6	-280.2	6.9	0.004	-0.22
12	FDis (E) + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-280.2	9.42	0.003	-0.21

13	FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-277.7	9.48	0.002	-0.22
14	FDis (E) + FDis (E)^2 + FDis (Dietary specialization)^2 + Pollinator visitation rate	7	-277.6	10.5	0.002	-0.22
15	FDis (E) + FDis (Dietary specialization)^2 + Pollinator visitation rate	6	-276.6	10.92	0.001	-0.22
16	FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	6	-276.2	11.71	0.001	-0.22
17	FDis (E) + FDis (E)^2 + FDis (Dietary specialization) + Pollinator visitation rate	7	-275.4	12.05	0.001	-0.22
18	FDis (E) + FDis (Dietary specialization) + Pollinator visitation rate	6	-275	12.41	0.001	-0.22
19	FDis (E)	4	-274.7	12.71	0.001	-0.18
20	FDis (E) + FDis (Dietary specialization)	5	-274.4	14.41	0	-0.19
21	FDis (E) + FDis (Dietary specialization)^2	5	-272.7	15.91	0	-0.18
22	FDis (E)^2 + FDis (Dietary specialization) + FDis (Dietary specialization)^2	6	-271.2	16.84	0	-0.18

		23	FDis (Dietary specialization)^2 + Pollinator visitation rate	5	-270.3	24.56	0	-0.17
		24	FDis (E)^2	4	-262.5	24.69	0	-0.14
		25	Pollinator visitation rate	4	-262.4	25.56	0	-0.15
		26	FDis (E)^2 + FDis (Dietary specialization)	5	-261.5	25.74	0	-0.15
		27	FDis (Dietary specialization) + FDis (Dietary specialization)^2	5	-261.4	26.11	0	-0.15
		28	FDis (E)^2 + FDis (Dietary specialization)^2	5	-261	28.03	0	-0.15
		29	FDis (Dietary specialization) + Pollinator visitation rate	5	-259.1	31.36	0	-0.15
		30	Null	3	-255.7	61.17	0	-0.01
		31	FDis (Dietary specialization)	4	-225.9	62.66	0	-0.03
		32	FDis (Dietary specialization)^2	4	-224.4	65.59	0	-0.01
Log (Fruit sugar content + 1) – Trait identity	7	**1**	**CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate**	**7**	**-306.3**	**0**	**0.99**	**-0.27**
		2	CWM (Oligolectic)^2 + CWM (Oil collectors) + Pollinator visitation rate	6	-296.2	10.07	0.01	-0.23

3	CWM (Oligolectic) + CWM (Oligolectic)^2 + Pollinator visitation rate	6	-291.7	14.6	0	-0.21
4	CWM (Oligolectic) + CWM (Oil collectors) + Pollinator visitation rate	6	-281.6	24.72	0	-0.2
5	CWM (Oligolectic)^2 + Pollinator visitation rate	5	-279	27.29	0	-0.17
6	CWM (Oil collectors) + Pollinator visitation rate	5	-273.9	32.35	0	-0.16
7	Pollinator visitation rate	4	-273.7	32.59	0	-0.14
8	CWM (Oligolectic) + CWM (Oligolectic)^2 + CWM (Oil collectors)	6	-271.5	34.76	0	-0.15
9	CWM (Oligolectic) + Pollinator visitation rate	5	-271.2	35.05	0	-0.15
10	CWM (Oligolectic) + CWM (Oligolectic)^2	5	-270.3	36.03	0	-0.13
11	Null	3	-237.6	68.71	0	-0.01
12	CWM (Oligolectic)^2 + CWM (Oil collectors)	5	-235.5	70.76	0	-0.04
13	CWM (Oligolectic)^2	4	-235.2	71.11	0	-0.02
14	CWM (Oil collectors)	4	-233.6	72.71	0	-0.01
15	CWM (Oligolectic)	4	-231.8	74.45	0	-0.01

	16	CWM (Oligolectic) + CWM (Oil collectors)	5	-228	78.28	0	-0.02

Table S13. Results of Moran's *I* autocorrelation test of model residuals. Observed and expected Moran's *I* values are shown. P-values > 0.05 indicate a lack of spatial autocorrelation.

Model ID (Response variable	Moran's *I* observed	Moran's *I* expected	*P*
FDis (R)	-0.47	-0.12	0.81
FDis (R-E)	-1.26	-0.22	0.96
FDis (Body length)	-0.52	-0.18	0.72
FDis (Inter-tegular span)	-0.51	-0.17	0.71
FDis (Forewing aspect ratio)	-0.28	-0.01	0.83
FDis (Dietary specialization)	-0.73	-0.12	0.97
FDis (Nesting location)	0.25	-0.01	0.18
FDis (Sociality)	-0.35	-0.17	0.35
FDis (Hairiness)	-0.22	-0.17	0.53
CWM (Body length)	0.27	-0.12	0.16
CWM (Inter-tegular span)	0.2	-0.12	0.2
CWM (Forewing aspect ratio)	-0.41	-0.22	0.62
CWM (Polylectic bees)	0.19	-0.12	0.24
CWM (Oligolectic bees)	0.19	-0.12	0.24
CWM (Above-ground nests)	-0.08	-0.12	0.46
CWM (Mixed nests)	-0.11	-0.12	0.49
CWM (Social bees)	0.43	-0.12	0.08
CWM (Solitary bees)	0.43	-0.12	0.08

CWM (Hairiness - Dense)	0.58	-0.12	0.05
CWM (Hairiness - Sparse)	0.58	-0.12	0.05
Fruit-set (Trait diversity)	0.21	0.97	0.55
Fruit-set (Trait identity)	-0.66	-1.72	0.33

Figure S1. Location of the study plots, which varied in management-related variables: herbaceous floral cover (%), light intensity (Lux), and forest coverage (%): 1 (7.8353°S – 34.8864°W); 2 (7.8426°S – 34.8806°W); 3 (8.0504°S – 34.9492°W); 4 (8.4756°S – 35.2424°W); 5 (8.5999°S – 35.2344°W); 6 (8.6044°S – 35.2266°W); 7 (8.6658°S – 35.0793°W); 8 (8.6847°S – 35.1330°W); 9 (8.6889°S – 35.1508°W); and 10 (8.6944°S – 35.1234°W). See Fig. 1 for further details.

Figure S2. Grid-based method used to systematically measure floral cover within each study plot. In red are the intersection points of the subplots; the blue lines delineate the subplots.

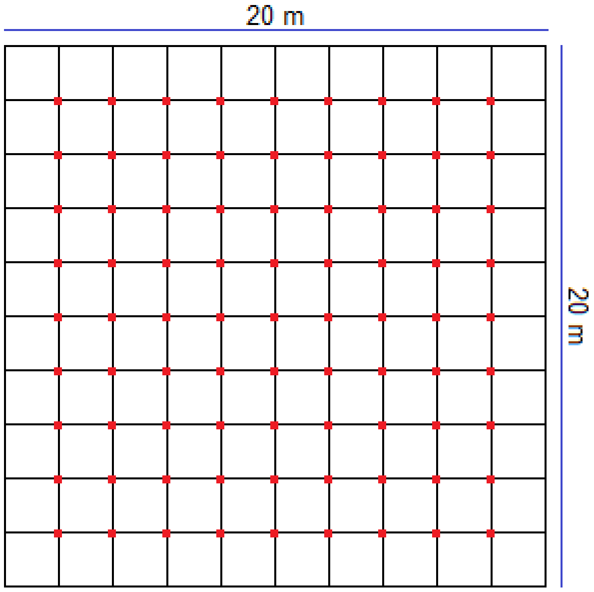


Figure S3. Floral cover associated with (A) the woody layer (i.e., trees and bushes), (B) the herbaceous layer, and (C) both strata in smallholder agroforestry systems in humid coastal areas of Pernambuco, northeastern Brazil. Each gray bar represents the relative amount of floral cover (black bar = 100%).

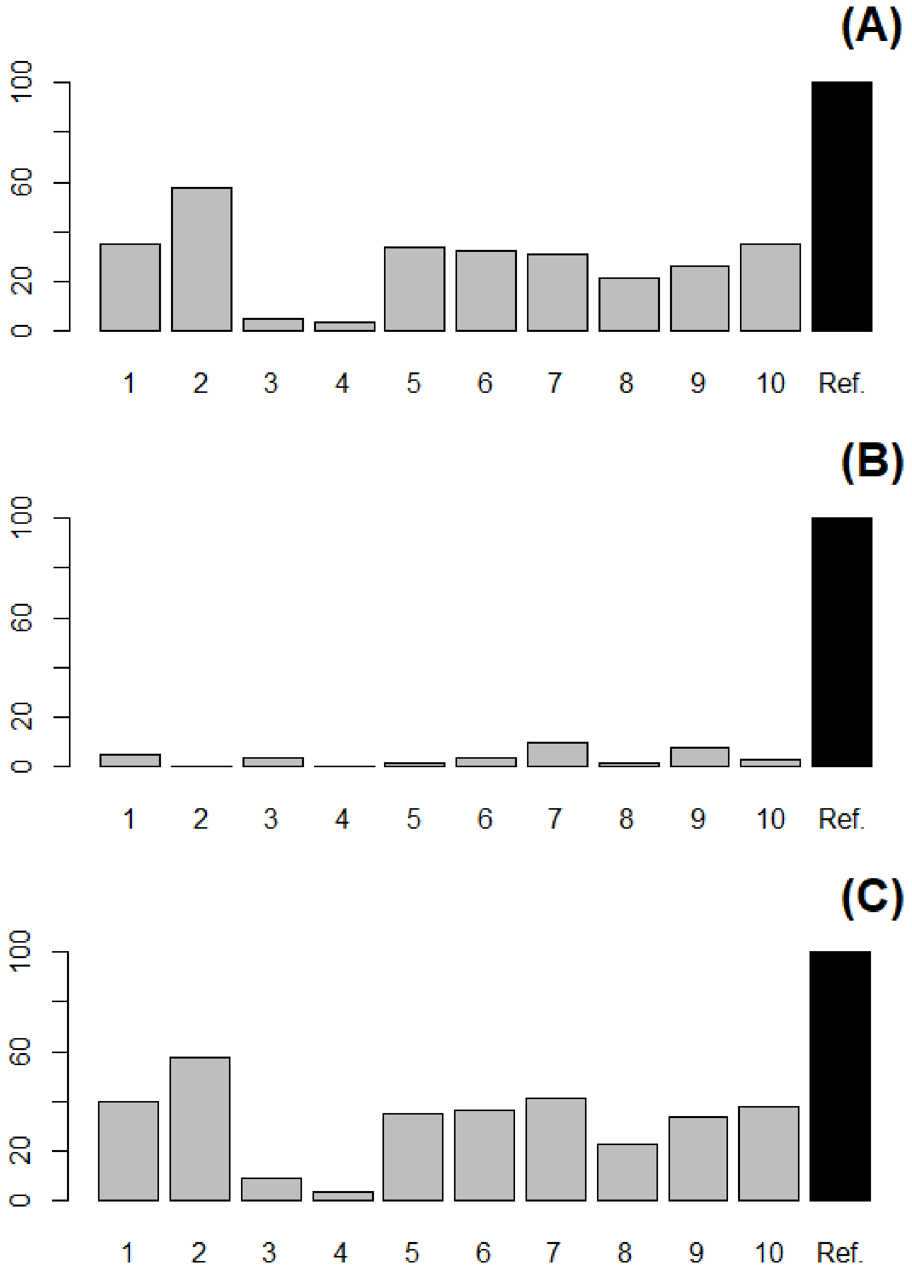


Figure S4. The (A) body length, (B) intertegular span, (C) forewing maximum length, and (D) forewing maximum width of the bee *Centris (Heterocentris) analis* (Fabricius. 1804) (Hymenoptera: Apidae: Centridini).

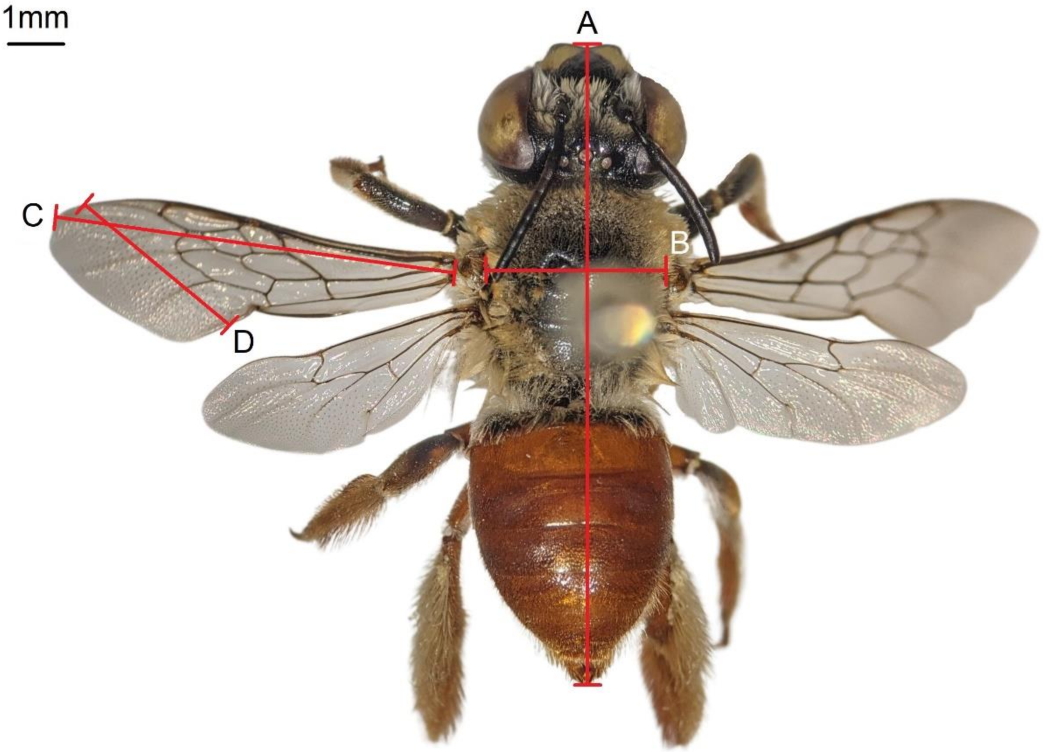


Figure S5. Acerola (*Malpighia emarginata* DC.) fruits at the same stage of ripeness.

6. CONSIDERAÇÕES FINAIS

6.1. Principais conclusões

Nossos resultados destacam que, em geral, os níveis de serviços de polinização podem ser semelhantes ou até maiores em sistemas agroflorestais do que em sistemas agrícolas convencionais, se os fatores locais e regionais forem adequadamente gerenciados. Assim, os serviços de polinização em sistemas agroflorestais podem ser otimizados principalmente pela melhoria dos recursos florais locais, aumento da cobertura de sombra e redução da distância entre os fragmentos agroflorestais e as florestas naturais próximas. No entanto, esses efeitos podem ser amplamente influenciados por fatores climáticos.

Primeiramente, nossa revisão (capítulo 1) revelou que os serviços de polinização podem ser maiores em sistemas agroflorestais em comparação com sistemas agrícolas convencionais, ou pelo menos equivalentes entre ambos. Até agora, café e cacau têm sido as culturas mais extensivamente estudadas, provavelmente devido à sua significância econômica e dependência de polinizadores. No entanto, isso enfatiza a urgência de investigar outras espécies de culturas, já que os sistemas agroflorestais poderiam oferecer uma alternativa sustentável para culturas economicamente importantes geralmente cultivadas através da agricultura intensiva. Não surpreendentemente, as abelhas têm sido o foco da maioria dos estudos, destacando seu papel crítico nos sistemas agroflorestais.

Além disso, utilizando o extenso corpo de literatura publicada disponível, nossa meta-análise (capítulo 2) forneceu evidências robustas que apoiam a ideia de que o aumento dos recursos florais locais em agroflorestas de café aumenta a diversidade de polinizadores de abelhas. No entanto, esse efeito pode ser influenciado por diversos fatores, incluindo condições climáticas, comportamento social dos polinizadores e as métricas usadas para avaliar os recursos florais. Embora a cobertura de árvores de sombra e a distância para as florestas naturais não pareçam afetar diretamente a diversidade de polinizadores, sua relação pode depender das condições climáticas. O aumento nos níveis de precipitação e temperatura é o principal fator que modera negativamente essa relação, embora não seja o único. Esses resultados devem ser considerados prioritariamente em relação aos cenários futuros de mudanças climáticas. Por exemplo, em certas regiões, temperaturas mais altas em áreas mais úmidas podem levar a uma precipitação ainda maior, apagando os efeitos positivos dos recursos florais locais e da cobertura de árvores de sombra na diversidade de polinizadores.

Por último, nossa abordagem de resposta-efeito (capítulo 3) demonstrou que a composição de traços funcionais das abelhas responde de forma diferente às práticas de manejo agroflorestal locais e regionais, enquanto a diversidade de traços funcionais dos polinizadores impacta a qualidade das frutas de maneiras complexas e divergentes. Esses resultados sugerem que as práticas de manejo agroflorestal influenciam indiretamente a qualidade das frutas ao moldar a diversidade funcional dos polinizadores por meio do manejo agroflorestal. Portanto, para otimizar a qualidade das frutas, é essencial manter níveis reduzidos de intensidade de luz e preservar diferentes graus de cobertura florestal natural ao redor das áreas agroflorestais, apoiando uma comunidade de polinizadores diversificada e promovendo práticas de polinização sustentável.

6.2. Contribuições teóricas e/ou metodológicas da tese

A tese sintetizou, por meio de diferentes abordagens, que o manejo agroflorestal é crucial para manter ou aumentar os serviços de polinização sustentáveis. Determinamos que o manejo da quantidade de recursos florais, da intensidade da luminosidade e da paisagem florestal são práticas essenciais a serem consideradas para manter diferentes facetas da diversidade de polinizadores e, assim, gerenciar os serviços de polinização. As condições climáticas locais podem mediar esses efeitos, por isso também devem ser consideradas. Especificamente, o aumento dos recursos florais locais, dentro do sistema agroflorestal, geralmente aumenta a diversidade taxonômica de polinizadores. No entanto, em cenários de aumento de temperatura e precipitação, o efeito dos recursos florais pode ser enfraquecido, tornando as estratégias de mitigação das mudanças climáticas antropogênicas cruciais. Por outro lado, embora a cobertura de árvores de sombra e a paisagem florestal (por exemplo, a distância até florestas naturais) não tenham um efeito global significativo na diversidade taxonômica, demonstramos que, a nível local, é imperativo manter níveis reduzidos de intensidade luminosa e preservar diferentes graus da paisagem florestal (por exemplo, cobertura de floresta natural) ao redor das áreas agroflorestais para promover uma alta diversidade funcional de polinizadores e otimizar a qualidade dos frutos. Concluímos que o manejo agroflorestal, aliado a estratégias de mitigação climática, é vital para a sustentabilidade dos serviços de polinização e para a qualidade e rendimento da produção de frutos.

6.3. Principais limitações do estudo

A principal limitação deste estudo foi a escassez de financiamento, o que limitou nossa capacidade de realizar trabalhos de campo mais extensivos. Embora tenhamos nos esforçado para coletar o máximo de dados possível dentro dos recursos alocados, o apoio financeiro limitado restringiu a coleta de dados *in situ* a apenas um capítulo da tese. Essa limitação dificultou nossa capacidade de explorar uma gama mais ampla de localidades, estender a duração dos esforços de amostragem ou empregar metodologias mais sofisticadas. Além disso, proibições devido à crise de emergência de saúde da doença coronavírus 2019 (COVID-19) restringiram os esforços de amostragem. Apesar dessas limitações, acreditamos que os resultados deste estudo ainda oferecem descobertas valiosas.

6.4. Propostas de investigações futuras

No geral, sugerimos que sejam conduzidas mais pesquisas para avaliar os efeitos das práticas de manejo agroflorestal sobre a diversidade taxonômica, funcional e filogenética dos polinizadores. Observamos que as pesquisas sobre várias práticas, como irrigação, configuração da paisagem e tratamentos agroquímicos em sistemas agroflorestais, permanecem limitadas. Além disso, é crucial que tais avaliações não apenas avaliem diretamente os efeitos nas várias facetas da diversidade de polinizadores, mas também considerem seu impacto nos serviços de polinização e suas consequências econômicas.

6.5. Orçamento

Este estudo foi financiado por:

1. Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) através de uma bolsa de doutorado (no. IBPG-0068-2.05/21) concedida ao estudante Diego Centeno Alvarado.
2. Universidade Federal Rural de Pernambuco (UFRPE) e Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) através do Programa de Apoio à Pós-Graduação (PROAP) com recursos concedidos ao estudante Diego Centeno Alvarado e ao Prof. Dr. Xavier Arnan.
3. *Organization for Tropical Studies* (OTS) através da bolsa de entomologia *Hovore-Horn* (no. 523/573) concedida ao estudante Diego Centeno Alvarado.
4. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) através da Bolsa de Produtividade em Pesquisa (no. PQ2: 307385/2020-5) concedida ao Prof. Dr. Xavier Arnan.

As despesas de amostragem incluíram a compra de material de escritório e de campo, aluguel de carro, combustível, hospedagem e alimentação. Aproximadamente R$ 10.225,44 foram gastos ao longo de 90 dias de coleta, representando um custo médio de R$ 113,62 por dia.

7. REFERÊNCIAS

ABROL, D.P. et al. Impact of insect pollinators on yield and fruit quality of strawberry**. Saudi J Biol Sci**, v. 26, n. 3, p. 524-530, 2019.

AIZEN, M.A. et al. How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. **Annals of Botany**, v. 103, p. 2005-2010, 2009.

ANDERSON, S.H. et al. Cascading effects of bird functional extinction reduce pollination and plant density. **Science**, v. 331, n. 6020, p. 1068-1071, 2011.

BAILES, E.J. et al. How can an understanding of plant-pollinator interactions contribute to global food security. **Current Opinion in Plant Biology**, v. 26, p. 72-79, 2015.

BAILLIE, J. et al. **Spineless: status and trends of the world's invertebrates.** London: IUCN, Zoological Society of London, 2012.

BARRERA, W.B.; BROSAS, J.V.; SACIL, M.D. Pollen sources of *Tetragonula biroi* (Friese, 1898) (Hymenoptera: Apidae, Meliponini) in two agroecosystems in Nagcarlan, Laguna, Philippines. **Palynology**, v. 45, n. 2, 2020.

BARRIOS, E. et al. Contribution of tress to the conservation of biodiversity and ecosystem services in agricultural landscapes. **Internation Journal of Biodiversity Science, Ecosystem Services & Management**, v. 14, n. 1, 2018.

BARTOMEUS, I. et al. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. **PeerJ**, v. 2, 2014.

BASCOMPTE, J. et al. The nested assembly of plant–animal mutualistic networks. **Proc Natl Acad Sci USA**, v. 100, p. 9383–9387, 2003.

BASTOLLA, U. et al. The architecture of mutualistic networks minimizes competition and increases biodiversity. **Nature**, v. 458, p. 1018–1020, 2009.

BEHERA, B.K.; PRASAD, R.; BEHERE, S. Public health, food security, and hunger. IN GURTNER, S; SOYEZ, K. (Eds.), **Challenges and Opportunities in Health Care Management.** Cham: Springer, 2022, p. 57-84.

BENNETT, E.M.; PETERSON, G.D.; GORDON, L.J. Understanding relationships among multiple ecosystem services. **Ecology Letters**, v. 12, n. 12, p. 1394–1404, 2009.

BENNETT, J.M. GloPL, a global data base on pollen limitation of plant reproduction. **Scientific Data**, v. 5, 2018.

BENTRUP et al. Temperate agroforestry systems and insect pollinators: A review. **Forests**, v. 10, n. 981, 2019.

BIESMEIJER, J.C. et al. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. **Science**, v. 313, n. 5785, p. 351–354, 2006.

BLASER, W.J. Climate-smart sustainable agriculture in low-to-intermediate shade agroforests. **Nature Sustainability**, v. 1, n. 5, 234-239, 2018.

BLÜTHGEN, N.; MENZEL, F.; BLÜTHGEN, N. Measuring specialization in species interaction networks. **BMC Ecol**, v. 6, n. 9, 2006.

BOHAN, D.A. et al. Networking Agroecology: Integrating the Diversity of Agroecosystem Interactions. In: WOODWARD, G.; BOHAN, D.A. (Eds.), **Ecological Networks in an Agricultural World. Advances in Ecological Research.** [s.l.] Academic Press, 2013. p. 1-67.

BPBES; REBIPP. **Relatório temático sobre polinização, polinizadores e produção de alimentos no Brasil.** São Paulo: Plataforma Brasileira de Biodiversidade e Serviços Ecossistêmicos, Rede Brasileira de Interações Planta-Polinizador.

BRITTAIN, C. et al. Pollination and plant resources change the nutritional quality of almonds for human health. **PLoS One**, v. 9, 2014.

BROUSSARD, M.A.; COATES, M.; MARTINSEN, P. Artificial pollination technologies: A review. **Agronomy**, v. 13, n. 5, 1351, 2023

BUCKLEY, Y.M. Generalized linear models. IN FOX, G.A.; NEGRETE-YANKELEVICH, S.; SOSA, V.J. (Eds.), **Ecological Statistics: Contemporary theory and application**. Oxford: Oxford University Press, 2015, p. 131-148.

BUTCHAT, S.H.M. et al. Global biodiversity: indicators of recent declines. **Science**, v. 328, n. 5982, p. 1164-1168, 2010.

CALLADA, S.M.G. et al. **Cashew systems in north-east Brazil: relationship between typology, productivity and characterization.** [s.l.] XXXIII Encontro da ANPAD, 2009.

CAMPBELL et al. High bee functional diversity buffers crop pollination services against Amazon deforestation. **Agriculture, Ecosystems and Environment**, v. 326, 2022.

CARDINALE, B.K. et al. Biodiversity loss and its impact on humanity. **Nature**, v. 486, p. 59-67, 2012.

CARVALHEIRO, L.G. et al. Natural and within farmland biodiversity enhances crop productivity. **Ecology Letters**, v. 14, p. 251-259, 2011.

CBD. **Decision adopted by the Conference of the Parties to the Convention on Biological Diversity.** Sharm El-Sheikh: Convention on Biological Diversity, 2018.

CENTENO-ALVARADO, D.; LOPES, A.V.; ARNAN, X. Fostering pollination through agroforestry: A global review. **Agriculture, Ecosystems & Environment**, v. 351, 108478, 2023.

CHAGNON, M. et al. Risks of large-scale use of systemic insecticides to ecosystem functioning and services. **Environ Sci Pollut Res**, v.22, p. 119–134, 2015.

COLLEN, B. et al. Monitoring change in vertebrate abundance: The living planet index. **Conserv Biol**, v. 23, n. 2, p. 317-327, 2009.

COLLEN, B.; BAILLIE, J.E.M. Barometer of life: Sampling. **Science**, v. 329, n. 5988, p. 140. 2010.

COUTINHO, J.G.E. et al. Landscape structure is a major driver of bee functional diversity in crops. **Frontiers in Ecology and Evolution Sec. Biogeography and Macroecology**, v. 9, 624835, 2021.

COULTHARD, E.; MCCOLLIN, D.; LITTLEMORE, J. The use of hedgerows as flight paths by moths in intensive farmland landscapes. **J. Insect Conserv**, v. 20, p. 345–350, 2016.

CRANMER, L.; MCCOLLIN, D.; OLLERTON, J. Landscape structure influences pollinator movements and directly affects plant reproductive success. **Oikos**, v. 121, p. 562–568, 2012.

DEHLING, D.M. The structure of ecological networks. In: DÁTTILO, W.; RICO-GRAY, V. (eds.) **Ecological Networks in the Tropics**. Cham: Springer, 2018. p. 29-42.

DESCAMPS, C. et al. Temperature and water stress affect plant-pollinator interactions in *Borago officinalis* (Boraginaceae). **Ecology and Evolution**, v. 8, p. 3443–3456, 2018.

DESCAMPS, C. et al. Warm temperatures reduce flower attractiveness and bumblebee foraging. **Insects**, 12, 493, 2021.

DIAS, A.S. et al. Gas exchanges and photochemical efficiency of the West Indian cherry cultivated with saline water and potassium fertilization. **Revista Brasileira de Engenharia Agrícola e Ambiental**, v. 22, n.9, 628-633, 2018.

DIRZO, R. et al. Defaunation in the Anthropocene. **Science**, v. 345, n. 6195, p. 401-406, 2014.

DOVER, J.; FRY, G.L.A. Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape. **Entomol Exp Appl**,v. 100, p. 221–233, 2001.

DRURY, C.F. et al. Nitrous oxide and carbon dioxide emissions from monoculture and rotational cropping of corn, soybean and winter wheat. **Canadian Journal of Soil Science**, v. 88, n. 2, p. 163-174, 2008.

ELITH, J.; LEATHWICK, J.R.; HASTIE, T. A working guide to boosted regression trees. **Journal of Animal Ecology**, v. 77, n. 4, p. 802-813, 2008.

EMBRAPA. **A cultura da acerola.** Brasília: Empresa Brasileira de Pesquisa Agropecuária, 2012.

EPULE, E.T.; BRYANT, C.R. Assessing the effects of agroecology and conventional farming techniques on small-scale peasant farmers’ crop yields in the Fako and Meme divisions of Cameroon. **African Journal of Agricultural Research**, v. 11, p. 849-866, 2016.

FIRBANK, L.G.; PETIT, S.; SMART, S.; BLAIN, A.; FULLER, R.J. Assessing the impacts of agricultural intensification on biodiversity: a British perspective. **Phil. Trans. R. B.**, v. 363, p.777-787, 2008.

FISHER, Z., TIPTON, E., ZHIPENG, H. Robumeta. <https://cran.r-project.org/web/packages/robumeta/>, 2017.

FAO. **The 10 elements of agroecology: Guiding the transition to sustainable food and agricultural systems.** Rome: FAO, 2018.

FAO. **The future of food and agriculture - Trends and Challenges.** Rome: FAO, 2017.

FAO. **Report of food security and nutrition in the world 2020. Transforming food systems for affordable healthy diets**. Rome: Food and Agriculture Organization of the United Nations, 2020.

FAO. **FAOSTAT Online database**. Rome: Food and Agriculture Organization of the United Nations, 2022.

FATEHI, P. et al. Tree density and forest productivity in a heterogeneous alpine environment: Insight from airborne laser scanning and imaging spectroscopy. **Forests**, v. 8, 2017.

FIERRO, M.M. et al. Effect of biotic factors on the spatial distribution of stingless bees (Hymenoptera: Apidae, Meliponini) in fragmented Neotropical habitats. **Neotropical Entomology**, v. 41, p. 95-104, 2012.

FRIMPONG-ANIN, K. et al. Dynamics of insect pollinators as influenced by Cocoa production systems in Ghana. **Journal of Pollination Ecology**, v. 5, n. 10, p. 74-80, 2011.

GARIBALDI, L.A. et al. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. **Ecology Letters**, v. 14, p. 1062-1072, 2011.

GARIBALDI, L.A. et al. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. **Science**, v. 339, p. 1608-1611, 2013.

GÉRARD, M. et al. Global warming and plant-pollinator mismatches. **Emerg Top Life Sci**, v. 4, n. 1, p. 77-86, 2020.

GODFRAY, H.; CHARLES, J.; GARNETT, T. Food security and sustainable intensification. **Phil Trans R Soc B**, 2014.

GÓMEZ-RUIZ, E.P.; LACHER JR., T.E. Climate change, range shifts, and the disruption of a pollinator-plant complex. **Scientific Reports**, v. 9, 14048, 2019.

GRAHAM, J.B.; NASSAUER, J.I, Wild bee abundance in temperate agroforestry landscapes: Assessing effects of alley crop composition, landscape configuration and agroforestry area. **Agroforest Syst**, v. 93, p. 837-850, 2019.

GREENLEAF, S.S. et al. Bee foraging ranges and their relationship to body size. **Oecologia**, v. 153, p. 589-596. 2007.

GREENWELL, B. et al. gbm: Generalized boosted regression models. <https://cran.r-project.org/package=gbm/>, 2019.

HAENKE, S. et al. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. **J Appl Ecol**, v. 51, p. 505–513, 2014.

HANLEY, N. et al. Measuring the economic value of pollination services: Principles, evidence and knowledge gaps. **Ecosystem Services**, v. 14, p. 124-132, 2015.

HANSEN, G.; STONE, D. Assessing the observed impact of anthropogenic climate change. **Nature Clim Change**, v. 6, p. 532-537, 2016.

HARVEY, C.A. et al. Climate-smart landscapes: opportunities and challenges for integrating adaptation and mitigation in tropical agriculture. **Conservation Letters**, p. 1-14, 2013.

HEDGES, L.V.; TIPTION, E.; JOHNSON, M.C. Robust variance estimation in meta-regression with dependent effect size estimates. **Research Synthesis Methods**, v. 1, p. 39-65, 2010.

HILL, D.B.; WEBSTER, T.C. Apiculture and forestry (bees and trees). **Agrofor Syst**, v. 29, p. 313–320, 1995.

HOOPER, D.U. et al. Species diversity, functional diversity, and ecosystem functioning. IN LOREAU, M.; NAEEM, S.; INCHAUSTI, P. (Eds.), **Biodiversity and Ecosystem Functioning**. Oxford: Oxford University Press, 2002, p. 195–208.

IBGE. **Censo Agropecuário 2017**. Rio de Janeiro: Instituto Brasileiro de Geografia e Estatística (IBGE), 2017.

IPBES. **Summary policymakers of the assessment report of the Intergovernmental Science- Policy Platform on Biodiversity and Ecosystem Services (IPBES) on pollinators, pollination and food production.** Bonn: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2016.

JHA, R. et al. NLP-driven citation analysis for scientometrics. **Natural Language Engineering**, v. 23, n. 1, p. 93-130., 2017.

KAY, S. et al. Spatial similarities between European agroforestry systems and ecosystem services at the landscape scale. **Agroforestry Systems**, v. 92, p. 1075-1089, 2018.

KEVAN, P.F.; MENZEL, R. The plight of pollination and the interface of neurobiology, ecology and food security. **The Environmentalist**, v. 32, p. 300–310, 2012.

KING, P.S. Moderators/moderating factors. IN GELLMAN, M.D.; TURNER, J.R. (Eds.) **Encyclopedia of Behavioral Medicine**. New York: Springer, 2013, p. 1256-1258.

TILMAN, D. Functional diversity. IN LEVIN, A. (Ed.) **Encyclopedia of Biodiversity.** New Jersey: Elsevier, 2000, p. 109–120.

KLAUS, F. et al. Hedgerows have a barrier effect and channel pollinator movement in the agricultural landscape. **J Landsc Ecol**, v. 8, p. 22-31, 2015.

KLEIN, A.M. et al. Importance of pollinators in changing landscapes for world crops. **Proceedings of the Royal Society B**, v. 274, p. 303-313, 2006.

KLEIN, A.M.; STEFFAN-DEWENTER, I.; TSCHARNTKE, T. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. **Journal of Applied Ecology**, v. 40, p. 837-845, 2003.

KORICHEVA, J.; GUREVITCH, J. Place of meta-analysis among other methods of research synthesis. IN KORICHEVA, J.; GUREVITCH, J.; MENGERSEN, K. (Eds.), **Handbook of Meta-Analysis in Ecology and Evolution**. Oxford: Princeton University Press, 2013, p. 105-206.

KREMEN, C. Managing ecosystem services: what do we need to know about their ecology? **Ecology Letters**, v. 8, p. 468–479, 2005.

KREMEN, C.; ILES, A.; BACON, C. Diversified farming systems: An agroecological, systems-based alternative to modern industrial agriculture. **Ecology and Society**, v. 17, n. 4, 2012.

KUYAH, S.; ÖBORN, I.; JONSSON, M. Regulating ecosystem services delivered in agroforestry systems. IN DAGAR, J.; TEWARI, V. (Eds.), **Agroforestry.** Singapore: Springer, 2017. p. 797-815.

LALIBERTÉ, E.; LEGENDRE, P.; SHIPLEY, B. FD: measuring functional diversity (FD) from multiple traits and other tools for functional ecology. <https://cran.r-project.org/web/packages/FD/>, 2022.

LAWSON, D.A.; RANDS, S.A. The effects of rainfall on plant-pollinator interactions. **Arthropod-Plant Interactions**, v. 13, p. 561–569, 2019.

LICHTENBERG, E.M. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. **Global Change Biology**, v. 23, p. 4946-4957, 2017.

LIPPER, L. et al. Climate-smart agriculture for food security. **Nature Climate Change**, v. 4, p. 1068-1072, 2014.

LOREAU, M.; HECTOR, A. Partitioning selection and complementarity in biodiversity experiments. **Nature**, v. 412, p. 72–76, 2001.

LOSAPIO, G. et al. Facilitation and biodiversity jointly drive mutualistic networks. **Journal of Ecology**, v. 109, n. 5, p. 2029-2037, 2021.

MACCAGNANI, B. et al. Agroecosystem Design Supports the Activity of Pollinator Networks. IN SMAGGHE, G. et al. (Eds.), **Entomovectoring for Precision Biocontrol and Enhanced Pollination of Crops.** Cham: Springer, 2020. p. 1-17.

MARTINELLI, G.C. et al. Decreasing uncertainties and reversing paradigms on the economic performance of agroforestry systems in Brazil. **Land Use Policy**, v. 80, p. 274-286, 2019.

MEIER, K. et al. Riparian buffer zones as elements of ecological networks: Case study on *Pamassius mnemosyne* distribution in Estonia. **Ecol Eng**, v. 24, p. 531–537, 2005.

MINISTÉRIO DE AGRICULTURA, PECUÁRIA E ABASTECIMENTO. **Plano Setorial para Adaptação à Mudança do Clima e Baixa Emissão de Carbono na Agropecuária 2020-2030.** Brasília; Ministério de Agricultura, Pecuária e Abastecimento, 2021.

MOHER, D. et al. Preferred reporting ítems for systematic reviews and meta-analyses: the PRISMA statement. **BMJ**, v. 339, b2535, 2009.

MOLÚA, E.L. **Climate variability, vulnerability and effectiveness of farm-level adaptation options: The challenges and implications for food security in Southwestern Cameroon.** Environment and Development Economics, v. 7, p. 529-545, 2002.

MORA, C.; ROLLO, A.; TITTENSOR, D.P. Comment on "Can we name Earth's species before they go extinct. **Science**, v. 341, n. 6143, p. 237, 2013.

MOREIRA, E.F.: BOSCOLO, D.; VIANA, B.F. Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. **PLoS ONE**, v. 10, n. 4, 2015.

MOREL, A.C. et al. The ecological limits of poverty alleviation in an African Forest-Agriculture landscape. **Frontiers in Sustainable Food Systems**, v. 3, n. 57, 2019.

MÚRUA, M. Different pollinators' functional traits can explain pollen load in two solitary oil-collecting bees. **Insects**, v. 11, n. 685. 2020.

NAIR, P.K.R. Classification of agroforestry systems. **Agroforestry Systems**, v. 3, p. 97-128, 1985.

NAQA, I.E.; MURPHY, M.J. What is machine learning? IN NAQA, I.E.; LI, R.; MURPHY, M. (Eds.), **Machine learning in radiation oncology.** Cham, Springer, 2015, p. 3-11.

NEUSCHULZ, E.L. et al. Pollination and seed dispersal are the most threatened processes of plant regeneration. **Scientific Reports**, v. 6, 29839, 2016.

NEVARD, L. et al. Transmission of bee-like vibrations in buzz-pollinated plants with different stamen architectures. **Scientific Reports**, v. 11, 2021.

NOTARO, K.A. Agroforestry systems, nutrients in litter and microbial activity in soils cultivated with coffee at high altitude. **Scientia Agricola**, v. 71, n. 2, p. 87-95, 2014.

NOVELLA-FERNANDEZ, R. et al. Interaction strength in plant-pollinator networks: Are we using the right measure? **PLoS ONE**, v. 14, p. 12, 2019.

OLESEN, J.M. et al. The modularity of pollination networks. **Proceedings of the National Academy of Sciences of the United States of America**, v. 104, n. 50, 19891-19896, 2007.

OLLERTON, J.; WINFREE, R.; TARRANT, S. How many flowering plants are pollinated by animals? **Oikos**, v. 120, p. 321-326, 2011.

DEVOT, A. et al. **Research for the AGRI committee: The impact of extreme climate events on agriculture production in the EU.** European Union: Policy Department for Structural and Cohesion Policies Directorate-General for International Policies, 2023.

OUIN, A.; BUREL, F. Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. **Agri Ecosyst Environ**, v. 93, p. 45-53, 2002.

PALMER, M.A.; FILOSO, S. Restoration of ecosystem services for environmental markets. **Science**, v. 325, n. 5940, p. 575–576, 2009.

PARMENTIER, S. **Scaling-up agroecological approaches: What, why and how.** Belgium, Oxfam-Solidarity, 2014.

PAVAGEAU, C. et al. Nesting sites of giant honeybees modulated by landscape patterns. **Journal of Applied Ecology**, v. 55, n. 3, p. 1230-1240, 2017.

PELLMYR, O. Pollination by animals. IN HERRERA, C.M.; PELLMYR, O. (Eds.), **Plant-Animal Interactions.** Oxford: Blackwell Science, 2009, p. 157-184.

PETCHEY, O.L.; GASTON, K.J. Functional diversity: back to basics and looking forward. **Ecology Letters**, v. 9, n. 6, p. 741-748, 2006.

PINHEIRO, J. et al. **nlme: Linear and nonlinear mixed effect models (v. 3.1-162).** <https://cran.r-project.org/web/packages/nlme/>, 2023.

POISOT, T. et al. The dissimilarity of species interaction networks. **Ecology Letters**, v. 15, n. 12, p. 1353-1361, 2012.

PONISIO, L.C. et al. On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. **Glob Chang Biol**, v. 22, p. 704–715, 2016.

PORTER, J.R. et al. Food security and food production systems. IN IPCC**, Climate Change 2014; Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.** New York: Cambridge University Press, 2014.p. 485-533.

POTTS, S.G. et al. Declines of managed honey bees and beekeepers in Europe. **Journal of Apicultural Research**, v. 49, n. 1, p. 15-22, 2009.

POTTS, S.G. et al. Global pollinator declines: trends, impacts and drivers. **Trends in Ecology & Evolution**, v. 25, n. 6, p. 345-353, 2010.

PRABHU, R. et al. **Agroforestry: realizing the promise of an agroecological approach.** Rome: FAO, 2014.

PRADO, S.G. et al. A comparison of coffee floral traits under two different agricultural practices. **Scientific Reports**, v. 9, 7331, 2019.

RAMOS-JILIBERTO, R., ESPANÉS, P.M., VÁZQUEZ, D.P. Pollinator declines and the stability of plant-pollinator networks. **Ecosphere**, v. 11, n. 4, 2020.

RANTA, P. et al. The fragmented Atlantic rain forest of Brazil: size, shape, and distribution of forest fragments. **Biodiversity and Conservation**, v. 7, p. 385–403, 1998.

RAVEN, P.H., WAGNER, D.L. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. **PNAS**, v. 118, n. 2, e2002548117, 2020.

REED, J. et al. Trees for life: The ecosystem service contribution of trees to food production and livelihoods in the tropics. **Forest Policy and Economics**, v. 84, p. 62-71, 2017.

RICHARDS, S.A. Likelihood and model selection. IN FOX, G.A.; NEGRETE-YANKELEVICH, S.; SOSA, V.J. (Eds.), **Ecological Statistics: Contemporary theory and application**. Oxford: Oxford University Press, 2015, p. 58-80.

RICKER-GILBERT, J.; JUMBE, C.; CHAMBERLIN, J. How does population density influence agricultura intensification and productivity? Evidence from Malawi. **Food Policy**, v.48, p. 114-128, 2014.

ROQUER-BENI, L. et al. A novel method to measure hairiness in bees and other insect pollinators. **Ecology and Evolution**, v. 10, n. 6, p. 2979-2990, 2020.

ROQUER-BENI, L. et al. Management-dependent effects of pollinator functional diversity on apple pollination services: A response-effect trait approach. **Journal of Applied Ecology**, v. 58, n. 12, 2843-2853, 2021.

ROUBIK, D.W. Pollination of cultivated plants in the tropics. Rome: FAO, 1995.

SAMPAIO et al. Sustainable Agricultural Uses in the Caatinga. In: SILVA, J.M.C.; LEAL, I.R.; TABARELLI, M. (Eds.), **Caatinga.** Cham: Springer, 2017. P. 413-428.

SÁNCHEZ, P.A.; LEAKEY, R.R.B. Land use transformation in Africa: three determinants for balancing food security with natural resource utilization. **Developments in Crop Science**, v. 25, p. 19-27, 1997.

SCHEFFERS, B.R. et al. What we know and don't know about Earth's missing biodiversity. **Trends Ecol Evol**, v. 27, n. 9, 501-510, 2012.

SCHEMBERGUE, A. et al. Sistemas agroflorestais como estratégia de adaptação aos desafios das mudanças climáticas no Brasil. **Revista Economia e Sociologia Rural**, v. 55, n. 1, 2017.

SIQUEIRA FILHO, J.A. Atlantic Forest fragments and bromeliads in Pernambuco and Alagoas: Distribution, composition, richness and conservation. IN SIQUEIRA FILHO, J.A.; LEME, E.M.C. (Eds.). **Fragments of the Atlantic Forest of Northeast Brazil: Biodiversity, conservation and the bromeliads**, Texas: Bromeliad Society International, Texas, 2007, p. 101–131.

SHANNON, C.E.; WEAVER, W. **The mathematical theory of communication.** Illinois: University of Illinois Press, 1949.

SHARMA, S.; DURAND, R.M.; GUR-ARIE, O. Identification and analysis of moderator analysis of moderator variables. **Journal of Marketing Research**, v. 18.

SHENNAN, C. et al. Organic and conventional agriculture: A useful framing? **Annu Rev Environ Resour**, v. 42, p. 317-346, 2017.

SILVA, M.A.C. et al. Mass transfer during the osmotic dehydration of West Indian cherry. **LWT – Food Science and Technology**, v. 45, n. 2, p. 246-252, 2012.

SMITH, C. et al. Specialist foragers in forest bee communities are small, social or emerge early. **Journal of Animal Ecology**, v. 88, n. 8, p. 1158-1167, 2019.

STATON, T. et al. Evaluating the effects of integrating trees into temperate arable systems on pest control and pollination. **Agricultural Systems**, v. 176, 2019.

STAVERT, J.R. et al. Hairiness: the missing link between pollinators and pollination. **PeerJ**, v. 4, 2016.

STEFFAN-DEWENTER, I.; POTTS, S.G.; PACKER, L. Pollinator diversity and crop pollination services are at risk. **Trends Ecol Evol,** v. 20, p. 651–652, 2005.

SUNDERLIN, W.D. et al. Livelihoods, forests and conservation in developing countries: An overview. **World Development**, v. 33, n. 9, p. 1383-1402, 2005.

SUNDRIYAL, M.; SUNDRIYAL, R.C. Wild edible plants of the Sikkim Himalaya: Nutritive values of selected species. **Econ Bot**, v. 58, p. 286–299, 2004.

TILMAN, D. Functional diversity. IN LEVIN, S.A. (Ed.), **Encyclopedia of Biodiversity**. New York: Academic Press, 2001, p. 109-120.

8. ANEXOS

8.1. SISBIO: Autorização para atividades com finalidade científica

Projeto: A diversidade das interações planta-inseto e serviços de polinização em sistemas agroflorestais de uma região tropical no Nordeste do Brasil

Número: 86051-1

Titular: Diego Centeno Alvarado

Instituição: Universidade Federal Rural de Pernambuco

Ministério do Meio Ambiente - MMA

Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio

Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 86051-1	**Data da Emissão: 29/11/2022 17:04:59**	**Data da Revalidação*: 29/11/2023**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: DIEGO CENTENO ALVARADO	CPF: 098.574.951-25
Título do Projeto: A diversidade das interações planta-inseto e serviços associados de polinização em sistemas agroflorestais de uma região tropical no Nordeste do Brasil	
Nome da Instituição: Universidade Federal Rural de Pernambuco	CNPJ: 24.416.174/0001-06

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Coleta e transporte de materiais	12/2022	12/2023

Observações e ressalvas

1	Deve-se observar as as recomendações de prevenção contra a COVID-19 das autoridades sanitárias locais e das Unidades de Conservação a serem acessadas.
2	Esta autorização NÃO libera o uso da substância com potencial agrotóxico e/ou inseticida e NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de atender às exigências e obter as autorizações previstas em outros instrumentos legais relativos ao registro de agrotóxicos (Lei nº 7.802, de 11 de julho de 1989, Decreto nº 4.074, de 4 de janeiro de 2002, entre outros).
3	Esta autorização NÃO libera o uso da substância com potencial agrotóxico e/ou inseticida e NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de atender às exigências e obter as autorizações previstas em outros instrumentos legais relativos ao registro de agrotóxicos (Lei nº 7.802, de 11 de julho de 1989, Decreto nº 4.074, de 4 de janeiro de 2002, entre outros)
4	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
5	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
6	Este documento somente poderá ser utilizado para os fins previstos na Portaria ICMBio nº 748/2022, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior.
7	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.
8	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
9	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
10	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infraestrutura da unidade.

Este documento foi expedido com base na Instrução Normativa nº Portaria ICMBio nº 748/2022. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

Autorização para atividades com finalidade científica

Número: 86051-1	**Data da Emissão: 29/11/2022 17:04:59**	**Data da Revalidação*: 29/11/2023**
De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.		

Dados do titular

Nome: DIEGO CENTENO ALVARADO	CPF: 098.574.951-25
Título do Projeto: A diversidade das interações planta-inseto e serviços associados de polinização em sistemas agroflorestais de uma região tropical no Nordeste do Brasil	
Nome da Instituição: Universidade Federal Rural de Pernambuco	CNPJ: 24.416.174/0001-06

Outras ressalvas

1		CBC Brasília-DF

Locais onde as atividades de campo serão executadas

#	Descrição do local	Município-UF	Bioma	Caverna?	Tipo
1	Sítio de Seu Jaciel	Rio Formoso-PE	Mata Atlântica	Não	Fora de UC Federal
2	Sítio de Dona Cristina	Sirinhaém-PE	Mata Atlântica	Não	Fora de UC Federal
3	Sítio de Seu Mauro	Igarassu-PE	Mata Atlântica	Não	Fora de UC Federal
4	Instituição SERTA	Glória do Goitá-PE	Mata Atlântica	Não	Fora de UC Federal

Atividades

#	Atividade	Grupo de Atividade
1	Captura de animais silvestres in situ	Fora de UC Federal
2	Coleta/transporte de espécimes da fauna silvestre in situ	Fora de UC Federal

Atividades X Táxons

#	Atividade	Táxon	Qtde.
1	Coleta/transporte de espécimes da fauna silvestre in situ	Diptera	1000
2	Captura de animais silvestres in situ	Diptera	-
3	Coleta/transporte de espécimes da fauna silvestre in situ	Hymenoptera	1000
4	Captura de animais silvestres in situ	Hymenoptera	-
5	Coleta/transporte de espécimes da fauna silvestre in situ	Coleoptera	1000
6	Captura de animais silvestres in situ	Coleoptera	-
7	Coleta/transporte de espécimes da fauna silvestre in situ	Lepidoptera	1000
8	Captura de animais silvestres in situ	Lepidoptera	-

A quantidade prevista só é obrigatória para atividades do tipo "Coleta/transporte de espécimes da fauna silvestre in situ". Essa quantidade abrange uma porção territorial mínima, que pode ser uma Unidade de Conservação Federal ou um Município.

A quantidade significa: por espécie X localidade X ano.

Este documento foi expedido com base na Instrução Normativa nº Portaria ICMBio nº 748/2022. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

Autorização para atividades com finalidade científica

Número: 86051-1	**Data da Emissão: 29/11/2022 17:04:59**	**Data da Revalidação*: 29/11/2023**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: DIEGO CENTENO ALVARADO	CPF: 098.574.951-25
Título do Projeto: A diversidade das interações planta-inseto e serviços associados de polinização em sistemas agroflorestais de uma região tropical no Nordeste do Brasil	
Nome da Instituição: Universidade Federal Rural de Pernambuco	CNPJ: 24.416.174/0001-06

Materiais e Métodos

#	**Tipo de Método (Grupo taxonômico)**	**Materiais**
1	Método de captura/coleta (Insetos)	Captura manual, Coleta manual, Puçá, Rede entomológica

Destino do material biológico coletado

#	**Nome local destino**	**Tipo destino**
1	Universidade de Pernambuco - Campus Garanhuns	Laboratório

Autorização para atividades com finalidade científica

Número: 86051-1	**Data da Emissão: 29/11/2022 17:04:59**	**Data da Revalidação*: 29/11/2023**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: DIEGO CENTENO ALVARADO	CPF: 098.574.951-25
Título do Projeto: A diversidade das interações planta-inseto e serviços associados de polinização em sistemas agroflorestais de uma região tropical no Nordeste do Brasil	
Nome da Instituição: Universidade Federal Rural de Pernambuco	CNPJ: 24.416.174/0001-06

Registro de coleta imprevista de material biológico

De acordo com a Instrução Normativa nº03/2014, a coleta imprevista de material biológico ou de substrato não contemplado na autorização ou na licença permanente deverá ser anotada na mesma, em campo específico, por ocasião da coleta, devendo esta coleta imprevista ser comunicada por meio do relatório de atividades. O transporte do material biológico ou do substrato deverá ser acompanhado da autorização ou da licença permanente com a devida anotação. O material biológico coletado de forma imprevista, deverá ser destinado à instituição científica e, depositado, preferencialmente, em coleção biológica científica registrada no Cadastro Nacional de Coleções Biológicas (CCBIO).

Táxon*	**Qtde.**	**Tipo de Amostra**	**Qtde.**	**Data**

* Identificar o espécime do nível taxonômico possível.

Este documento foi expedido com base na Instrução Normativa nº Portaria ICMBio nº 748/2022. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).