UNIVERSIDADE ESTADUAL DE SANTA CRUZ PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE

Diversidade taxonômica de abelhas (Hymenoptera: Anthophila) e vespas sociais (Vespidae: Polistinae) em paisagens agrícolas

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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade. Área de concentração: Ecologia e Conservação da Biodiversidade. Discente: José Victor Alves Ferreira. Orientadora: Drª Maíra Benchimol

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SUMÁRIO

RESUMO

A conversão de habitats nativos em áreas agrícolas é uma das principais ameaças a perda global de biodiversidade. Diante da grande extensão de áreas cultiváveis, estratégias de conservação que conciliem produção agrícola com manutenção da biodiversidade e dos serviços ecossistêmicos se tornam necessárias. Para isso, é preciso entender como grupos biológicos respondem a expansão agrícola, sobretudo aqueles que apresentam um potencial de favorecer a produtividade agrícola, como diversos insetos. Em particular, as abelhas desempenham um papel fundamental na polinização de plantas nativas e cultiváveis, e as vespas sociais, atuam no controle biológico de insetos pragas. Neste sentido, esta tese de doutorado teve como objetivo investigar como abelhas e vespas sociais respondem aos efeitos de matrizes agrícolas, especialmente em agroflorestas de cacau-cabruca do sul da Bahia, Brasil. No primeiro capítulo, intitulado "*Effect of agricultural matrices on the biodiversity metrics of bees (Hymenoptera: Anthophila): A review*", nós avaliamos o efeito de matrizes agrícolas sobre a abundância e riqueza de espécies de abelhas em paisagens agrícolas em todo o globo, por meio de uma revisão sistemática e meta-análise. No segundo capítulo, intitulado "*Species richness and abundance of social wasps (Vespidae: Polistinae) associated with shaded cocoa agroforests (Theobroma cacao L.) in southern Bahia state, Brazil*", nós conduzimos um estudo descritivo em que apresentamos a primeira lista de espécies de vespas sociais registradas em agroflorestas de cacau sombreadas no sul da Bahia. No terceiro capítulo, intitulado "*Landscape forest cover and regional context shape the conservation value of shaded cocoa agroforests for bees and social wasps*", nós avaliamos o valor de conservação das agroflorestas de cacau sombreado para a diversidade taxonômica (alfa e beta) de abelhas e vespas sociais, em relação a remanescentes florestais de Mata Atlântica, e o papel da cobertura florestal, em escalas de paisagem e regional, na modulação da resposta destes insetos. No quarto e último capítulo, intitulado "*Taxonomic diversity of bees and social wasps in shaded cocoa agroforests is shaped by environmental predictors at multiple spatial scales*", nós investigamos os efeitos do manejo, estrutura do habitat e da cobertura florestal sobre a diversidade taxonômica de abelhas e vespas sociais em agroflorestas de cacau sombreado do sul da Bahia. Nossos resultados demonstraram que, apesar da agricultura representar uma ameaça à conservação da diversidade, as agroflorestas de cacau possuem um alto valor de conservação para abelhas e vespas sociais, desde que mantidas em paisagens e/ou regiões com alta cobertura florestal.

Considerando o atual cenário de mudança do uso do solo na região estudada – altamente relevante para a conservação da biodiversidade – e o alto valor ecológico das agroflorestas de cacau-cabruca, sugerimos que o incentivo à manutenção desse sistema, aliado à restauração de habitats nativos, representa uma medida efetiva para conservação da biodiversidade, com benefícios potenciais para a produtividade do cacau no sul da Bahia.

Palavras-chave: Agrofloresta de cacau, conservação da biodiversidade, controle biológico, ecologia de paisagem, matriz agrícola, polinizadores, predadores.

ABSTRACT

The conversion of native habitats into agricultural areas is one of the main threats to global biodiversity loss. In view of the large extent of arable land, conservation strategies that reconcile agricultural production with the maintenance of biodiversity and ecosystem services are becoming urgent. To this end, it is necessary to understand how biological groups respond to agricultural expansion, especially those that have the potential to favour agricultural productivity, such as insects. In particular, bees play a fundamental role in the pollination of native and cultivated plants, and social wasps act in the biological control of insect pests. In this sense, this thesis aimed to investigate how bees and social wasps respond to the effects of agricultural matrices, especially in cocoa-cabruca agroforests in southern Bahia, Brazil. In the first chapter, entitled “Effect of agricultural matrices on the biodiversity metrics of bees (Hymenoptera: Anthophila): A review”, we evaluate the effect of agricultural matrices on the abundance and species richness of bees in agricultural landscapes across the globe, through a systematic review and meta-analysis. In the second chapter, entitled “Species richness and abundance of social wasps (Vespidae: Polistinae) associated with shaded cocoa agroforests (Theobroma cacao L.) in southern Bahia state, Brazil”, we conduct a descriptive study in which we present the first list of social wasp species recorded in shaded cocoa agroforests in southern Bahia. In the third chapter, entitled “Landscape forest cover and regional context shape the conservation value of shaded cocoa agroforests for bees and social wasps”, we assess the conservation value of shaded cocoa agroforests for the taxonomic diversity (alpha and beta) of bees and social wasps, in relation to Atlantic Forest remnants, and the role of forest cover, at landscape and regional scales, in modulating the response of these insects. In the fourth and final chapter, entitled “Taxonomic diversity of bees and social wasps in shaded cocoa agroforests is shaped by environmental predictors at multiple spatial scales”, we investigated the effects of management, habitat structure and forest cover on the taxonomic diversity of bees and social wasps in shaded cocoa agroforests in southern Bahia. Our results showed that, despite agriculture threatening the conservation of diversity, cocoa agroforests have a high conservation value for bees and social wasps, as long as they are maintained in landscapes and/or regions with high forest cover. Considering the current scenario of land use change in the region studied - highly relevant for biodiversity conservation - and the high ecological value of cocoa-cabruca agroforests, we suggest that encouraging the maintenance of this system, combined with the restoration of native habitats, represents an effective measure for biodiversity conservation, with potential benefits for cocoa productivity in southern Bahia.

Keywords: Agricultural matrix, biodiversity conservation, biological control, cocoa agroforest, landscape ecology, predators, pollinators.

INTRODUÇÃO GERAL

O desenvolvimento da agricultura resultou em transformações sem precedentes na história humana e contribuiu não apenas para mudanças sociais e comportamentais da nossa espécie, mas também para mudanças substanciais das características bióticas e abióticas do planeta. Apesar de ter iniciado há cerca de 10 mil anos, a agricultura teve uma expansão mais acentuada somente nos últimos 300 anos (Ramankutty et al. 2018). Em especial, com a chamada Revolução Verde, ocorrida no século XX, a agricultura passou a contar com inúmeras novas tecnologias que nos permitiu atingir níveis de produção até então impraticáveis (Tilman et al. 2001), contribuindo inclusive para o surgimento de uma possível nova era, o Antropoceno (Waters and Turner 2022). Apesar do inquestionável papel da agricultura para o fornecimento de alimentos à população mundial, a rápida expansão agrícola fomentou debates sobre os potenciais prejuízos deste novo modelo de produção aos ecossistemas naturais, como muito bem documento por Rachel Carson em sua clássica e marcante obra Primavera Silenciosa (1962).

Diante da visível modificação das paisagens naturais, sobretudo como consequência de atividades antrópicas, ecólogos e conservacionistas começaram a questionar a magnitude e a extensão dos efeitos da agricultura sobre comunidades biológicas e processos ecossistêmicos. Tal perspectiva contribuiu, por exemplo, para o surgimento da Ecologia de Paisagem, que objetiva compreender como o arranjo espacial e a composição da paisagem afetam o padrão de distribuição das espécies e relações ecológicas entre organismos e ecossistemas (Metzger 2001). Sendo uma área de estudo relativamente recente e que lida com sistemas extremamente complexos, a Ecologia de Paisagem ainda carece de modelos mecanicistas capazes de prever com maior precisão as predições de seus modelos teóricos. Apesar disso, este campo da ecologia tem se tornado indispensável para nos ajudar a lidar com um dos principais desafios para a humanidade no século XXI: como conciliar produção agrícola com a conservação da biodiversidade?

Anos de conhecimento acumulado em como conciliar produção com manutenção de espécies nativas em paisagens agrícolas resultaram em duas ideias que têm sido amplamente discutidas: a separação (*land sparing*) e o compartilhamento de terras (*land sharing*). A separação de terras propõe que a intensificação agrícola, e consequentemente o aumento da produtividade, reduz a necessidade de converter ambientes naturais em áreas de cultivo, favorecendo a preservação e restauração de habitats nativos (Phalan

2018). Por outro lado, a partilha de terras propõe conciliar, em uma mesma paisagem, a produção agrícola com a conservação da vida selvagem, aumentando o valor de conservação das áreas de cultivo (Perfecto and Vandermeer 2010). Diante do atual cenário de crise global da biodiversidade (Potts et al. 2010; Betts et al. 2017), não temos porquê questionar o fato de que manter e restaurar grandes extensões de habitats nativos livres da ação humana direta é uma medida necessária e urgente para garantirmos a funcionalidade dos ecossistemas em uma escala mais ampla (Edwards et al. 2019). Entretanto, se considerarmos que as áreas agrícolas ocupam cerca de 40% da área terrestre não congelada do planeta (Ramankutty et al. 2008), a proposta do compartilhamento de terras deve ser considerado um dos principais mecanismos para a conservação da biodiversidade (Ellis et al. 2010; Melo et al. 2013), sobretudo em regiões tropicais (Arroyo-Rodríguez et al. 2020).

De acordo com a perspectiva *land sharing*, a conservação da vida selvagem em paisagens agrícolas é um desafio que depende de diversos fatores que atuam em múltiplas escalas espaciais. Como passo inicial, compreender quais fatores afetam a diversidade de espécies de grupos biológicos chave para o funcionamento de ecossistemas se torna essencial. Dentre potenciais mecanismos, a “hipótese da quantidade de habitat” tem sido amplamente utilizada para explicar a diversidade de espécies em paisagens antrópicas, em que independentemente do número de manchas de habitats, a quantidade de habitat seria o principal preditor da diversidade de espécies em escala de paisagem (Watling et al. 2020). Apoiada na relação espécie-área, uma das relações mais sólidas no campo da ecologia, a hipótese da quantidade de habitat prevê que o número de espécies na paisagem responde positivamente a área de habitat disponível (Fahrig 2013). Entretanto, a força dessa relação também depende de uma série de fatores, como por exemplo, a qualidade da matriz na qual esses habitats estão inseridos. Do ponto de vista funcional, uma matriz pode ser definida como a área de “não-habitat”, que geralmente resulta de ações antrópicas (Boscolo et al. 2016), e que apresenta um papel fundamental na retenção ou perda de espécies em uma paisagem (Gascon et al. 1999; Boesing et al. 2018). Por exemplo, uma matriz de alta qualidade (i.e., com alta permeabilidade e oferta de recursos) favorece o movimento dos organismos entre remanescentes nativos e pode atuar como habitat suplementar para múltiplos táxons (Fahrig 2001). Portanto, à medida que a qualidade da matriz aumenta, é esperado que os efeitos negativos da perda de habitat tendam a ser menos intensos, favorecendo a retenção de um maior número de espécies e, consequentemente, da provisão de processos ecológicos (Galán-Acedo et al. 2019; Deane and Riva 2025).

Diante da reconhecida importância da matriz como modulador das respostas das espécies, ecólogos e conservacionistas tem investigado o papel de sistemas agroflorestais como aliados na mitigação dos efeitos negativos da perda de habitat (Perfecto and Vandermeer 2010; Arroyo-Rodríguez et al. 2020). Uma vez que sistemas agroflorestais incorporam componentes arbóreos, resultando em um ambiente potencialmente adequado para mais espécies comparado a monoculturas, as agroflorestas tendem a mitigar os efeitos negativos da expansão agrícola sobre a biodiversidade (Oakley and Bicknell 2022). Um maior valor de conservação é atribuído a sistemas agroflorestais que associam múltiplas espécies arbóreas, incluindo espécies nativas, com espécies de interesse econômico (Gama-Rodrigues et al. 2021). Esse é o caso das agroflorestas de cacau (*Theobroma cacao* L.) sombreadas na Mata Atlântica do sul da Bahia, localmente conhecidas como “cabrucas” (Cassano et al. 2009). Este sistema se caracteriza pela associação do cacaueiro com árvores emergentes (Figura 1 e 2), em geral espécies arbóreas e de grande porte nativas da Mata Atlântica. Apesar de comumente apresentar espécies de árvores exóticas, como a seringueira (*Hevea brasiliensis*), a jaqueira (*Artocarpus heterophyllus*) dentre outras, para ser considerada cabruca a agrofloresta de cacau deve conter no mínimo 20 árvores nativas da Mata Atlântica por hectare, como previsto pelo Decreto 15.180/2014 e Portaria Conjunta SEMA/INEMA N° 03 de 16 de abril de 2019. Esta associação resulta em um sistema de cultivo altamente diverso, estruturalmente complexo e economicamente viável, classificando as cabrucas como um sistema amigável à biodiversidade e um exemplo de estratégia *land sharing* (Cassano et al. 2009; Gama-Rodrigues et al. 2021).

Por volta da década de 1980, a região sul da Bahia se destacava como a principal região cacaueira do Brasil, responsável por cerca de 95% da produção nacional e 20% da produção global. Mas em 1989, com a chegada e proliferação do fungo vassoura-de-bruxa (*Moniliophthora perniciosa*), a produtividade dessas agroflorestas reduziu vertiginosamente. Os impactos econômicos associados a forte redução da produtividade foi um dos principais fatores responsáveis pela intensificação do desmatamento na região cacaueira e adoção de sistemas de produção mais intensivos (Alger and Caldas 1994; Cassano et al. 2009). Ainda assim, as agroflorestas de cacau-cabruca ainda representam um dos principais tipos de uso do solo na região, abrangendo mais de 80 municípios

(Mapbiomas Cacau 2023). E se considerarmos que estes sistemas estão inseridos em um *hotpoint* dentro da Mata Atlântica (Dias et al. 2014), as cabrucas possivelmente desempenham um papel fundamental para conservação da biodiversidade do sul da Bahia.

Figura 1. Agrofloresta de cacau sombreado (cabruca): **A)** com menor e **B)** maior grau de manejo.

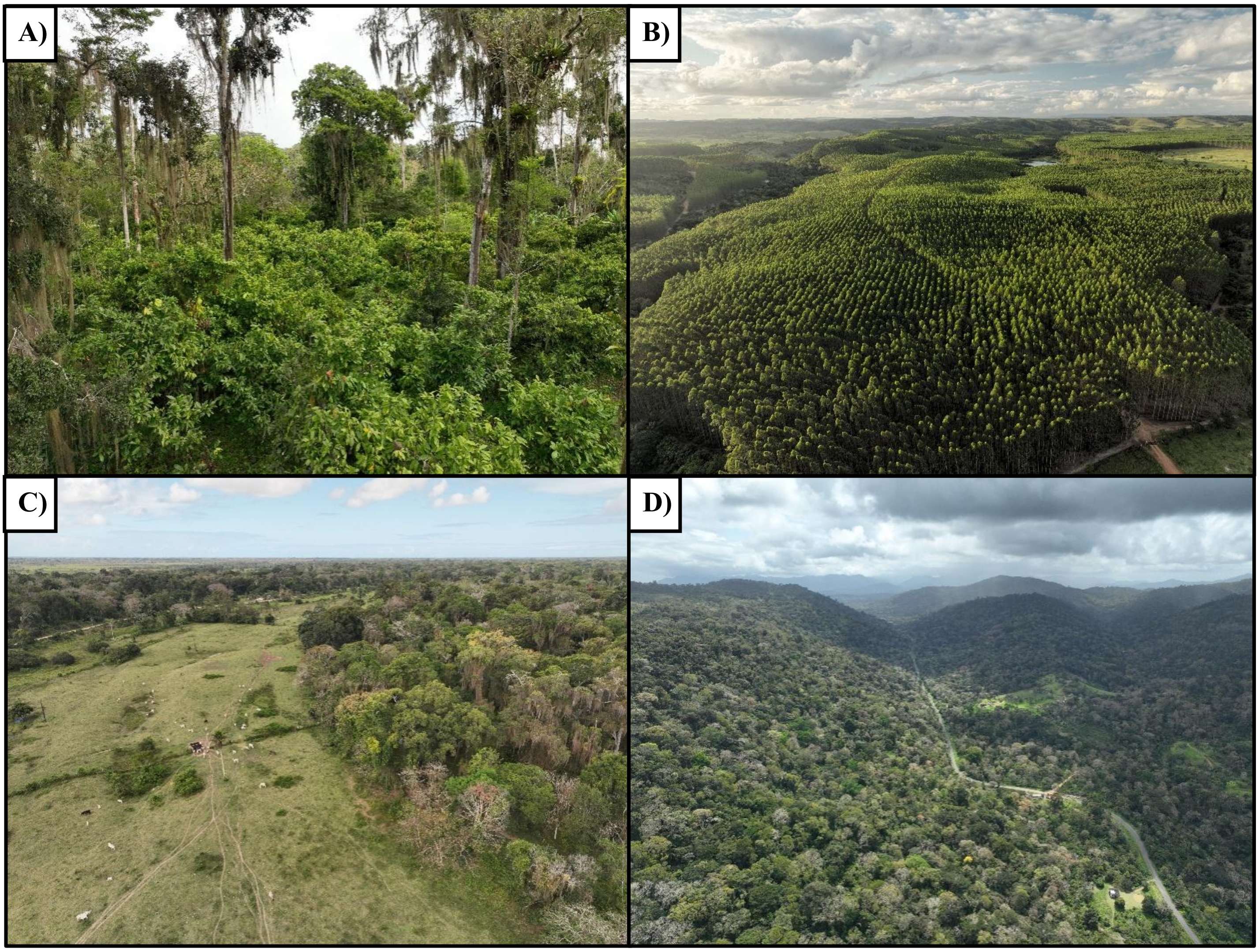

Figura 2. Fotografias aéreas indicando: (**A)** uma agrofloresta de cacau sombreado (cabruca); (**B)** monocultura de eucalipto, um dos principais tipos de uso do solo da região sul Bahia; (**C)** pastagem destinada a criação de gado, adjacente a uma agrofloresta de cacau sombreado (cabruca) e **(D)** extensa agrofloresta de cacau sombreado (cabruca).

Neste contexto, o projeto Eco-nomia das Cabrucas (https://www.youtube.com/watch?v=WEHoZvrw9Ok), conduzido pelo Laboratório de Ecologia Aplicada à Conservação (LEAC) da Universidade Estadual de Santa Cruz (UESC), busca compreender as relações entre diversidade de espécies, serviços ecossistêmicos e produtividade no sistema agroflorestal de cacau, considerando o contexto espacial e a intensificação do manejo local das agroflorestas. Mais especificamente, o projeto tem avaliado a influência de três principais preditores sobre padrões de biodiversidade e processos ecológicos: i) as características locais das agroflorestas - apesar da definição de cabruca prever uma quantidade mínima de árvores nativas por hectare, essas agroflorestas apresentam uma considerável variação em relação ao número e diversidade de árvores sombreadoras. Além disso, o tipo de manejo adotado pelos produtores, que consiste principalmente na aplicação de insumos agrícolas, roçagem do sub-bosque, poda e desbaste de cacaueiros e árvores sombreadoras, também tendem a apresentar uma grande variação entre propriedades; ii) a cobertura florestal em escala de paisagem - considerado um dos principais determinantes do número de espécies em paisagens agrícolas, pesquisas buscam entender o papel da variação da quantidade de remanescente florestal sobre a diversidade biológica nas agroflorestas de cacau-cabruca; iii) contexto regional - além da variação em escala de paisagem, a área de estudo do Eco-nomia das Cabrucas abrange três importantes regiões no sul da Bahia, caracterizadas pelo contexto predominante de uso do solo. A primeira região (moderadamente florestada), corresponde aos municípios de Ilhéus e Uruçuca, e apresenta uma predominância de agroflorestas de cacau-cabruca. A segunda região (altamente florestada), que inclui os municípios de Una, Arataca e Santa Luzia, tem como principal tipo de cobertura do solo a vegetação de Mata Atlântica, especialmente devido à Reserva Biológica de Una e do Refúgio de Vida Silvestre de Una, que representam as maiores extensões de florestas da região. Finalmente, a terceira região (severamente desmatada), que abrange os municípios de Belmonte, Mascote, Canavieiras e Itapebi, apresenta as maiores extensões de silvicultura (monocultura de eucalipto) e pasto (destinado à criação de gado) da região.

Até o momento, múltiplos táxons foram investigados no projeto Eco-nomia das Cabrucas, incluindo aves (Cabral et al. 2021), répteis e anfíbios (Cervantes-López et al. 2025), e processos ecológicos (Cassano et al. 2021; Araújo-Santos et al. 2021; Barillaro et al. 2024; Bandeira and Morante-Filho 2024). Apesar das diferentes respostas entre os táxons investigados, estes estudos têm demonstrado que as características locais, de paisagem e região de fato são importantes preditores da diversidade. Além disso, como também demonstrado por estudos anteriores, as cabrucas desempenham um importante papel na conservação da diversidade de múltiplos táxons (Faria and Baumgarten 2007; Ferreira et al. 2020, 2025). Mas apesar do reconhecido potencial destas agroflorestas para a conservação da biodiversidade, o papel das cabrucas e do contexto espacial em que estão inseridas para a conservação dos insetos, em especial de abelhas (Hymenoptera: Anthophila) e vespas sociais (Vespidae: Polistinae), ainda permanece desconhecido.

As abelhas (Figura 3) são os principais agentes de polinização em todo o mundo, um processo que garante ou favorece a reprodução de ~87% das espécies de angiospermas (Ollerton et al. 2011). Além de garantir a reprodução de plantas nativas, o serviço ecossistêmico de polinização ofertado por estes insetos favorece a produção agrícola (Klein et al. 2003; Garibaldi et al. 2013), com um incremento subestimado de 12 bilhões de dólares por ano, no Brasil (Giannini et al. 2015), e cerca de 235–577 bilhões de dólares, em todo o mundo (Lautenbach et al. 2012; Potts et al. 2016). Por outro lado, as vespas sociais (Figura 3), popularmente conhecidas como marimbondos ou cabas, são predadores que participam ativamente no controle de insetos herbívoros. Apesar da falta de estudos que estimem o valor do controle biológico ofertado por estas vespas, elas certamente exercem um papel fundamental na regulação da cadeia trófica em ecossistemas naturais e agrícolas (Brock et al. 2021). Desta forma, compreender como abelhas e vespas respondem a conversão de habitats nativos em áreas agrícolas é fundamental não apenas para a proposta de estratégias de conservação destes, mas também para a intensificação dos serviços ecossistêmicos de polinização e controle biológico ofertado por esses insetos, com impactos diretos sobre o funcionamento de ecossistemas naturais e agrícolas.

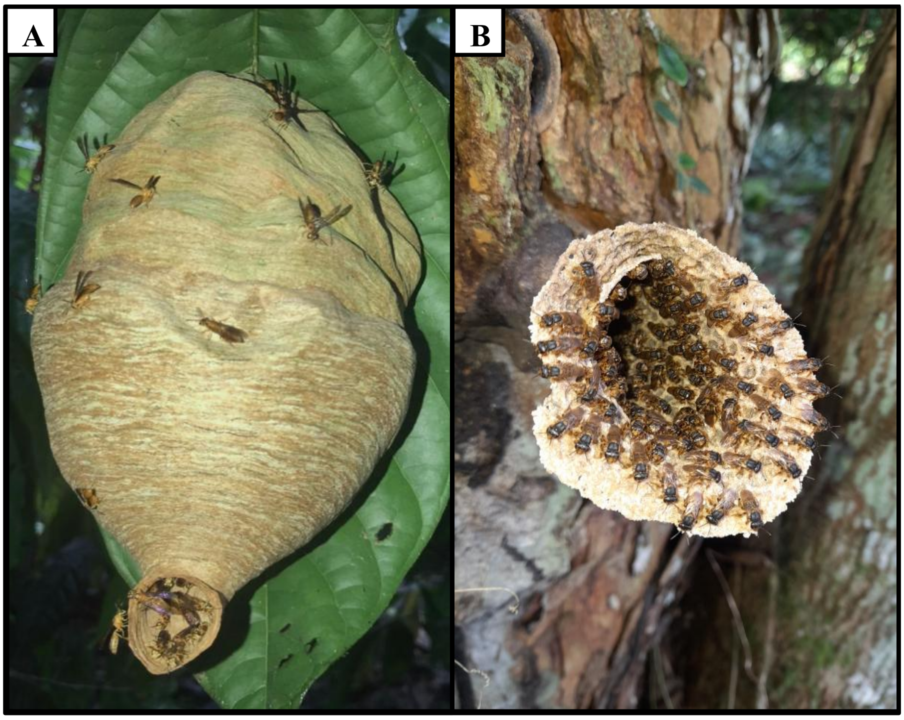

Figura 3. A) Ninho de *Angiopolybia pallens*, construído em um cacaueiro. Conhecida popularmente como marimbondo peito-de-moça, esta é a espécie de vespa social mais abundante em agroflorestas de cacau-cabruca. **B)** Ninho de abelhas-sem-ferrão, *Scaptotrigona xanthotricha*, construído em uma árvore sombreadora em uma agrofloresta de cacau-cabruca.

Diante de tal perspectiva, esta tese de doutorado teve como objetivo investigar como abelhas e vespas sociais respondem aos efeitos de matrizes agrícolas, sobretudo em agroflorestas de cacau-cabruca do sul da Bahia, Brasil. Especificamente, são apresentados quatro capítulos:

No primeiro capítulo, intitulado "*Effect of agricultural matrices on the biodiversity metrics of bees (Hymenoptera: Anthophila): A review*", nós realizamos uma revisão bibliográfica de estudos que compararam a abundância de abelhas e/ou a riqueza de espécies entre habitats agrícolas e nativos. Além de descrever o padrão geral observado por esses estudos (n = 32), nós também conduzimos uma meta-análise com um subconjunto de dados (14 estudos e 38 comparações). Nesta abordagem, nós consideramos moderadores que podem influenciar o efeito das matrizes agrícolas, incluindo o tipo de resposta avaliado (abundância ou riqueza de espécies), o tipo de floração (com ou sem floração massiva) e ciclo de vida (anual ou perene) da cultura agrícola, bem como a região (tropical ou temperada) na qual os estudos foram conduzidos.

No segundo capítulo, intitulado "*Species richness and abundance of social wasps (Vespidae: Polistinae) associated with shaded cocoa agroforests (Theobroma cacao L.) in southern Bahia state, Brazil*", nós conduzimos um estudo descritivo no qual apresentamos a primeira lista de espécies de vespas sociais registradas em agroflorestas de cacau sombreadas no sul da Bahia e discutimos sobre o potencial dessas agroflorestas para reterem a diversidade desses insetos.

No terceiro capítulo, intitulado "*Landscape forest cover and regional context shape the conservation value of shaded cocoa agroforests for bees and social wasps*", nós avaliamos o valor de conservação das agroflorestas de cacau para a diversidade taxonômica (alfa e beta) de abelhas e vespas sociais, tendo como referência remanescentes florestais de Mata Atlântica. Além disso, nós investigamos se o valor de conservação das agroflorestas depende da cobertura florestal em escalas de paisagem e/ou regional.

Finalmente, no quarto capítulo, intitulado "*Multiscale drivers of bee and wasp species richness and composition in shaded cocoa agroforests*", nós investigamos os efeitos das características locais (estrutura da vegetação e intensidade do manejo) e da composição da paisagem (cobertura florestal) sobre a diversidade taxonômica de abelhas e vespas sociais em agroflorestas de cacau sombreado do sul da Bahia.

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CAPÍTULO 1

Effect of agricultural matrices on the biodiversity metrics of bees (Hymenoptera: Anthophila): a review

Article accepted for publication in Sociobiology

Effect of agricultural matrices on the biodiversity metrics of bees (Hymenoptera: Anthophila): a review

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ABSTRACT: Agriculture has been globally responsible for biodiversity decay. Given that bees are key pollinators, their diversity reduction can affect biodiversity conservation and agricultural production. Although agricultural matrices have been reported as pervasive to bees, these effects are not always consistent and may vary according to evaluated parameters. To fill this gap, we conducted a global review of studies that compared bee abundance and/or species richness between agricultural and native habitats. In addition to describing the overall pattern observed in the studies (n = 32), we also conducted a meta-analysis with a subset of data (14 studies and 38 comparisons). To do this, we calculated the effect size from the standardized mean difference among agriculture-native habitats. We considered moderators that may influence this effect, including response type, flowering type, crop life cycle, and region. Based on the review, half of the studies (50%) concluded that agricultural matrices negatively affect biodiversity metrics of bees. In comparison, only five (15.6%) and eight studies (25%) observed a positive and neutral effect, respectively. Three studies (9.4%) observed a varied effect (positive or negative), depending on the type of response assessed (richness or abundance) or the management intensity. Additionally, meta-analysis supports this finding by revealing an overall negative effect (general effect = -0.43; IC: -0.75; -0.10), especially for abundance. Negative effects were consistent for no mass-flowering crops, perennial crops, and temperate regions. We thus recommend that agricultural landscapes across the globe should maintain native habitats to ensure high bee diversity and potentially contribute to the delivery of ecosystem services.

Key-words: biodiversity conservation, biodiversity-friendly matrices, cropland, pollinators, species loss

INTRODUCTION

Agriculture is one of the primary pervasive activities affecting biodiversity worldwide, responsible for converting natural ecosystems into human-modified landscapes (Newbold et al., 2015; Campbell et al., 2017; Tilman et al., 2017). In fact, agricultural areas already occupy more than a third of the ice-free land surface (Ramankutty et al., 2008; Ellis et al., 2010), and estimates of human population growth suggest that the demand for agricultural lands is expected to increase by 50-90% by 2050 (Springmann et al., 2018). The expansion and intensification of agricultural lands comprise the primary strategies employed to increase production and yields but usually negatively impact biodiversity (Zabel et al., 2019). In particular, the expansion of agricultural lands is expected to occur primarily in tropical regions (Laurance et al., 2014), which directly contributes to reduced species diversity of several faunal groups, including terrestrial insects (van Klink et al., 2020; Raven and Wagner 2021).

Agricultural expansion and intensification have driven many insect species to local extinctions, including species that could directly enhance productivity (Raven and Wagner 2021). Since insects provide a wide range of ecological functions, such as pest control and pollination (Yang and Gratton 2014), reducing their diversity can strongly impact the functioning of native ecosystems. Furthermore, insects are closely related to agricultural productivity and are responsible for substantial productivity gains in different crops due to their provision of ecosystem services (Losey and Vaughan 2006). For example, around 87 of the top 115 crops produced worldwide benefit from animal pollination (Klein et al., 2007), leading to global yields ranging from US$195 billion to ~US$387 billion annually (Porto et al., 2020). Among animals, bees are considered the main pollinating agents of native (Ollerton et al., 2011) and cultivated (Klein et al., 2007; Paz et al., 2021) plant species, playing a vital role in regulating and maintaining natural and agricultural ecosystems. In fact, the impact of bee diversity on agricultural productivity varies according to the degree of pollination dependence of each crop (Giannini et al., 2015), but in general, an increase in bee richness and abundance exerts a positive effect on crop yield (Garibaldi et al., 2013; Rogers et al., 2014).

Although several studies have demonstrated an overall loss of bee diversity in agricultural land-use types surrounding native habitats (hereafter, agricultural matrices; Ferreira et al., 2022; Ockermüller et al., 2023; Rahimi et al., 2022), such effects are not always consistent. For example, agricultural matrices may retain a greater diversity of bees than native habitats (Schüepp et al., 2012; Almeida et al., 2020), although this effect may vary depending on the type of response variable under investigation (e.g., abundance or species richness) (Briggs et al., 2013; Kammerer et al., 2021). In addition, some studies failed to detect a significant effect of agricultural matrices on bee diversity (Sheffield et al., 2008; Serralta-Batun et al., 2024). It is also important to emphasize that both positive (Hoehn et al., 2010; Almeida et al., 2020) and negative effects (Aguiar et al., 2015; Shaw et al., 2020; Ferreira et al., 2022) on bee diversity have been observed in different types of crops. For example, crops with massive flowering can benefit bee species richness, as they offer more food resources (Westphal et al., 2003; Diekötter et al., 2014). In addition, perennial crops present greater stability than annual crops (Asbjornsen et al., 2014) since they experience longer periods without disturbances, resulting from activities such as planting and harvesting. As a direct result, perennial crops favor the long-term establishment of bee nests, which is less likely to occur in annual crops (Asbjornsen et al., 2014; Oakley and Bicknell 2022). Furthermore, bee responses may also differ among regions (Millard et al., 2021), as communities inhabiting tropical regions tend to be more susceptible to land-use changes than those in temperate regions (Newbold et al., 2020; Millard et al., 2021). Therefore, understanding how different agricultural crop systems affect bee diversity globally is vital to propose sound mitigation strategies for insect conservation in human-modified landscapes.

Here, we performed a comprehensive global review of studies evaluating patterns of bee's biodiversity metrics in both agricultural matrices and native habitats, and subsequently performed a meta-analysis with a subset of studies that provided specific data on the type of response investigated (abundance and/or species richness), food availability within the agricultural matrix (i.e. flowering type: mass-flowering or no mass-flowering), life-cycle of crop (perennial or annual crops), and the region in which the study was conducted (tropical or temperate). Overall, we expected a negative effect of agricultural matrices on biodiversity metrics compared to natural habitats due to the lower variety of food items and nesting sites within crops. Specifically, we also expected: i) a stronger negative effect of agricultural matrices on species richness than on abundance, given the greater sensitivity of certain species (e.g., rare ones) to the negative impacts of agriculture (Kleijn et al., 2015), while tolerant species can be benefited and therefore become hyperabundant in disturbed landscapes (Ferreira et al., 2015, 2022); ii) a lower negative effect of crops exhibiting massive flowering, as a consequence of their greater food availability (Diekötter et al., 2014); iii) a higher negative effect of annual compared to perennial crops, as the former exhibit lower viability for nesting establishment and bee survival (Asbjornsen et al., 2014; Oakley and Bicknell 2022); and iv) a more substantial negative effect on bee biodiversity metrics in tropical regions compared to temperate regions, considering that tropical pollinators tend to be more sensitive to the habitat disturbance (Newbold et al., 2020; Millard et al., 2021).

MATERIALS AND METHODS

Literature search

We first performed a comprehensive literature search in the Web of Science database (www.webofknowledge.com), aiming to identify all studies published until 23 August 2023 that investigated the effect of agricultural matrices on species diversity (i.e., abundance and/or richness) in croplands. For this, we used the following combination of words, in English, located in the title, keywords, or abstract: (((bee OR bees) AND (agricultur* OR plantation* OR matrix OR monoculture OR polyculture OR agroforest* OR crop*) AND (abundance OR richness OR "species number" OR diversity))). We ended up finding 2,836 articles. On 20 October 2023, we performed an additional search on Google Scholar (https://scholar.google.com) to potentially increase the number of studies and reduce publication bias by including gray literature (e.g. theses and dissertations). For this, we used the same words mentioned above in English, Portuguese, and Spanish. Considering the large number of studies found in Google Scholar searches (in total, 83,200 studies) and that our search was ordered by relevance of the articles, we limited our search to the published research found on the first 20 pages for each language (Lisón et al., 2020). In addition, we identified that the final pages (within our 20-page range) presented studies unrelated to our topic of study, which increased our confidence in searching for articles. Therefore, we ended up with 200 studies per language (English, Portuguese, and Spanish). We also included data from three other studies conducted by our study group, one of which was published after our reviews (Ferreira et al., 2024) and the other two are unpublished data. The first database unpublished refers to the collection of orchid bees (Apidae: Euglossini) in shaded cacao agroforests and Atlantic Forest remnants in southern Bahia, Brazil. The bees were collected using traps with attractive baits (cineole, eugenol, vanillin, and methyl cinnamate) for a period of 48 hours at each site sampled (see Ferreira et al. (2024) for more details about the study area). The second database corresponds to the collection of bees in soybean monocultures and native Cerrado remnants, in the central region of Mato Grosso, Brazil (see Oliveira et al. (2022) for more details about the study area).

Screening process

As inclusion criteria, we selected only studies that i) performed bee sampling in at least one agricultural matrix (treatment) and one native habitat (control) within the same regional context; ii) used the same sampling techniques for treatment and control; and iii) provided data on the species abundance and/or richness in both treatment and control groups. We excluded studies that i) considered semi-natural habitat (such as semi-natural pastures intended either to raising animals or plant species of agricultural interest) as a control habitat; ii) considered cattle pastures as treatment; iii) present data collected at the environmental edge (i.e., <50 m from the edge of native habitats or agricultural matrix, because this short distance makes it difficult to determine whether the bees found in this transitional area are in fact associated with the native environment or the agricultural matrix); and iv) represented duplicate databases (in this case, we kept the most recent study). For studies that performed bee surveys across time series, we calculated the mean and total dispersion of both treatment and control groups along the studied period.

After reading the title and abstract of the 2836 articles found in the Web of Science database and the 600 studies from Google Scholar (200 for each language - English, Spanish, and Portuguese), we ended up with 263 studies. After a thorough reading, only 32 articles were considered potentially suitable to be included in our review based on the abovementioned criteria. However, 18 failed to provide the required information (i.e., mean or dispersion value) to enable meta-analysis. Although we requested the data from the corresponding authors of the studies, many authors did not respond to our request, even after we tried at least two times, which made it unfeasible to perform the data analyses with the total number of studies gathered in our literature search. In summary, all 32 selected studies were used for the review, whereas a subset of 14 studies (with 38 comparisons) were used for meta-analysis (Fig. 1 and Fig. 2; Supplementary Table 1).

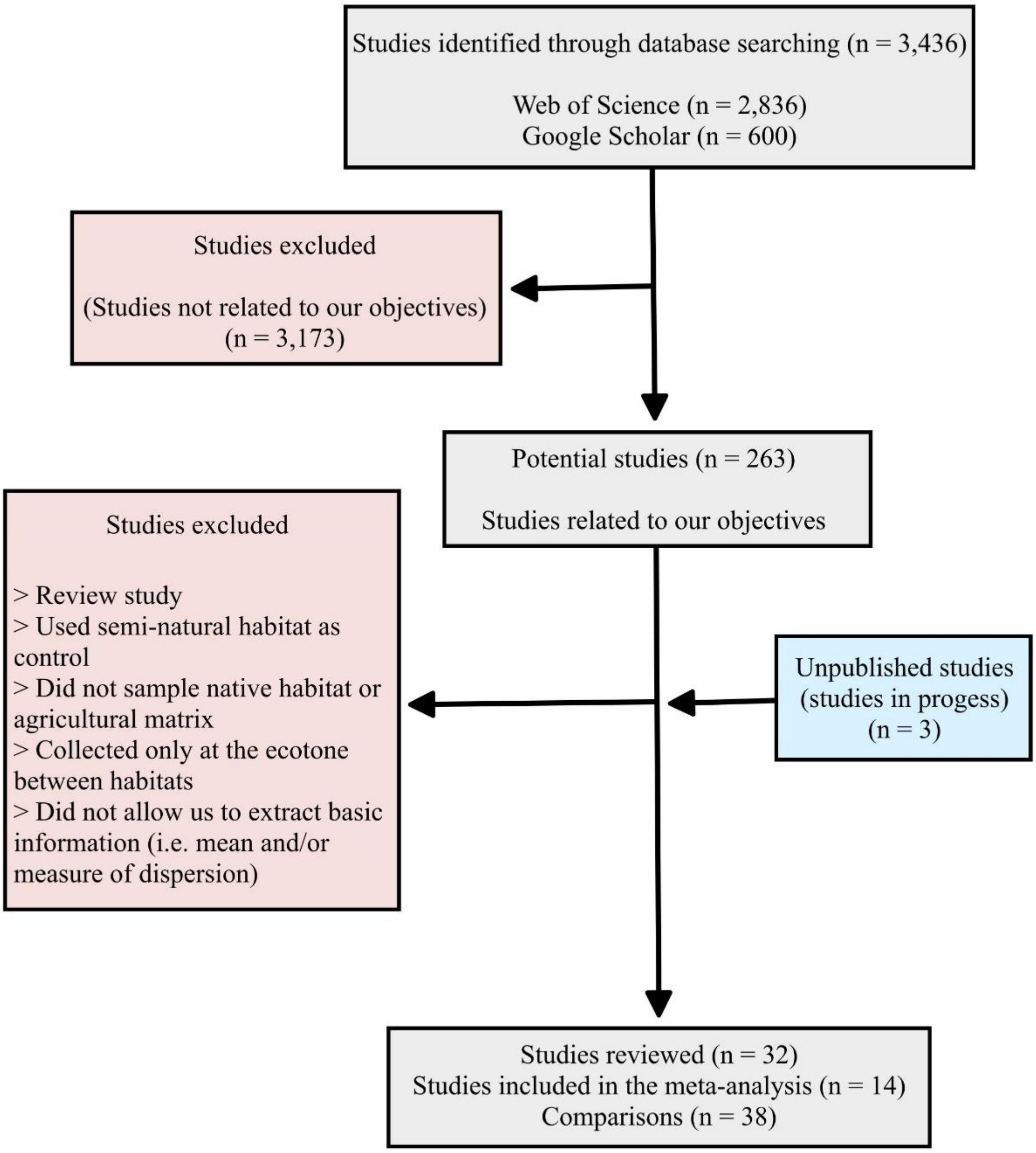

Fig. 1 - Diagram of the stages of selection and exclusion of studies used in our review (n = 32) and meta-analysis (n = 14) evaluating the effects of agricultural matrices on bee richness and/or abundance

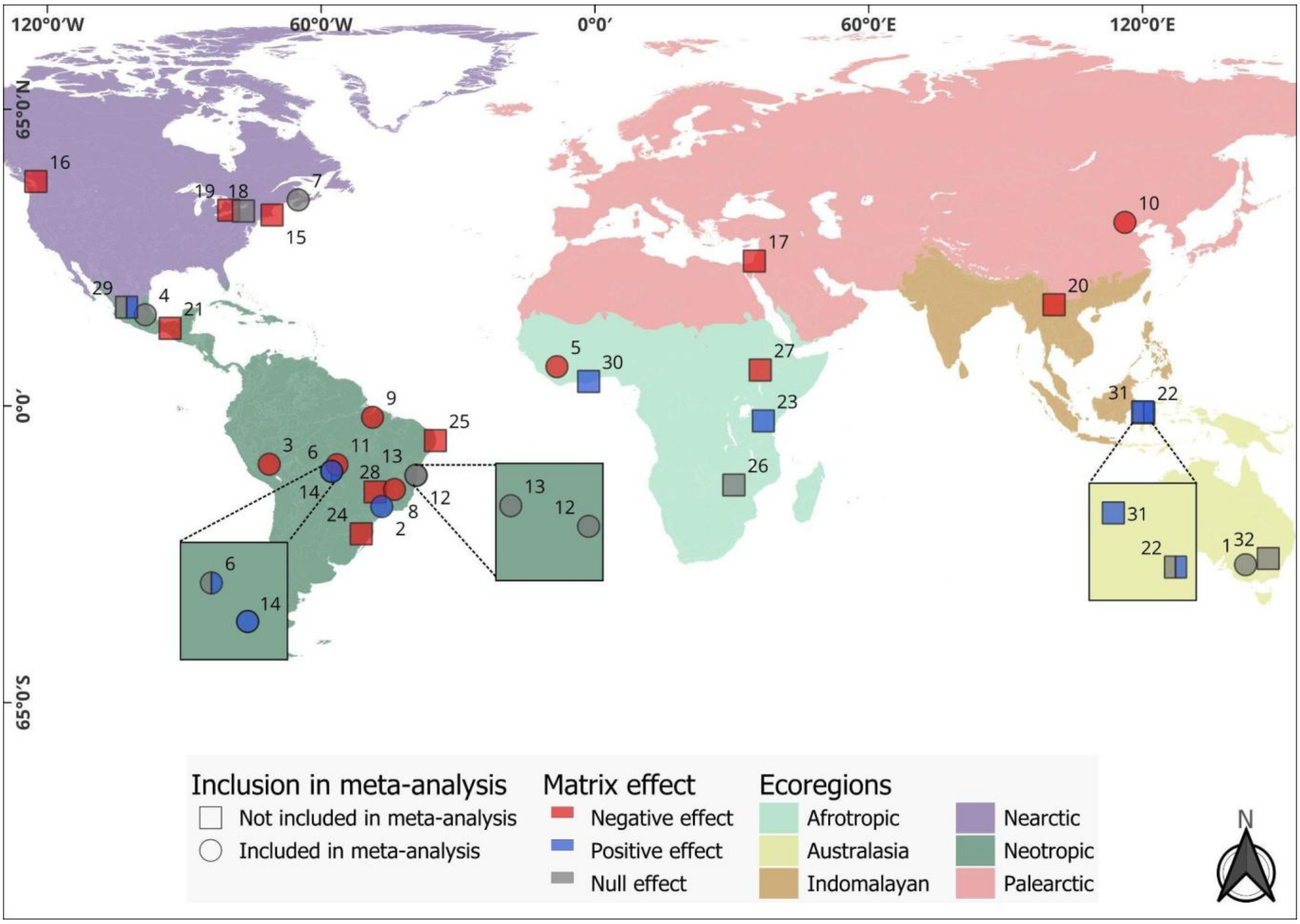

Fig. 2 - Global distribution of the 32 studies used in our review. Circle and square symbols represent, respectively, the 14 studies included, and the 18 studies not included in our meta-analysis. The effect of agricultural matrix on bee diversity, defined based on the main conclusions of the reviewed studies, is represented by the symbol colors - red = negative, blue = positive and gray = neutral. See Supplementary Table 1 for details of each study.

Exploratory analysis and data extraction

From the 32 studies that met our inclusion criteria, we reviewed and classified each one according to the evaluated effect of agricultural matrix on bee biodiversity metrics – i.e., positive, negative, or neutral, based on the conclusions of each study. Exotic bees were not disregarded, since not all studies attested to the decision to include or not include exotic species or provided a data set that allowed for this type of separation. We classified and quantified all 32 studies according to the characteristics of the agricultural matrices, i.e., i) flowering type (mass flowering or no mass-flowering), ii) life-cycle of crops (perennial or annual crops), iii) type of native habitat (natural or agricultural); iv) type of agricultural matrix; v) country, and vii) the region (tropical or temperate) in which the study was conducted. In particular, we conducted a literature search to obtain information on the type of flowering and life cycle of each crop included in our review. Concerning the type of flowering, we did not obtain this information for all crops. Therefore, we classified only soybean, sunflower, and rapeseed as mass flowering crops. Regarding the life cycle, we classified all crops with a duration of one or two years, such as sugarcane, as annuals, and as perennials, all crops exceeding two years, such as apple, coffee, and oil palm. The classification of each crop is described in the table presented in Supplementary Table 1.

Meta-analysis

For the 14 studies used in the meta-analysis, we extracted the following information: i) type of response variable (abundance and/or species richness); ii) sample size (i.e., number of transect or site sampled); iii) mean estimate of the response variable in the treatment and control groups; iv) dispersion estimate of the response variable (i.e., standard deviation or standard error) in the treatment and control groups, v) type of native habitat; vi) type of agricultural matrix; and vii) the geographical region where the study was performed (tropical or temperate). When mean and dispersion estimates were not explicitly provided in the studies, but graphs were available, we extracted them by using the software GetData Graph Digitizer (http://www.getdata-graph-digitizer.com/) or requesting directly from the authors (authors who responded and kindly sent the data are explicitly mentioned in the acknowledgments section). We also obtained the geographic coordinates of each study from Google Earth when the authors did not explicitly provide this information. In the case where more than one coordinate was reported (i.e., when more than one site was surveyed), we estimated the centroid to represent the study area.

We calculated individual effect sizes using standardized mean differences (Cohen’s d) between the mean of the treatment (agricultural matrix) and the control (native habitat), divided by the standard deviation within each group. Positive and negative values indicate, respectively, the agricultural matrix's positive and negative effect on bee diversity. We used the *escalc* function from the metafor package (Viechtbauer 2010) to estimate the effect sizes. As some studies carried out the bee sampling at different distances within the same habitat (native and/or agricultural matrix), we calculated mean and dispersion values by combining all distances within each study. We corrected the potential bias for small samples by converting Cohen’s d to Hedge’s g effect size.

We used the *rma function* to calculate the mean effect across all studies (i.e., all comparisons) and a 95% confidence interval. In particular, confidence intervals including zero indicate that it was not possible to verify an effect of agricultural matrices on bee diversity. Considering that several studies included more than one comparison and that this could result in pseudo-replication bias, we applied a bootstrap procedure and calculated the effect size for 10,000 resamples (with replacement) using only one individual comparison per study at a time (Almeida-Rocha et al., 2017).

Finally, to investigate the heterogeneity between studies, we conducted subgroup analyses defined by the type of response (abundance or richness), flowering type (mass flowering or no mass-flowering), life-cycle of crops (perennial or annual crops), and region (tropical or temperate). For each subgroup, we repeated the same general approach of random effects meta-analysis using the bootstrap procedure and generated a mean effect size and a 95% confidence interval.

To assess the meta-analysis robustness regarding a possible publication bias, a visual inspection was first performed through a funnel plot, in which the effect size variation (standard error) was plotted as a function of the standardized mean difference of each study. We then performed a Trim and Fill analysis (Duval and Tweedie 2000) to estimate the number of missing studies that would be necessary to make the funnel plot symmetric, and how the inclusion of such studies would impact the mean effect size. We also used Rosenthal's fail-safe number (fsn) to estimate the number of studies with non-significant effect that, if included in our meta-analysis, would render our results non-significant. We used the bootstrap approach for both the Trim and Fill and FSN tests. All analyses were conducted in R software (R Core Team 2022).

RESULTS

General patterns

In general, we observed that half of the studies (50%) concluded that agricultural matrices negatively affect bee biodiversity metrics (i.e., a reduction in species richness and/or abundance), while only five studies (15.6%) reported a positive effect of the matrix. Our review also revealed that eight studies (25%) recorded a neutral effect of agricultural matrices on bee diversity. Three studies (9.4%) observed a varied effect, depending on the type of evaluated response (neutral for species richness and positive for abundance) or management intensity (neutral effect when considering intensive management systems or positive when considering less intensive management).

Of the total reviewed studies (n = 32), the most common agricultural matrices were cocoa and coffee, with four studies each (12.5%), followed by soybean (n = 3 studies, 9.4%), and almond, apple, blueberry, canola, cranberry, prickly pear, and oil palm (n = 2 studies each, 6.3%). Alfalfa, banana, cherry, peach, raspberry, rice, sugarcane, sunflower, and wheat were investigated in only one study each (3.1%). Four studies (12.5%) did not specify or define a single matrix type, and we considered them mixed cropping systems. Most studies (27 studies-84.4%) featured agricultural matrices classified as non-mass-flowering, with only five (15.6%) being mass-flowering. In addition, only six studies (18.3%) were classified as annual crops, while 26 studies (81.7%) were classified as perennial crops. Approximately one-third of the studies (n = 11, 34.4%) were conducted in Brazil, followed by Canada and Mexico (n = 3 studies each, 9.4%). Australia, China, the USA, and Indonesia (n = 2 studies each, 6.3%), and Ghana, Israel, Zimbabwe, Ethiopia, Peru, Costa Rica, and Tanzania had only one study, each (3.1%). Consequently, most studies (n = 23 - 71.9%) were conducted in tropical regions, in contrast to nine (28.13%) in temperate areas.

Meta-analysis

Regarding the meta-analysis, the majority of comparisons (21 comparisons - 55.3%) indicated that the agricultural matrix had a negative effect, while only six (15.8%) and 11 comparisons (29%) indicated positive and neutral effects, respectively (Fig. 3). When considering all studies with the bootstrap approach, our results indicated that agricultural matrices exerted a general and negative effect on bee diversity (effect size = -0.43; 95% CI = lower: -0.75; upper: -0.10) (Fig. 4; Supplementary Table 2). We also observed a high heterogeneity among the studies' effect sizes (I2 = 78%). Regarding publication bias, despite the funnel plot suggesting an asymmetry (Supplementary Figure 3), the Trim and Fill test indicated that only nine studies needed to be included in the dataset to complete a symmetric funnel plot. The fail-safe-number analysis indicates that 23 studies without effect would be needed to cause the observed average effect to be non-significant. Considering our research efforts (including different databases and grey literature), we consider our results robust and unbiased.

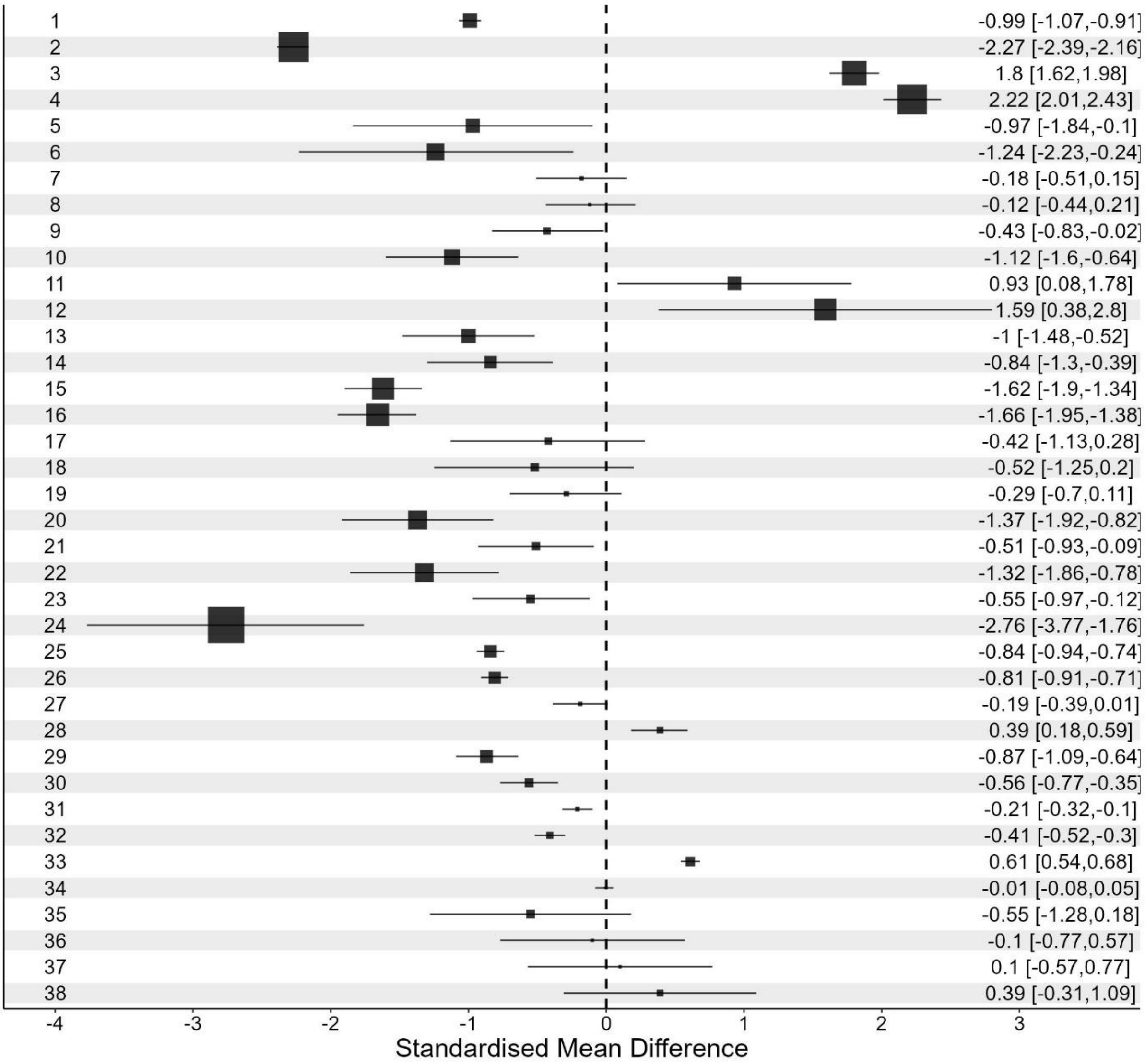

Fig. 3 - Effect size of the 38 pairwise from 14 studies investigated in meta-analysis. The horizontal bars indicate a 95% confidence interval. Black square indicates the individual effect (size is proportional to effect size). Negative and positive values indicate, respectively, a negative and positive effect of the agricultural matrix on bee diversity. Results in which the confidence interval includes a value of zero, indicate that the result was not significant.

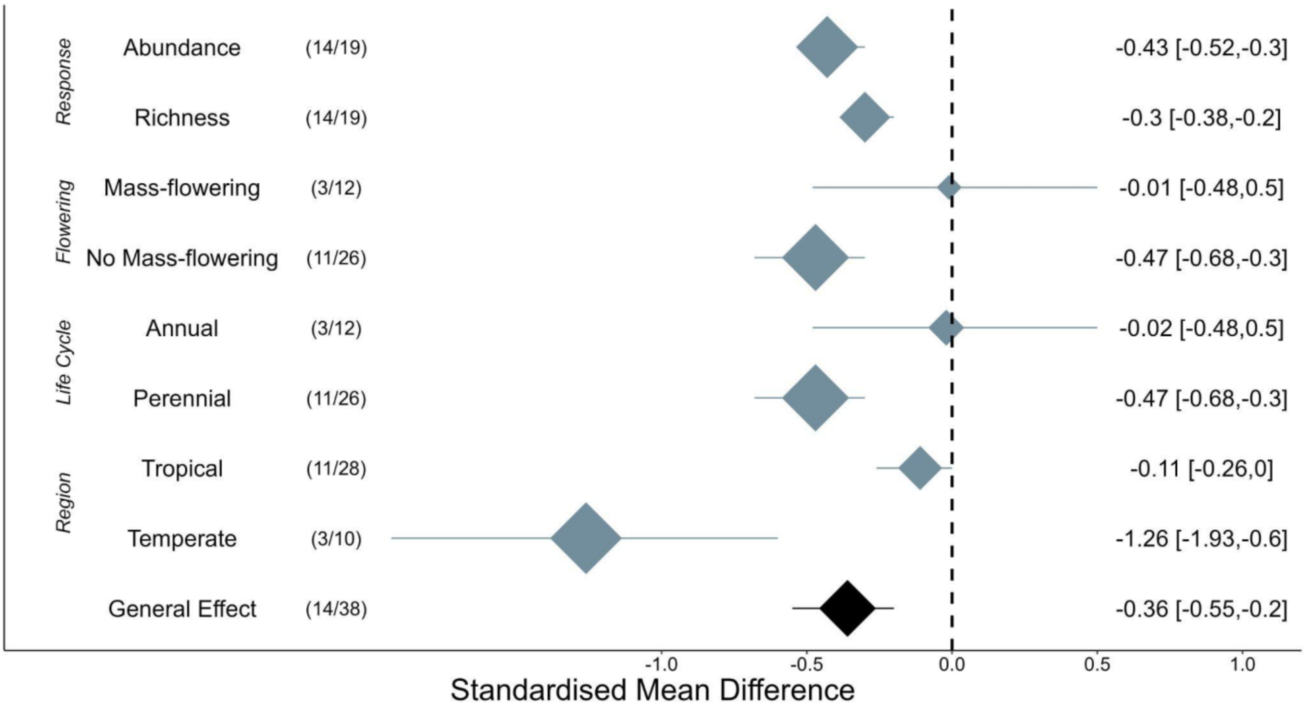

Fig. 4 - Effect size, calculated with the bootstrap approach, for the different subgroups: type of response (abundance or richness of bees), type of flowering (massive and no-mass flowering), life-cycle (annual or perennial), biogeographic region (tropical or temperate). The horizontal bars indicate a 95% confidence interval. Black diamond indicates the overall effect estimated from the 14 studies that were included in the meta-analysis. Negative and positive values indicate, respectively, a negative and positive effect of the agricultural matrix on bee diversity. Results in which the confidence interval includes a value of zero, indicate that the result was not significant.

Our results also evidenced that agricultural matrices present a negative effect on both abundance (effect size = -0.43; 95% CI = lower: -0.52; upper: -0.34; I2 = 74%) and species richness (effect size = -0.30; 95% IC = lower: -0.38; upper: -0.21; I2 = 79%), when evaluated separately (Fig. 4). We also observed that agricultural matrices composed of crops with no mass-flowering presented a negative effect on bee diversity (effect size = -0.47; 95% CI = lower: -0.68; upper: -0.26; I2 = 82%), while no effect was detected in mass-flowering (effect size = -0.01; 95% CI = lower: -0.48; upper: 0.46; I2 = 30%). Our analyses also evidenced a negative effect of perennial crops on bee diversity (effect size = -0.47; IC 95% = lower: -0.68; upper: -0.26; I2 = 82%), although this pattern was not detected for annual crops (effect size = -0.02; 95% CI = lower: -0.48; upper: 0.45; I2 = 31%). It is important to draw attention to the fact that, in our database, the matrices classified as mass-flowering coincided with matrices classified as annual crops (consequently the same applies to no mass-flowering crops being also perennial crops). Thus, we cannot distinguish the effects of both moderators, which will be discussed together. Finally, regarding the region in which the study was conducted, the agricultural matrix had a negative effect only in the temperate region (effect size = -1.26; IC 95% = lower: -1.93; upper: -0.59; I2 = 30%), while no general effect was observed for the tropics (effect size = -0.11; IC 95 % = lower: -0.26; upper: -0.04; I2 = 77%) (Fig. 4).

DISCUSSION

As far as we are aware, this is the first review investigating the effect of distinct agricultural matrices on bee abundance and species richness at a global scale. Differently to a previous meta-analysis investigating the effects of anthropogenic disturbances on bee diversity, which did not find a consistent effect of agriculture on species abundance and richness (Winfree et al., 2009), we observed that agricultural matrices present a lower richness and abundance of bees than native habitats. However, the conclusions of this previous study included only seven and eight comparisons for abundance and richness, respectively, which probably led to an underestimation of the effects. Furthermore, our observed pattern was consistent mainly when evaluating matrices composed of crops without mass flowering and with a perennial life cycle. Our findings also indicated that the negative impact of agricultural matrices is more intense in studies conducted in the temperate region. Based on our outcomes, we highlight that the conversion of natural habitats to agricultural lands is consistently more detrimental to bee conservation than previously thought, driven mainly by monocultures in temperate regions.

Overall, most studies in our review reported a negative effect of agricultural matrices on bee diversity. Likewise, we revealed a similar result in our meta-analysis, therefore reinforcing that agricultural systems represent a severe threat to the maintenance of bee diversity. In particular, converting native habitats into agricultural areas is one of the leading causes of pollinator biodiversity loss, including bees (Potts et al., 2010; IPBES 2016). The reduction in the quantity and diversity of resources, combined with the frequent use of pesticides (common in agricultural areas), have serious impacts at a population and community level (Brittain and Potts 2010; Belsky and Joshi 2020). However, such effects are not always observed, which may explain why 25% of the studies evaluated in our review did not detect an impact on the abundance or richness of bee species. For example, despite the recognized impact of agriculture on bee diversity, Schüepp et al. (2024) observed that the taxonomic and functional diversity of bees did not differ between agroecosystems and forests, suggesting that such agricultural systems may even favor bee communities by providing supplementary resources and facilitating the movement of these insects between native environments.

Contrary to our expectations, we did not find a greater magnitude of effect on species richness than abundance. However, our results evidenced that both the richness and abundance of bees were negatively impacted by agricultural matrices, indicating a more pronounced effect on abundance. A possible explanation for this finding can be associated with the greater sensitivity of social bees to anthropogenic disturbances compared to solitary bees (Winfree et al., 2009). In fact, social bees constitute a highly abundant group of bees (Michener 2007) characterized by their great success in acquiring floral resources due to the collective effort of numerous workers dedicated to nurturing offspring, maintaining the nest, and collecting essential resources for the colony. Nonetheless, social bees tend to exhibit a higher dependency on structurally complex vegetation, as many bee species inhabit pre-existing cavities, such as those found in the trunks of old trees (Wille 1983). Consequently, replacing native habitats with agricultural crops, particularly in systems characterized by the complete removal of native vegetation, could exert a more significant impact on social bee species, potentially resulting in a further reduction in bee abundance within these areas.

Our results demonstrate that matrices composed of no mass-flowering crops and perennial crops negatively affect bee diversity. However, we failed to detect a consistent effect for matrices with mass flowering and annual crops. This finding is intriguing as we assumed that the moderators flowering type and life cycle of agricultural crops are associated with the food resource availability and the nesting site provision for bees. We cannot overlook the fact that there was a overlap between moderators (i.e., crops with mass-flowering are often annuals, and crops without mass-flowering are often perennials), which may represent a limitation in our interpretations. Nevertheless, the fact that no mass-flowering crop (lower food availability) coincides with crops more favorable to bee nesting (i.e., perennial crops) suggests that the availability of food resources may be the primary limiting factor for bee maintenance in agricultural matrices (Roulston and Goodell, 2011). In this instance, besides the reduced diversity of food resources available in agricultural areas, the smaller amount of these resources in agricultural matrices without mass flowering impact negatively impacts the maintenance of bee populations. On the other hand, agricultural crops with mass flowering may provide a large supply of food resources, such as nectar and pollen, and therefore favoring some bee species that, during the flowering peak, may even present a greater abundance in the matrix compared with native habitats (Almeida et al., 2020). This could explain the fact that we did not find a significant effect of these flowering type crops on bee diversity. However, this result should be observed with caution, especially because only 12 comparisons from three studies were included in the meta-analysis. Mass-flowering crop systems, such as sunflower and soybean, are frequently associated with more intensive management practices and with high amounts of pesticide, which can trigger significant loss of pollinators (Brittain et al., 2010).

We also observed a negative effect of perennial agricultural matrices on bee diversity, which exhibit higher structural stability compared to annual crops and, therefore, could favor the establishment of various bee species (Hoehn et al., 2010; Vides-Borrell et al., 2019). The potential benefits of perennial crops in fostering bee nesting may be limited to only some species with simpler nesting requirements, such as species that excavate their nests in the soil (Ferreira et al., 2015). Thus, the demands for adequate nesting can depend not only on substrate diversity but also on a diversity of resources that do not seem to be supplied by perennial agricultural crops. Therefore, this result supports the idea that even agricultural crops that could have reduced negative effects on bee diversity substantially affect these insects. Hence, these findings demonstrate that, although some perennial agricultural crops support high species richness, these environments are insufficient to harbor and retain high bee diversity.

Our findings also demonstrate that even bee communities are considered less sensitive, as in the case of communities located in temperate regions, which are threatened and negatively impacted by agricultural activities, emphasizing the importance of recovering natural habitats for the conservation of these pollinators. Studies conducted in these regions often use semi-natural habitats as controls, and this could also explain the fact that few studies conducted in temperate zones were included in our meta-analysis since we excluded studies that did not use natural habitat as a control. Therefore, despite the more significant history of agricultural activities in temperate regions, bee assemblages remain sensitive to replacing native habitats by agricultural areas. In addition, although many studies highlight the importance of semi-natural habitats for maintaining bees in agricultural landscapes in temperate regions (Papanikolaou et al., 2017; Rutschmann et al., 2022), our results reinforce the role and importance of strictly native habitats for maintaining bee diversity across temperate zones.

Despite most comparisons in tropical regions showed a negative or neutral effect, we failed in detecting a consistent impact of agricultural matrices on bee diversity in this region. The positive effect observed in some comparisons might be attributed to the characteristics of the investigated matrix and the distance from the native habitat. For instance, out of the six comparisons in tropical regions that showed a positive effect, five involved coffee (Medeiros et al., 2019), sunflower (Almeida et al., 2020), or soybeans matrices (Ferreira et al., 2020). Notably, these last two are mass flowering crops, and the authors clearly stated that collections were conducted during the reproductive period of these crops. Therefore, it is likely that during this period, when there is a greater supply of food resources, there is a spillover of bees to the matrix due to the abundant floral resources (Montero-Castaño et al., 2016).

Furthermore, the distance from the native habitat is also an important factor, as there is a positive relationship between proximity to the native habitat and bee abundance and species richness (Ricketts et al., 2008; Bailey et al., 2014). In this regard, it is noteworthy that in four of these six comparisons with a positive effect, collections were carried out within 150 m or less from the native habitat, and in all cases, the collections were conducted at a maximum distance of 600 m, which is accessible for many bee species (Zurbuchen et al., 2010; Kendall et al., 2022). It is also important to consider the fact that the amount of habitat at a given scale, for example at a landscape scale, is negatively related to the isolation of native remnants (Fahrig et al. 2013). Considering that tropical regions retain the largest amount of native remnants, on a global scale (Hansen et al. 2022), this results in less isolation and facilitates the access of bees to the agricultural matrix, which possibly contributed to explaining the lack of effect on the abundance and richness of species in tropical regions. Therefore, we emphasize that the neutral effect of agricultural matrices in tropical regions should be interpreted with caution and suggest long-term monitoring studies of bee diversity, considering not only the reproductive period of agricultural crops but also the vegetative phases and fallow periods in the case of annual crops.

We recognize that, despite our effort to include as many studies as possible in our dataset, we were able to perform meta-analysis, including data from only 14 studies. As a result, this potentially reduced our inferential power regarding the effect of agricultural matrices on bee abundance and species richness. This is especially the case for Africa, Southeast Asia, and parts of Oceania, which have had a very limited number of studies, highlighting the importance of increasing research efforts in these sub-regions. However, there is also a need to conduct further studies, we reinforce the importance of researchers in providing the raw data on their studies, enabling maximum data utilization (Stodden et al., 2018). In addition, we draw attention to the challenge of defining a global effect of the agricultural matrix, considering the wide range of characteristics of each cropping system, the lack of standardization of the sampling method and the different responses of groups of bees, which possibly contribute to the high heterogeneity observed among the studies included in the meta-analysis. Such characteristics include i) the type of management adopted (e.g. organic production systems versus conventional systems - Morandin & Winston, 2005; Holzschuh et al., 2007); ii) the collection method (e.g. collection with pan traps tends to underestimate bee diversity in native forest habitats, compared to more open environments (Prado et al., 2017), such as agricultural matrices; iii) the proximity to the native habitat (Bailey et al. 2014) and iv) the amount of habitat on a landscape scale, which can influence the response of bees to matrix effects (Ricketts et al., 2008; Rahimi et al., 2022), among others. Nonetheless, we clearly observed that half of the reviewed studies concluded that agricultural matrices negatively affected bee abundance and species richness, and meta-analysis supports this finding by also revealing an overall negative effect.

Finally, our study outcomes reinforce that bee assemblages are threatened by the advance of agricultural lands on native habitats, even in crops that are structurally more stable (as perennial crops) and in regions where bee communities are considered more resilient (as temperate regions). Regarding the provision of the pollination ecosystem service, we also showed that the effects of the agricultural matrices can be doubly negative in agricultural landscapes because both the abundance (Sabbahi et al., 2005) and richness of pollinator species (Rogers et al., 2014; Dainese et al., 2019) are positively related to the increase in productivity, and both (abundance and species richness) are negatively affected by agricultural matrices. Thus, our results demonstrate that agricultural lands mostly fail to maintain a high diversity of these key pollinators and potentially provide pollination services (Kleijn et al., 2015), which reinforces the importance of preserving native habitats for the conservation of bees. Therefore, we suggest that habitat restoration programs should be prioritized in agricultural landscapes, which can be done by implementing specific laws and effective governmental surveillance. Even temperate areas need to increase native lands, which are likely to provide multiple benefits beyond bee maintenance and pollination services, including carbon storage and significant biodiversity maintenance.

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SUPPLEMENTARY MATERIAL

Supplementary Table 1 - Summary of the 32 studies located and reviewed (including the 14 studies used in the meta-analysis), with the study number refers to the ones presented in Figure 2. WOS = Web of Science; DS = Data source; IM = Inclusion in the meta-analysis; Temp. = Temperate; Trop. = Tropical; Peren. = Perennial.

Study	**Article Title**	**DS**	**IM**	**Matrix type**	**Region**	**Country**	**Flowering type**	**Life cycle**	**Matrix effect**[1]	**Key results**
1	Keystone resources available to wild pollinators in a winter tree crop plantation	WOS	Yes	Almond	Temp.	Australia	No mass	Peren.	Neutral	Inconclusive
2	Landscape structure shapes the diversity of beneficial insects in coffee producing landscapes	WOS	Yes	Coffee	Trop.	Brazil	No mass	Peren.	Positive	Bee richness was positively correlated with the amount of native habitat at a landscape scale. But species abundance and richness were greater in the matrix
3	Are orchid bees useful indicators of the impacts of human disturbance?	WOS	Yes	Banana	Trop.	Peru	No mass	Peren.	Negative	Orchid bees show a clear negative response to human disturbance along a tropical forest-agriculture gradient

Supplementary Table 1 - Summary of the 32 studies located and reviewed (including the 14 studies used in the meta-analysis), with the study number refers to the ones presented in Figure 2. WOS = Web of Science; DS = Data source; IM = Inclusion in the meta-analysis; Temp. = Temperate; Trop. = Tropical; Peren. = Perennial.

Study	Article Title	DS	IM	Matrix type	Region	Country	Flowering type	Life cycle	Matrix effect[1]	Key results
4	Prickly pear crops as bee diversity reservoirs and the role of bees in Opuntia fruit production	WOS	Yes	Prickly pear	Trop.	Mexico	No mass	Peren.	Neutral	There were no significant differences between habitats in any of the bee community parameters (richness, abundance, diversity and species composition)
5	Conservation Value and Permeability of Neotropical Oil Palm Landscapes for Orchid Bees	WOS	Yes	Oil palm	Trop.	Costa Rica	No mass	Peren.	Negative	Species richness, abundance and community similarity to the forest declined in the agricultural matrix as distance from the forest increased
6	Contribution of the Cerrado as Habitat for Sunflower Pollinating Bees	WOS	Yes	Sunflower	Trop.	Brazil	Mass	Annual	Neutral / Positive	Species richness did not differ between the Cerrado and the sunflower plantation (but bee diversity decreased proportionally as distance from the edge increased) and abundance was greater in sunflower
7	Diversity of cavity-nesting bees (Hymenoptera : Apoidea) within apple orchards and wild habitats in the Annapolis Valley, Nova Scotia, Canada	WOS	Yes	Apple	Temp.	Canada	No mass	Peren.	Neutral	Species richness and numbers of bees in commercially managed orchards, abandoned orchards, and natural habitats were similar, and patterns of species composition were not exclusive to specific habitats
8	Does a coffee plantation host potential pollinators when it is not flowering? Bee distribution in an agricultural landscape with high biological diversity in the Brazilian Campo Rupestre	WOS	Yes	Coffee	Trop.	Brazil	No mass	Peren.	Negative	There was no temporal difference in species richness or abundance. However, both varied in relation to the type of vegetation and were greater in the native-coffee transition area

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Study	Article Title	DS	IM	Matrix type	Region	Country	Flowering type	Life cycle	Matrix effect[1]	Key results
9	Effects of habitat type change on taxonomic and functional composition of orchid bees (Apidae: Euglossini) in the Brazilian Amazon	WOS	Yes	Oil palm	Trop.	Brazil	No mass	Peren.	Negative	Functional diversity has been reduced with land use change caused by palm oil plantations
10	Effects of Plant Diversity, Vegetation Composition, and Habitat Type on Different Functional Trait Groups of Wild Bees in Rural Beijing	WOS	Yes	Peach, Cherry and Apple	Temp.	China	No mass	Peren.	Negative	Natural shrub areas supported the greatest bee diversity overall, in large bees, solitary bees, and below-ground nesting bees
11	Critical role of native forest and savannah habitats in retaining neotropical pollinator diversity in highly mechanized agricultural landscapes	WOS	Yes	Soybean	Trop.	Brazil	Mass	Annual	Negative	The richness of bee species was significantly lower in the soybean matrix compared to the interior of the forest and the species composition also differed significantly
12	Landscape forest cover and regional context shape the conservation value of shaded cocoa agroforests for bees and social wasps	WOS	Yes	Cocoa	Trop.	Brazil	No mass	Peren.	Positive	Species richness was similar between cocoa agroforestry and native forestry
13	*Provisional title*: Taxonomic diversity of orchid bees (Euglossini) in cocoa agroforests and Atlantic Forest remnants in southern Bahia, Brazil	Unpublished	Yes	Cocoa	Trop.	Brazil	No mass	Peren.	Neutral	Abundance and richness did not differ between cocoa agroforestry and native forest

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Study	**Article Title**	**DS**	**IM**	**Matrix type**	**Region**	**Country**	**Flowering type**	**Life cycle**	**Matrix effect[1]**	**Key results**
14	*Provisional title*: Bee diversity in soybean cultivation areas, as well as Cerrado remnants, in the state of Mato Grosso, Brazil	Unpublished	Yes	Soybean	Trop.	Brazil	Mass	Annual	Positive	The abundance and richness of species were significantly greater in the soybean matrix than in the Cerrado remnant
15	Bee (Hymenoptera, Apoidea) diversity and abundance on cranberry in southeastern Massachusetts	WOS	No	Cranberry	Temp.	USA	No mass	Peren.	Negative	Non-apid bees were more abundant and diverse in abandoned and natural peatlands than in cultivated peatlands
16	Diversity and abundance of native bee pollinators on berry crops and natural vegetation in the lower fraser Valley, British-Columbia	WOS	No	Blueberry, Raspberry and Cranberry	Temp.	Canada	No mass	Peren.	Negative	The abundance and diversity of native bees was greater in natural vegetation compared to fruit crops
17	Diversity patterns of wild bees in almond orchards and their surrounding landscape	WOS	No	Almond	Temp.	Israel	No mass	Peren.	Negative	The natural habitats had a significantly higher abundance of wild bees compared to the orchard
18	Diversity and abundance of bees (Hymenoptera: Apoidea) foraging on highbush blueberry (Vaccinium corymbosum L) in central New York	WOS	No	Highbush blueberry	Temp.	USA	No mass	Peren.	Neutral	Species richness was high in both cultivated and uncultivated sites
19	Restored native prairie supports abundant and species-rich native bee communities on conventional farms	WOS	No	Mix: corn, berry, soybeans, squash and pumpkins	Temp.	Canada	Mix	Annual	Negative	The restored prairie supported twice as many species and three times as many bees compared to the other cover types

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Study	Article Title	DS	IM	Matrix type	Region	Country	Flowering type	Life cycle	Matrix effect[1]	Key results
20	Contrasting responses of hoverflies and wild bees to habitat structure and land use change in a tropical landscape (southern Yunnan, SW China)	WOS	No	Rice	Trop.	China	No massa	Annual	Negative	The richness of wild bees recorded was higher in natural forest sites compared to rice fields
21	The Role of the Agricultural Matrix: Coffee Management and Euglossine Bee (Hymenoptera: Apidae: Euglossini) Communities in Southern Mexico	WOS	No	Coffee	Trop.	Mexico	No mass	Peren.	Negative	The composition of euglossini bees differed between forest and coffee monocultures and abundance was significantly higher in the native habitat
22	Alpha and beta diversity of plants and animals along a tropical land-use gradient	WOS	No	Cocoa	Trop.	Indonesia	No mass	Peren.	Neutral / Positive	Species richness varied according to the cultivation system. In intensive systems, species richness was similar to forestry and in less intensive systems (cocoa-native tree association) species richness in the matrix was greater
23	Agricultural intensification with seasonal fallow land promotes high bee diversity in Afrotropical drylands	WOS	No	Mix: maize, beans, sunflower, wheat and barley	Trop.	Tanzania	Mix	Annual	Positive	Bee species richness increased with agricultural intensity and increasing temperature
24	Bee assemblage in habitats associated with Brassica napus L.	WOS	No	Canola	Trop.	Brazil	Mass	Annual	Negative	Diversity indices (Shannon, Simpson and Pielou) were higher in pastures and forests than in canola crops
25	Do euglossine males (Apidae, Euglossini) leave tropical rainforest to collect fragrances in sugarcane monocultures?	WOS	No	Sugarcane	Trop.	Brazil	No mass	Annual	Negative	Species richness in the agricultural matrix showed a drastic reduction, compared to the forest

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Study	Article Title	DS	IM	Matrix type	Region	Country	Flowering type	Life cycle	Matrix effect[1]	Key results
26	Drivers of diversity and community structure of bees in an agroecological region of Zimbabwe	WOS	No	Mix: mainly cereals	Trop.	Zimbabwe	No mass	Annual	Neutral	Bee diversity was high, both in fields and natural forests
27	Fragmentation and Management of Ethiopian Moist Evergreen Forest Drive Compositional Shifts of Insect Communities Visiting Wild Arabica Coffee Flowers	WOS	No	Coffee	Trop.	Ethiopia	No mass	Peren.	Negative	The abundance of non-apis bees and the taxonomic richness of flower-visiting insects decreased significantly in coffee forests compared to natural forests
28	Land-use changes in a neotropical biodiversity hotspot and its effects on Euglossini bees	WOS	No	Soybean	Trop.	Brazil	Mass	Annual	Negative	Few species were recorded in anthropogenic land uses and most had lower abundances in cultivated areas than in native habitats
29	The effect of adjacent habitat on native bee assemblages in a perennial low-input agroecosystem in a semiarid anthropized landscape	WOS	No	Prickly pear	Trop.	Mexico	No mass	Peren.	Neutral / Positive	Total taxon richness and guild taxon richness were not affected by habitat type, but total native bee abundance was significantly higher in areas of native habitat compared to orchards
30	The Utility of Aerial Pan-Trapping for Assessing Insect Pollinators Across Vertical Strata	WOS	No	Mix: mainly oil palm	Trop.	Ghana	No mass	Peren.	Positive	Bee species richness differed significantly between habitat types and agricultural sites were more diverse than undisturbed forest and regenerating forest
31	Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity	WOS	No	Cocoa	Trop.	Indonesia	No mass	Peren.	Positive	Local bee density and diversity were highest in open areas, followed by agroforestry systems and were lowest in primary forests

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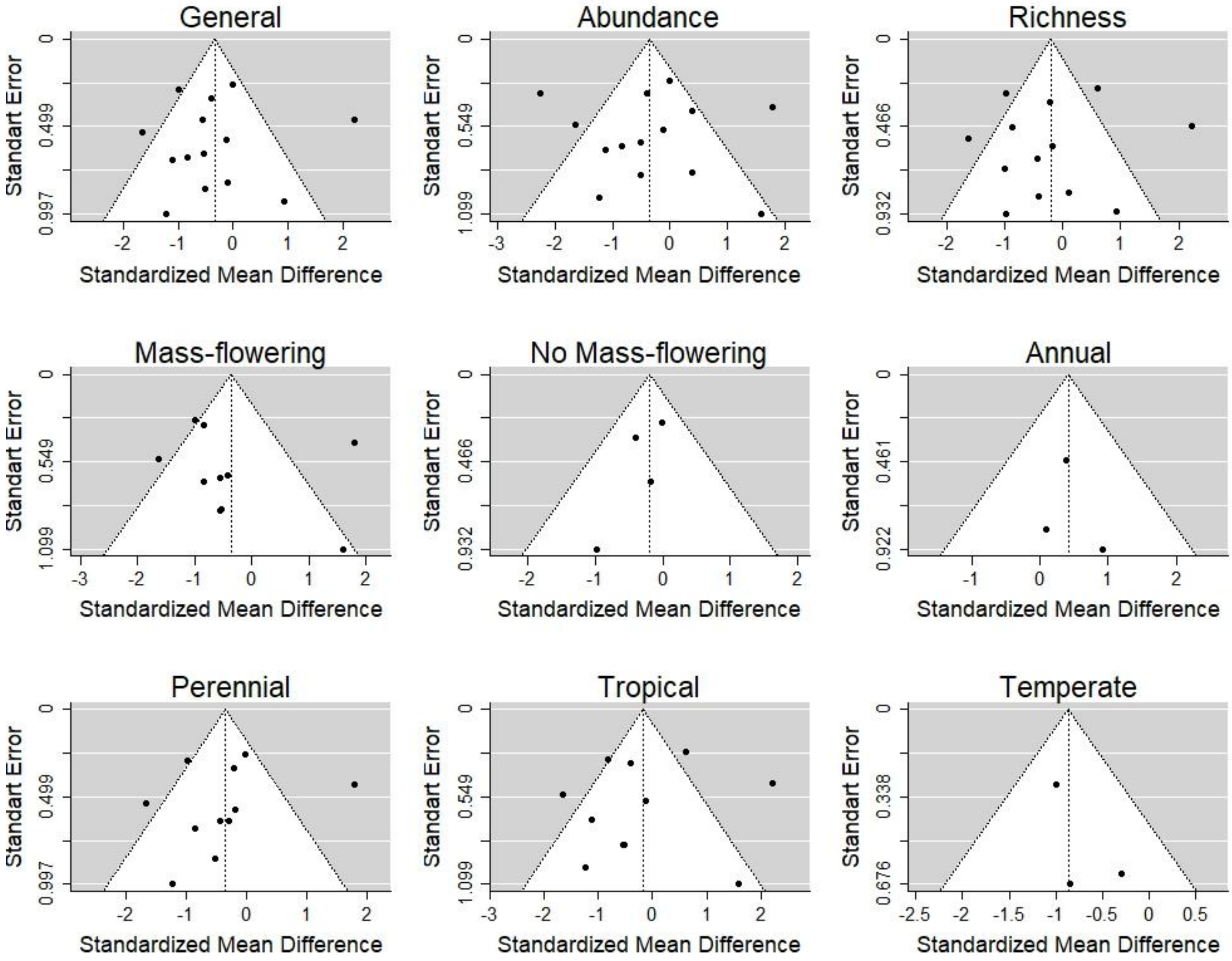
Study	Article Title	DS	IM	Matrix type	Region	Country	Flowering type	Life cycle	Matrix effect[1]	Key results
32	Supporting wild pollinators in a temperate agricultural landscape: Maintaining mosaics of natural features and production	WOS	No	Alfafa, Trigo and Canola	Temp.	Australia	Mix	Annual	Neutral	Inconclusive

[1] Refers to the matrix effect (positive, negative or neutral) according to the results observed in each study.

Supplementary Table 2 - Random effect meta-analysis results for the overall effect of the agricultural matrix and each moderator on bee diversity. CI = Confidence Interval; I² = percentage of total heterogeneity observed between studies.

Group	Pairwise	Study	Estimate	CI lower	CI upper	P value	I²
General effect (bootstrap)	38	14	-0.36	-0.55	-0.18	<0.001	78.73
Abundance	19	14	-0.43	-0.52	-0.34	<0.001	73.99
Richness	19	14	-0.30	-0.38	-0.21	<0.001	78.60
Tropical	28	11	-0.11	-0.26	0.04	0.15	76.67
Temperate	10	3	-1.26	-1.93	-0.59	<0.001	30.18
Annual	12	3	-0.02	-0.48	0.45	0.94	30.56
Perennial	26	11	-0.47	-0.68	-0.26	<0.001	82.26
Mass-flowering	12	3	-0.01	-0.48	0.46	0.96	30.31
No mass-flowering	26	11	-0.47	-0.68	-0.26	<0.001	82.20

Supplementary Figure 3 – Funnel graph for the general meta-analysis and for the different subgroups: type of response (abundance or richness of bees), type of flowering (massive and no-mass flowering), life-cycle (annual or perennial), biogeographic region (tropical or temperate).



Species richness and abundance of social wasps (Vespidae: Polistinae) associated with shaded cocoa agroforests (Theobroma cacao L.) in southern Bahia state, Brazil

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Species richness and abundance of social wasps (Vespidae: Polistinae) associated with shaded cocoa agroforests (Theobroma cacao L.) in southern Bahia state, Brazil

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ABSTRACT: Traditional cocoa agroforests of southern Bahia in Brazil, locally known as "cabrucas", are highly relevant for sheltering forest species, being thus recognized as a biodiversity-friendly agricultural system. However, despite their role in biodiversity conservation, little is known about the ability of cocoa agroforests to maintain social wasp assemblages in human-modified landscapes. Here, we present the first list of social wasp species recorded in shaded cocoa agroforests in southern Bahia. In total, we collected 25 species of social wasps belonging to nine genera, representing 20% of the known species richness for the entire northeastern region of Brazil. In particular, *Angiopolybia pallens* (Lepeletier), *Agelaia angulata* (Fabricius), and *Agelaia centralis* (Cameron) were the most abundant species, with 186, 70, and 36 individuals, respectively. Notably, we recorded six species for the Bahia state - *Agelaia flavipennis* (Ducke), *Polybia emaciata* Lucas, *Polybia quadricincta* (Saussure)*, Agelaia angulicollis* (Spinola), *Parachartegus smithii* (Saussure) and *Protopolybia acutiscutis* (Cameron), the former three having been recorded for the first time in the Northeast region of Brazil. Two of them are new occurrence records for the Atlantic Forest biome. Based on our findings, we emphasize that cocoa agroforests can contribute to maintaining the diversity of social wasps in human-modified landscapes.

Key-words: agricultural system, agroecosystem, biological control, biodiversity-friendly, new species records, taxonomic diversity

INTRODUCTION

Brazil, a country with high biodiversity, is home to more than 90,000 described species of insects (Rafael et al., 2024). However, a considerable portion of this diversity remains unknown or restricted to specific regions of the country, as is the case with social wasps of the subfamily Polistinae, alongside Eumeninae and Masarinae, which encompasses the three subfamilies of Vespidae occurring in Brazil. Overall, 1,050 species of Polistinae wasps are recognized worldwide, with about a third of these species (381) recorded in Brazil (Somavilla et al., 2021).

Given that social wasps are predatory insects (Michelutti et al., 2017), particularly Lepidoptera immatures, these organisms play an important role in regulating trophic chains in natural systems (Brock et al., 2021). In addition, social wasps also perform a fundamental role in natural biological control, especially insect pests in agricultural systems (Prezoto et al., 2019; Southon et al., 2019). Despite being relatively well-studied insects, which means that these wasps' evolutionary, behavioral, and ecological biology are reasonably well-known (Prezoto et al., 2021), there are still many gaps in the geographic distribution of social wasps. Even in highly diverse biomes that concentrate most studies on social wasps, such as the Atlantic Forest, there are regions where the taxonomic diversity of these insects remains poorly explored or even unknown (Souza et al., 2020; dos Santos et al., 2020).

One of the possible limitations in understanding the geographic distribution of social wasps is associated with the fact that natural habitat is primarily the focus of most species' inventories, which limits the understanding of species diversity in other environments (Somavilla et al., 2019; Somavilla et al., 2020). However, surveying wasp species associated with agricultural systems may be relevant for understanding the species diversity patterns in anthropogenic areas and identifying species of agricultural interest. In addition, several insect species are associated with agricultural areas, which comprise a significant extent of human-modified landscapes worldwide (Melo et al., 2013; Somavilla et al., 2016; Ferreira et al., 2020). Along with life-history attributes, the ability of native species to use agricultural areas depends on the crop system and its local level of intensification, factors that can affect resource availability for most insect species (Oakley & Bicknell, 2022).

Shaded cocoa agroforests (*Theobroma cacao* L.) of southern Bahia in Brazil are agroecosystems exhibiting high value for biodiversity maintenance in human-modified landscapes (Cassano et al., 2009). Historically, cocoa has been cultivated in a system popularly known as cabruca, where cocoa trees are planted under the shade of large trees. Thus, the association of emergent trees with cocoa trees creates high structural complexity systems, making them highly relevant for biodiversity conservation (Cassano et al., 2009). However, in the 1980s, after the incidence of the witch's broom fungus (*Moniliophthora perniciosa*), there was an expansion of intensive cocoa cultivation areas, such as cocoa monocultures or full-sun cocoa production (Alger & Caldas, 1994; Gama-Rodrigues et al., 2021), with negative impacts on biodiversity (Niether et al., 2020; Ferreira et al., 2020). Despite this, cocoa production in the cabruca system still represents one of the region's main economic activities, covering a total of ~11% of the 83 cocoa-producing municipalities in southern Bahia state (Mapbiomas, 2023).

These agroforests maintain a higher amount of large canopy trees to provide shade for cocoa trees, creating, therefore, greater structural complexity of the vegetation and consequently providing high resource availability (Cassano et al., 2009). In addition, the role of these agroforests in biodiversity conservation may be even more relevant if we consider that these agroecosystems are located in the Atlantic Forest, a biodiversity hotspot (Myers et al., 2000) highly threatened by deforestation, which has destroyed about 80% of its original vegetation (Vancine et al., 2024). However, the species diversity of social wasps associated with these agroforests remains unknown. Therefore, surveys of wasp species in this type of agricultural system can enhance our understanding of the actual geographic distribution of these insects in Brazil and assess the value of agroforests for wasp conservation in human-modified landscapes.

In our study, we aimed to identify which species of social wasps are associated with the shaded cocoa agroforests in southern Bahia, a region retaining high species diversity and endemism for various floristic and faunal groups within the Brazilian Atlantic Forest (Martini et al., 2007; Dias et al., 2014).

MATERIAL AND METHODS

Study Area

Our study was conducted in the southern region of Bahia state, Brazil, specifically in the municipalities of Arataca, Belmonte, Canavieiras, Ilhéus, Itapebi, Mascote, Santa Luzia, Una, and Uruçuca (Fig. 1; Table S1). The region is in the Atlantic Forest biome, considered a global biodiversity hotspot (Myers et al., 2000), being characterized by a hot and humid climate, with average annual temperatures of 24°C and annual precipitation ranging from 1700 to 2000 mm (Gouvêa, 1969). Given the changes in land use over the last few decades, the region is currently composed of a mosaic of environments consisting mainly of remnants of forests, cattle pastures, and shaded cocoa agroforests (Cabral et al., 2021).

Social wasp collection

We sampled social wasps in 30 cocoa agroforests from December 2022 to February 2023, a single field campaign per agroforestry. The agroforests were selected to meet the objectives of the "Eco-nomia das Cabrucas" project, whose sites were chosen to ensure a gradient of forest cover on a landscape scale, which the forest cover ranged from 4.4% to 79.4%, within a radius of 1,000 m surrounding of each agroforest. Each agroforest was spaced at least 2 km apart to ensure sampling independence, covering a total area of 5,386 km². In each agroforest, we established a transect of approximately 50 m, located about 100 m from the nearest edge. Along the transect (Fig. 1A), we deployed three flight interception traps of the Townes Malaise model, spaced approximately 50 m apart (Fig. 1B). Additionally, we installed six 500 ml plastic bottle traps (Fig. 1C) containing three types of attractive baits: guava juice, orange juice, and sardine solution. The bottle traps were installed at about 1.5 m above the ground, spaced approximately 10 m apart from each other, and the different baits were distributed alternately (Fig. 1A). We used industrialized guava and orange juices with a concentration of 50% and 35% natural juice, respectively, according to the manufacturer's specifications. The sardine solution comprised 125 g of crushed sardines and oil diluted in 1 L of water (methodology adapted from Souza et al. 2015). All traps remained installed for an uninterrupted period of about 72 hours. The specimens collected were identified using the identification keys proposed by Somavilla and Carpenter (2021) and Richards (1978) and also through comparisons with previously identified species from the Invertebrate Collection of the National Institute for Amazonian Research (INPA), where the material is deposited. The collections were carried out in accordance with Brazilian legislation, under authorization

(SISBIO 83493-1) issued by the Chico Mendes Institute for Biodiversity Conservation (ICMBio), together with permission from the landowners.

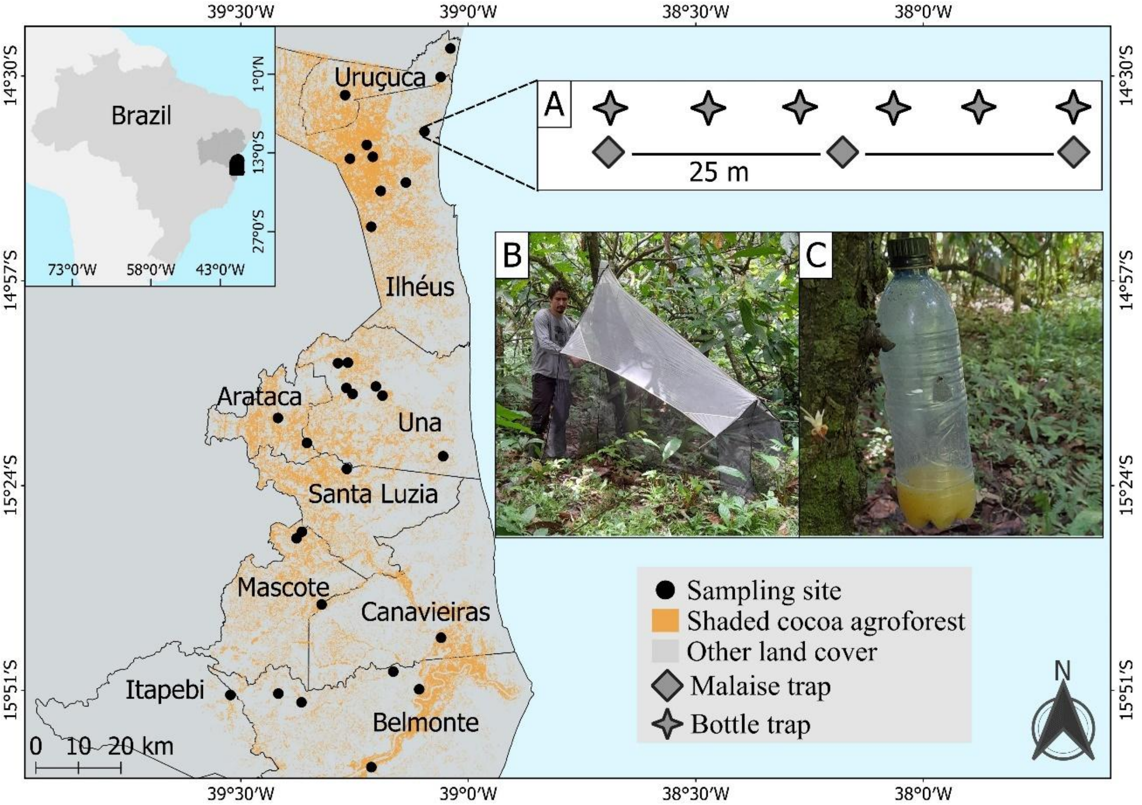

Figure 1. Location of the 30 cocoa agroforests sampled in nine municipalities in southern Bahia state, Brazil. The map was constructed using QGIS software 3.34.1 (QGIS Development Team 2023), based on the raster of overgrown cocoa agroforestry cover in the south of Bahia (Mapbiomas Cacau, 2023). Diagram representing the distribution pattern of the Malaise traps (B) and bottle traps (C) in each sampled agroforest.

Data analysis

Using the *iNEXT* package (Hsieh et al., 2016), we constructed a curve with the extrapolated species richness to assess whether increasing the sampling effort (i.e., the number of sampled cocoa agroforests) would lead to higher species richness. We employed a presence-absence matrix and extrapolated species richness to twice our sampling effort (i.e., 60 agroforest sites). The graph and extrapolated species richness were calculated using the R software (Team R Core 2018).

RESULTS

In total, we collected 363 specimens of social wasps representing nine genera and 25 species (Table 1). In particular, *Polybia* Lepeletier, 1836, *Ageleia* Lepeletier, 1836, *Mischocyttarus* Carpenter, 1993, and *Protopolybia* Ducke, 1905, comprised the genera with the highest number of species, with 10, five, three, and two species, respectively. In contrast, *Angiopolybia* Araujo, 1946, *Apoica* Lepeletier, 1836, *Leipomeles* Möbius, 1856; and *Metapolybia* Ducke, 1905, each presented a single species. We also observed that *Angiopolybia pallens* (Lepeletier, 1836), *Agelaia angulata* (Fabricius, 1804), *Agelaia centralis* (Cameron, 1907), *Polybia rejecta* (Fabricius, 1798), and *Polybia occidentalis* (Olivier, 1792) showed the highest number of individuals recorded in the cocoa agroforests, with 186, 70, 36, 19, and 12 wasps, respectively (Table 1). Together, these species accounted for 20% of the species richness observed and 89% of all individuals collected in all surveyed agroforests. We recorded, for the first time, six species for the Bahia state - *Agelaia flavipennis* (Ducke, 1905), *Polybia emaciata* Lucas, 1879, *Polybia quadricincta* Saussure, 1854*, Agelaia angulicollis* (Spinola, 1851), *Parachartegus smithii* (Saussure, 1854) and *Protopolybia acutiscutis* (Cameron, 1906), in which the three formers having been recorded for the first time in the Northeast region of Brazil and two for the Atlantic Forest biome. Based on the species accumulation curve (Fig. 3), increasing sampling effort can lead to a sharp increase in the species richness (36.2 species, confidence interval: lower = 24.1 and upper = 48.4). Although we did not search for social wasp nests, during our collections, we observed three nests of different species established in agroforests: *Angiopolybia pallens*, *Polybia* sp., and *Apoica pallens* (Fabricius, 1804) (Fig. 2C, D and E), emphasizing the capacity of this system to offer suitable sites and conditions for the establishment of these wasps' nests.

Table 1. Social wasp species recorded in 30 cocoa agroforest located in southern Bahia state, Brasil. New records for the (*) state of Bahia and (**) the Atlantic Forest.

Specie	Bottle trap	Malaise trap	Abundance (%)
Agelaia angulata (Fabricius, 1804)	9	61	70 (19.3)
Agelaia angulicollis (Spinola, 1851) * / **		1	1 (0.3)
Agelaia centralis (Cameron, 1907)	6	30	36 (9.9)
Agelaia flavipennis (Ducke, 1905) *	3		3 (0.8)
Agelaia vicina (Saussure, 1854)		3	3 (0.8)
Angiopolybia pallens (Lepeletier, 1836)	149	37	186 (51.2)
Apoica pallens (Fabricius, 1804)	1		1 (0.3)
Leipomeles dorsata (Fabricius, 1804)		6	6 (1.7)
Metapolybia cingulata (Fabricius, 1804)		1	1 (0.3)
Mischocyttarus bahiensis Zikán, 1949		1	1 (0.3)
Mischocyttarus labiatus (Fabricius, 1804)		1	1 (0.3)
Mischocyttarus santacruzi Raw, 2000		1	1 (0.3)
Parachartegus smithii (Saussure, 1854) *		1	1 (0.3)
Polybia (*Myraptera*) sp.1 White, 1941	2		2 (0.6)
Polybia belemensis Richards, 1970		1	1 (0.3)
Polybia dimidiata (Olivier, 1792)		1	1 (0.3)
Polybia emaciata Lucas, 1879 *		1	1 (0.3)
Polybia flavifrons Smith, 1857		4	4 (1.1)

Polybia jurinei Saussure, 1854	1	2	3 (0.8)
Polybia occidentalis (Olivier, 1792)		12	12 (3.3)
Polybia quadricincta Saussure, 1854 *		1	1 (0.3)
Polybia rejecta (Fabricius, 1798)	2	17	19 (5.2)
Polybia ruficeps Schrottky, 1902	2		2 (0.6)
Protopolybia acutiscutis (Cameron, 1906) * / **	1	1	2 (0.6)
Protopolybia exigua (Saussure, 1854)		4	4 (1.1)
Abundance	**176**	**187**	**363**
Species richness	**10**	**21**	**25**

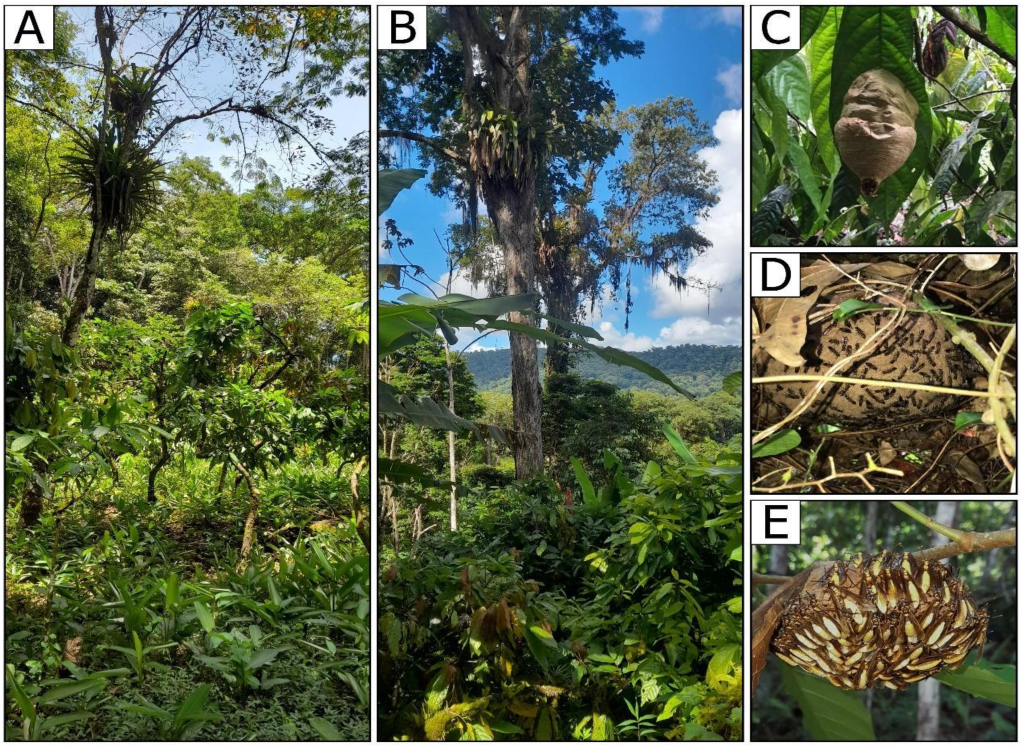

Figure 2. Shaded cocoa agroforests typically observed in southern Bahia, Brazil (A and B). Social wasp nests recorded in surveyed agroforests during our data collection: (C) *Angiopolybia pallens* (Lepeletier, 1836), (D) *Polybia* sp. Lepeletier, 1836 and (E) *Apoica pallens* (Fabricius, 1804).

DISCUSSION

As far as we know, this is the first study to describe the assembly of social wasps associated with shaded cocoa agroforests in Brazil. Our study recorded a considerable species number (n = 25), especially compared to another study conducted in native forest remnants near our studied region (Aragão & Andena, 2016). In this previous study, the authors recorded 26 social wasp species over one year of sampling using three collection methods (attractive solution, light trap, and Malaise trap). In addition to the similar number of species observed between the studies, only 10 (40%) of the 25 species observed in cocoa agroforests were shared by these forest fragments (Aragão & Andena, 2016). This suggests that, in addition to the southern region of Bahia possibly having a high richness of social wasps, in which only two studies recorded a total of 41 species, the cocoa agroforests typical of this region potentially contribute to the species pool at a regional level.

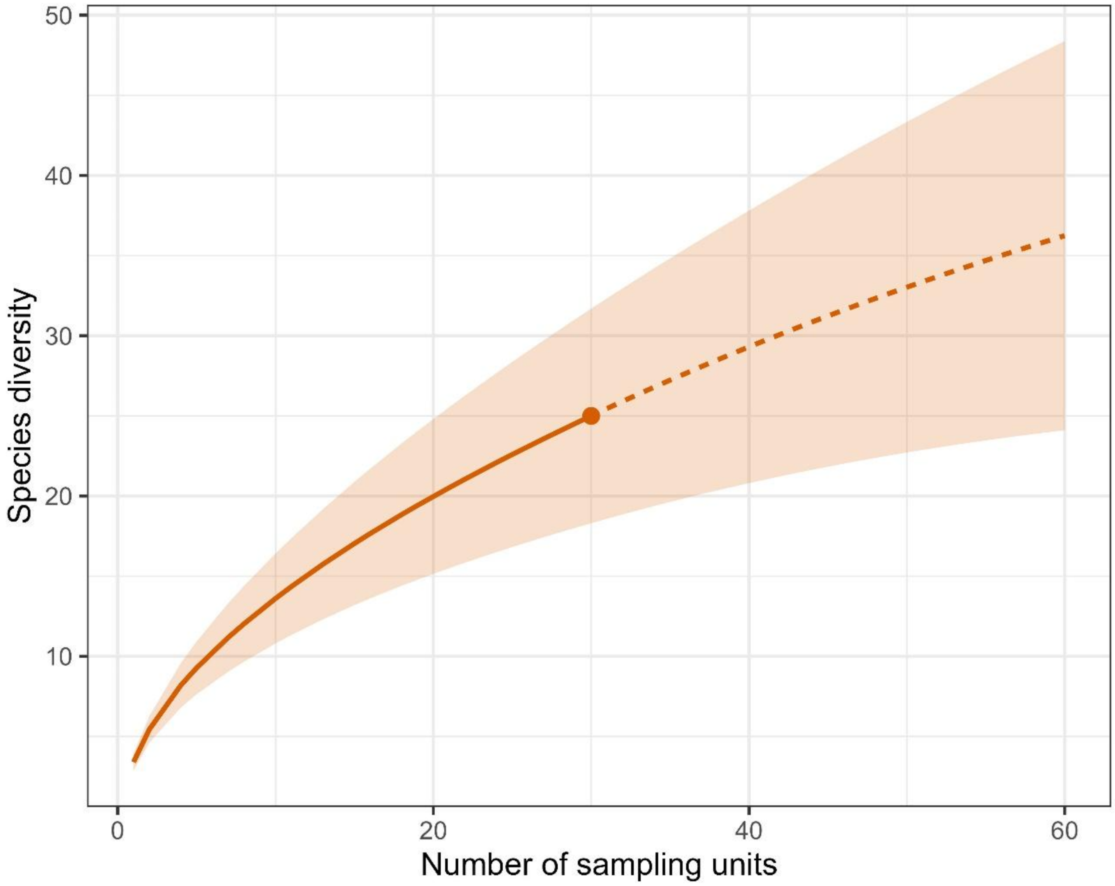

Figure 3. Species richness curve of social wasps observed (solid line) and extrapolated (dashed line) based on the number of sampling sites (i.e., 60 cocoa agroforests). The dot represents the total richness observed in the 30 sampled agroforests, and the shadow represents a 95% confidence interval.

A bibliographic survey of research about social wasps from the northeastern region of Brazil identified that 15 (~58%) of the 26 regional studies were conducted in the Bahia state (dos Santos et al., 2020). Based on these studies, 86 species of social wasps were documented for the state, representing 70% of the species known in the northeastern region of Brazil. This high species richness observed for Bahia may be associated with its vast territorial extension, Brazil's fifth largest state, and the high diversity of biomes within its territory: Caatinga, Cerrado, and Atlantic Forest (IBGE, 2024). Our study, therefore, recorded one-third of the known species for the Bahia state and one-quarter of the species recorded in northeastern Brazil. On a broader scale, a survey of Polistinae species recorded in the different phytophysiognomies of the Atlantic Forest identified a total of 170 species (Souza et al., 2020). Considering the scale of this survey and the diversity of habitats, which included everything from agroecosystems to important refuges for biodiversity, such as National Parks, cocoa agroforests presented a representative species richness, corresponding to 15% of the species richness recorded for the Atlantic Forest. Thus, as well as being the first inventory of social wasp species in cocoa agroforests in Brazil, our study suggests the potential importance of these agricultural systems for conserving Polistinae wasps in human-modified landscapes.

Regarding the general pattern observed of wasp assembly, the observed predominance of species of the tribe Epiponini was expected, given that this tribe has more than 250 species distributed in 19 genera, being the most endemic of the Neotropical region (Somavilla et al., 2021). In addition, Epiponini species are widely distributed throughout Brazil and recorded in all states of the country (Barbosa et al., 2016). However, despite the high proportion of species recorded in our study, we acknowledge the limitation regarding our sampling effort. Since sampling effort strongly influences species richness (Azovsky, 2011), maintaining traps in the field for longer periods or sampling more sites would increase the number of observed species, as evidenced by the estimated species number. For example, we did not collect any species from the Polistini tribe, genus *Polistes*. This result is unexpected since this tribe contains many species, widely distributed in Brazil and relatively common in anthropized environments (Prezoto et al., 2021). We also acknowledge that other collection methods, such as active searching, should be used to better represent social wasp species in a community (Silveira, 2002). Therefore, we suggest that future studies expand the number of sampled agroforests or increase sampling efforts within agroforests, which could contribute to new species records for this agricultural system.

Our study documented the first records of six social wasp species for the Bahia state, with three of them being recorded for the first time in the country's northeastern region. Among these new records, *A. flavipennis*, *P. smithii*, *P. emaciata*, and *P. quadricincta* were already expected to occur in Bahia since these species have been widely recorded in different biomes and Brazilian states (CTFB 2024). On the other hand, the occurrence of *A. angulicollis* and *P. acutiscutis* is more restricted in Brazil. In the case of both species, knowledge of their distribution had previously been restricted to the north of the country, except for records for Mato Grosso and Maranhão (Prezoto et al., 2021), especially for the Amazon biome. Given the absence of *A. angulicollis* and *P. acutiscutis* in the various studies conducted in the Amazon region, in large forest fragments (Somavilla et al., 2015; Gomes et al., 2020), urban fragments (Graça & Somavilla, 2019) or even agroecosystems (Somavilla et al., 2016), we can consider that both species are indeed rare. Therefore, in addition to contributing to the knowledge of the social wasp assemblage associated with cocoa agroforest, our study expands knowledge regarding the geographical distribution and occurrence of species, including species rarely observed in social wasp inventories.

In general, our findings highlighted two points warranting attention. Firstly, despite social wasps being a well-studied group with numerous studies on their behavior, ecology, and evolution (Prezoto et al., 2021), the distribution of these insect species in Brazil still presents sampling gaps (Barbosa et al., 2016). In particular, most research is still concentrated in the southeast region of Brazil, with a limited number of surveys being conducted in the northeast region (Barbosa et al., 2016). For example, the state of Sergipe does not present any published studies to date on social wasps (dos Santos et al., 2020). Second, our results demonstrated that, compared to forest remnants near our study area (Aragão & Andena, 2016), cocoa agroforests exhibit a considerable number of social wasp species. As well as providing food resources, shaded cocoa agroforests offer favorable conditions for establishing social wasp nests, as observed during our collections. Therefore, this agricultural system can act as a supplementary habitat for these insects, with important implications for species conservation and also for intensifying the provision of ecosystem services such as biological control provided by wasps (Brock et al., 2021). Despite the recognized importance of cocoa agroforests for biodiversity conservation (Cassano et al., 2009), the relevance of these systems for conservation is still underestimated, especially if we consider that these agroforests are located in the Atlantic Forest, one of the hotspots with the highest levels of habitat loss and degradation (Myers et al., 2000). Moreover, the Bahia state still presents high rates of deforestation of the Atlantic Forest (SOS et al., 2021), jeopardizing the maintenance of its biodiversity. In this harsh scenario, agroforests can act as an important refuge for native species, including social wasps. Therefore, we suggest that future studies on social wasps should focus on conducting inventories in poorly studied regions, such as Northeast Brazil, surveying both natural habitats and anthropogenic areas like agricultural systems. This information will help us understand the real geographic distribution of species and enhance our understanding of the role of agricultural systems in maintaining native forest species in human-modified landscapes.

Author contributions: José V. A. Ferreira: Conceptualization, methodology, project administration, funding acquisition, formal analysis, writing-original draft, writing-review & editing. José C. Morante-Filho: Conceptualization, methodology, supervision, project administration, funding acquisition, writing-review & editing. Alexandre Somavilla: Conceptualization, methodology, writing-original draft, writing-review & editing. Danielle Storck-Tonon: Methodology, supervision, writing-review & editing. Maíra Benchimol: Methodology, supervision, project administration, funding acquisition, writing-review & editing.

Data availability: The datasets generated and/or analyzed during the current study are available upon request to the corresponding author.

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CAPÍTULO 3

Landscape forest cover and regional context shape the conservation value of shaded cocoa agroforests for bees and social wasps

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Landscape forest cover and regional context shape the conservation value of shaded cocoa agroforests for bees and social wasps

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ABSTRACT: *Context:* The expansion of agricultural lands threatens biodiversity maintenance across the tropics. Although some agroforestry systems may be biodiversity-friendly, their conservation value likely depends on the landscape and regional contexts in which they are embedded – a poorly tested hypothesis. *Objectives:* We assessed the conservation value of shaded cocoa agroforests for bees and social wasps, and evaluated whether such value depends on the remaining forest cover at the landscape and/or regional scales. *Methods:* Using a paired design, we compared α- (species number) and β-diversity of each taxon between cocoa agroforests and neighbouring rainforests in 30 landscapes from three regions with different deforestation levels from the Brazilian Atlantic Forest. We assessed whether the species number ratio (cocoa/forest) and β-diversity related to landscape-scale forest cover, and whether such a relationship differed among regions (interacting effect). *Results:* Cocoa agroforests held more bee and wasp species than forests, and β-diversity between habitats was moderate (bees) to high (wasps). Bees' species number ratio peaked at the intermediate-deforested region, and β-diversity decreased with increasing forest cover, indicating that both land uses shared more species in more forested landscapes, especially in the high- and intermediate-deforested regions. Yet, for social wasps, β-diversity varied only within regions, with habitats sharing more species in the low-deforested region. *Conclusions:* Our findings highlight that the conservation value of shaded cocoa agroforests for bees and social wasps depends on local and regional landscape forest cover. With cocoa agroforest being highly permeable matrix which increases with higher forest cover especially, for bees in high- and intermediate-deforested regions.

Key-words: agricultural systems, biodiversity-friendly matrices, deforestation, insect conservation, land sharing

INTRODUCTION

Biodiversity provides key ecosystem services for human well-being, so its conservation represents one of the most important challenges facing humanity in this century (Cardinale et al. 2012). Over the last decades, the foremost strategies to promote biodiversity conservation have been primarily focused on native habitat protection and restoration (Ellis 2019; Riva et al. 2024). Indeed, establishing protected areas and promoting restoration programs are vital to curb the accelerated rates of species loss especially in tropical areas (Edwards et al. 2019). However, as deforestation has been mainly caused by agricultural activities, some researchers advocate in implementing land-sparing strategies, i.e., setting aside lands used for intensive farming practices while other lands are used for conservation (land-sparing approach; Green et al. 2005; Phalan 2018). Conversely, a strategy referred to as land-sharing suggests that human-modified landscapes should consist of mosaics of diverse environments, incorporating biodiversity-friendly agricultural areas and native habitats (Green et al. 2005; Phalan et al. 2011). Therefore, combining forest preservation with biodiversity-friendly anthropogenic matrices may lead to conservation outcomes, which can be achieved by integrating biodiversity maintenance with production in agricultural lands (Perfecto and Vandermeer 2010; Melo et al. 2013; Mendenhall et al. 2016; Arroyo-Rodríguez et al. 2020).

Regardless of the conservation strategy adopted, the number of species retained in anthropogenic landscapes tends to be especially influenced by the amount of habitat at the landscape scale (Watling et al. 2020; Arroyo-Rodríguez et al. 2020). As predicted by the ‘habitat amount hypothesis’ (Fahrig 2013), increased habitat availability in the landscape favours increased taxonomic diversity (higher conservation value). However, the importance of matrix quality for wildlife has also been highlighted in several theoretical models (see e.g. landscape supplementation and complementation hypotheses, neighbouring effect, and cross-habitat spillover hypothesis: Dunning et al. 1992; Tscharntke et al. 2012), and increasingly verified by empirical research (Gascon et al. 1999; Galán-Acedo et al. 2019). This is the case of complex agroforestry systems, such as shaded cocoa agroforests, which produce cocoa under the shade of canopy trees, thus providing important resources to native species (Kremen and Merenlender 2018; Silva et al. 2020; Gama-Rodrigues et al. 2021). Since these agroforests can act as supplementary habitat for several forest species, the spillover of organisms between forest patches and shaded cocoa agroforests can influence community structure and associated processes

(Tscharntke et al. 2012; Boesing et al. 2018), such as pollination (Ricketts et al. 2008) and biological pest control (Landis et al. 2000). However, the conservation value of shaded cocoa agroforests likely depends on the amount of remaining forest cover at the landscape scale (Martínez-Penados et al. 2024) and/or on the disturbance level at the regional scale (Pardini et al. 2010).

Bees and social wasps are closely related insects that can use agricultural landscapes, where they play important roles for ecosystem functioning, including the delivery of ecosystem services (Ollerton et al. 2011; Giannini et al. 2020; Prezoto 2021). For example, bees are key pollinating agents and the conservation in the proximity of crop are fundamental for increasing agricultural productivity (Giannini et al. 2020; González-Chaves et al. 2022). Social wasps also provide valuable benefits for agriculture, as they are important predatory agents for biological control (Brock et al. 2021). However, the conservation value of cocoa agroforests for bees and wasps is not well understood (but see Klein et al. 2004; Hoehn et al. 2010).

The cocoa plantations from southeastern Bahia state, Brazil, are typically located under the shade of canopy trees. In fact, because of its high structural complexity, these agroforests can harbour a wide range of resources for native species, including birds (Cabral et al. 2021), bats (Faria and Baumgarten 2007), and ground mammals (Ferreira et al. 2020a). This implies that these agroforests can be of high conservation value, especially because they are located in a biodiversity hotpoint within the Atlantic Forest hotspot (Martini et al. 2007), where only ~23% of its original forest cover remains, but a large number of endemic species are preserved (Vancine et al. 2024). In addition, such conservation value may depend on the landscape and regional contexts in which they are embedded. For example, Cabral et al. (2021) demonstrated that forest bird diversity in shaded cocoa agroforests increases with increasing the percentage of forest cover in the surrounding landscape. Likewise, seed dispersal (Araújo-Santos et al. 2021) and medium- and large-sized mammal species richness (Ferreira et al. 2020a) can also be enhanced in cocoa agroforests embedded in more forested landscapes. However, to our knowledge, no study to date has assessed whether the conservation value of cocoa agroforests for invertebrates, including bees and wasps, can depend on the percentage of forest cover at the landscape scale, and whether such dependence can vary across regions with different deforestation levels.

Here, we sampled bees and social wasps in both shaded cocoa agroforests and adjacent native forests in 30 landscapes embedded within a gradient of landscape forest cover across three regions with different deforestation levels in the Brazilian Atlantic Forest. We particularly assessed (i) the conservation value of cocoa agroforests for each taxon, and (ii) the role of regional and landscape forest cover in modulating such a conservation value. To this end, we first tested for differences in species number (i.e. number of species per sampling unit) between pairwise cocoa agroforests and forests. We then assessed the additive and interacting effect of forest cover and region (three categories: high, intermediate and low deforestation levels) on the species number ratio (cocoa/forest) and beta diversity of each taxon. Given the high structural complexity of shaded cocoa agroforests (Faria and Baumgarten 2007; Cassano et al. 2009), which may provide food and nest resources for bees and wasps, we expected to find similar species number and composition in both environments. However, as species diversity in cocoa agroforestry likely depends on sources of individuals from neighbouring forest, we expect that the conservation value of agroforests will decrease in landscapes with lower forest cover, especially in the most deforested region. Therefore, we predict that landscape-scale forest cover is positively related to species number ratio, but negatively related to beta diversity, especially in highly deforested regions.

METHODS

Study regions

This study is part of the "Eco-nomia das Cabrucas" project, which assesses the conservation value of shaded cocoa agroforests (locally known as ‘cabruca’) in the southern Bahia region, Brazil (e.g. Araújo-Santos et al. 2021; Cabral et al. 2021; Fig. 1). Shaded cocoa plantations are distributed across the Atlantic Forest biome, which has a hot (mean annual temperature ≈ 24 °C) and humid climate, with annual precipitation ranging from 1700 to 2000 mm, without a clear dry season (Gouvêa 1969). This species-rich biome has a large number of endemic plant and animal species, but it is also one of the most deforested in Brazil (Faria et al. 2021). Cocoa production was the main economic activity in southern Bahia in the 1960s and 1970s, but the introduction of the witches' broom fungus (Moniliophthora perniciosa) decreased cocoa production in the 1980s and 1990s (Alger and Caldas 1994). Despite such a decrease in cocoa production, this anthropogenic land use is still dominant (Fig. 1), covering about 22% of the studied area. However, the remaining forest and cocoa plantations are not evenly distributed (Fig. 1).

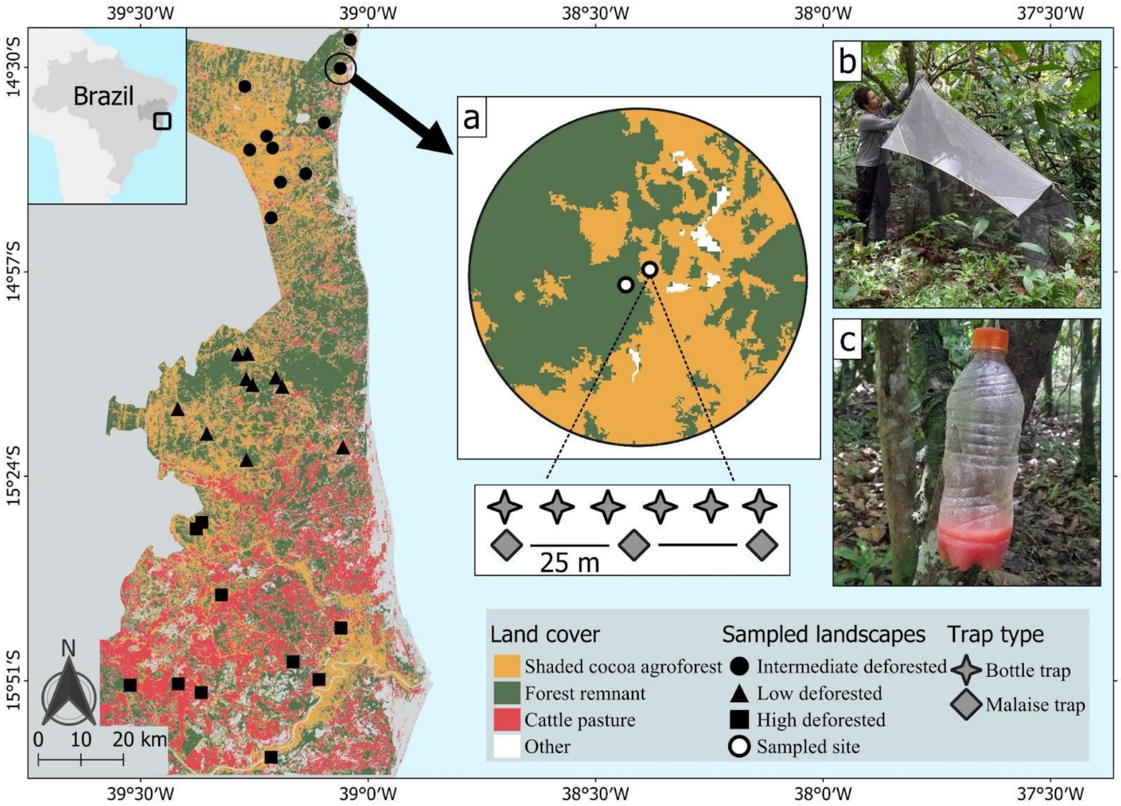

Figure 1 Location of sampled landscapes across regions with different deforestation levels (high deforested = squares; intermediate deforested = triangles; low deforested = dots). In each landscape, we sampled bees and social wasps in a cocoa agroforest (dark orange) and a neighbouring forest (dark green), within a 50 m transect (a). In each transect we located both Malaise traps (b) and bottle traps (c).

The southern region was highly deforested ("high-deforested region" hereafter), and nowadays ≈26.7% of forest cover remains, embedded in an anthropogenic matrix composed of cattle pastures (36.3%), cocoa agroforests (15.4%), and eucalyptus monocultures (4.6%). At the other extreme, the presence of two large reserves – the Una Biological Reserve (18,715 ha) and Una Wildlife Refuge (23,262 ha) – in the low-deforested region has contributed to the maintenance of ≈54.1% of forest cover. Here, the anthropogenic matrix is dominated by shaded cocoa agroforest (24%). Finally, the intermediate-deforested region, in the north, maintains ≈43% of forest cover and 33% of shaded cocoa agroforest.

Study design and insect collection

We sampled bees and social wasps from December 2022 to February 2023 using a paired design. We conducted the collections during this period because we assumed that the higher average temperatures (Liuth et al. 2013) and the peak flowering of some tree species in southern Bahia at this time of year (Vinet & Zhedanov 2013) could favour the activity of bees and wasps, therefore likely increasing our capture success. In particular, we selected 30 cocoa agroforest sites distributed across the three regions (i.e. 10 sites per region; Fig. 1), and then selected a paired site within the closest forest (Fig. 1a). Due to logistical problems, it was not possible to keep the distance between each pair of sites fixed (mean isolation distance ± SD = 397 ± 195.2 m, range = 148 to 827 m), but we take it into account in our statistical models (see below). Within each site, we established a 50-m transect 100 m apart from the nearest forest or cocoa agroforest edge to avoid potential confounding edge effects (Fig. 1a). In each transect, we deployed three Malaise traps, Townes model (Fig. 1b), separated 25 m between each other (i.e. at distances 0, 25, and 50 m). Malaise traps are efficient for Hymenoptera and can be used for collecting bees (Prado et al. 2017) and wasps (Somavilla and De Oliveira 2017). However, as a complementary method, we also placed six 500-ml plastic bottle traps distributed along the transect and spaced ~10 m apart from each other (Fig. 1c) with three types of baits (about ~150 ml of bait per trap): (i) orange juice, (ii) guava juice, and (iii) sardine solution. Each bait type was alternated among traps. The guava and orange juice baits consisted of industrialised juice, with a concentration of 50% and 35% of natural juice, respectively (according to manufacturer specifications). The sardine bait consisted of a solution of crushed sardines and water, at a concentration of ~125 g of sardines and oil / 1 litre of water (adapted from Souza et al. 2015). This method is recommended to complement the collection of social wasps (Souza et al. 2015). However, given that our collections were standardised and that some bees were also collected using this methodology, we included in our database individuals captured from both bees and social wasps. All Malaise and bottle traps remained active for 72 consecutive hours and simultaneously sampled bees and social wasps in both habitat types within each landscape. All collected individuals were identified by A.S., J.A.S., T.M. and M.L.O., who are experts in both taxa, and deposited in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Brazil). Governmental Licence was previously obtained by the ICMBIO under the number 83493-1.

Forest cover at the landscape scale

We measured the percentage of forest cover in the landscape surrounding each pair of sites, i.e. taking the midpoint between both sampling sites as the centre of the landscape. To this end, we used two sources of information, the Mapbiomas Collection 7 (Mapbiomas 2021) and MapBiomas Cacau (Mapbiomas 2023), which are freely available land cover and land use maps developed by a multi-institutional Brazilian network involving universities, NGOs, and technology companies. This was necessary because in shaded agroforests, cocoa trees are grown under the shade of emergent trees, resulting in a structure with some elements of a native forested area. As a consequence, the MapBiomas Collection 7 mapping does not distinguish forest and shaded cocoa agroforests. Therefore, to solve this problem, we used a combination of both mappings (MapBiomas Cacau and Collection 7) to estimate only the forest cover, which included remnants of primary and secondary forest. The processing of satellite images and quantification of forest cover were carried out with the QGIS software (QGIS Development Team 2024).

As we do not know a priori the landscape size that best predicts the response of bees and social wasps to landscape forest cover, we measured the percentage of forest cover across different-sized buffers, i.e. in concentric radii of 1000, 1250, 1500, 1750, and 2000 m. The minimum radius of the buffers was defined to include the average dispersal capacity of bees and social wasps, which generally do not exceed distances of more than 1000 m (Zurbuchen et al. 2010; Prezoto 2021). Moreover, this was the minimum buffer size needed to encompass the sample sites in the habitats (forest and cocoa agroforest) within the landscape. We then used the multifit function (Huais 2018) to select the scale of forest cover effect (i.e. the scale at which forest cover had the strongest effect on each response variable; Jackson and Fahrig 2015; Online Resource 1). To this end, we assessed the effect of forest cover on each response variable and each insect group with Generalised Linear Models (GLMs), and then compared the obtained models across scales using the Akaike Information Criterion (AIC). In all response variables but one (bee beta diversity) forest cover effects were almost the same across scales (i.e. ΔAIC < 0.7, in all cases; Online Resource 1). For the beta diversity of bees, the greatest effect of forest cover was predicted in 1000-m radius landscapes. Therefore, we selected this landscape size as the best fitting scale for all response variables because it also had the advantage of preventing spatial overlap among landscapes, which contributes to increasing independence among sampling sites (Eigenbrod et al. 2011). Importantly, at this scale, the selected landscapes encompassed a wide range of the forest cover gradient (i.e. 8.5-60.7% in the high-deforested region; 9.2-78% in the intermediate deforested region; 23.3-82% in the low-deforested region). In addition, we also detected that forest cover was significantly correlated with shaded cocoa agroforests ($r = -0.61$, $p < 0.001$) in 1000-m radius landscapes.

Data analyses

Considering that bees and social wasps may respond differently to habitat modification, we conducted all analyses separately for each taxon. We also calculated the species number (i.e. number of species recorded in each site), and tested for differences between habitats (i.e. cocoa agroforest vs forest) with GLMMs. We built a model for each region (i.e. high-deforested, intermediate-deforested, and low-deforested), using the number of species as the response variable, the habitat type as a fixed factor and the landscape (which includes an agroforest and the neighbouring forest remnant) as a random factor. We used the Poisson distribution for all models, which is recommended for count data (Crawley 2012). Using the DAHRMa package (Hartig 2022), we verified the suitability of the models, considering the overdispersion and heteroscedasticity of the residuals. In particular, we assessed the additive and interacting effect of forest cover and region on two response variables: (i) the species number ratio, and (ii) beta diversity. The species number ratio is the number of species in the cocoa agroforest site divided by the number of species in the neighbouring forest site. Note that a ratio > 1 indicates that the cocoa agroforest site holds more species than the neighbouring forest site, whereas a ratio < 1 indicates the opposite. As suggested for continuous response variables (Crawley 2012), we fixed a Gaussian distribution error to these GLMs. When the categorical factor (region) was significant, we used the emmeans package (Lenth 2024) as a post-hoc test to identify the regions that differed from each other. To account for the potential confounding effect of inter-site (cocoa agroforest to forest sites) distance into the models, we included this covariable in the models, after verifying that forest cover, region and inter-site distance were independent predictors (variance inflation factor, VIF < 3). We also used the DHARMa package (Hartig 2022) to verify that the residuals of the models followed a Gaussian distribution and that there was no overdispersion or heteroscedasticity in the models. We followed a similar analytical procedure to assess the effect of forest cover and region on beta diversity between paired sites. We considered total beta diversity based on presence-absence data (Jaccard dissimilarity, βJAC), and also the nestedness (βJNE) and turnover (βJTU) components to assess whether changes in species dissimilarity were mainly driven by differences in the number of species (gain or loss of species) between sites, or by the replacement of species, respectively (Baselga 2010). All beta diversity indexes were calculated with the Betapart package (Baselga and Orme 2012). As they varied from 0 to 1, we fixed a beta distribution family with the betareg package (Cribari-Neto and Zeileis 2010). We considered all results with a p-value ≤ 0.05 to be significant. The graphs were built with the ggplot2 package (Wickham 2016) and all analyses were conducted with R version 4.3.2 (R Core Team 2023).

RESULTS

In total, we sampled 514 bees from 44 species, and 540 social wasps from 33 species. The most abundant bee species in cocoa agroforests were Partamona sp.1 (84 individuals), Partamona sp.3 (27), Trigona spinipes (24), Apis mellifera (19), and Trigona gr. fuscipennis (15). Together, these five species accounted for 66.3% of all bees collected in the cocoa agroforests. In the forests, the top five most abundant bees were Partamona sp1 (100 individuals), Trigona braueri (71), Plebeia sp.1 (21), Megalopta sp.1 (13), and Partamona sp.3 (13), which totalled 84.2% of bee individuals sampled in the forest sites (Online Resource 2). The number of bee species was higher in cocoa agroforests (38 species) than in forest (21 species), with 23 species being exclusive to cocoa agroforests, and 6 species exclusive to forests (15 species were recorded in both habitats) (Fig. 2).

Regarding social wasps, the top five most abundant species in cocoa agroforests were Angiopolybia pallens (186 individuals), Agelaia angulata (70), Agelaia centralis (36), Polybia rejecta (19), and Polybia occidentalis (12), totalling 89% of all social wasps recorded in cocoa agroforests. The most abundant social wasp species in the forest were Angiopolybia pallens (84 individuals), Agelaia angulata (41), Agelaia centralis (25), Agelaia flavipennis (5), and Leipomeles dorsata (3), totalling 89.3% of all wasps collected in forests (Online Resource 2). The total number of species was also higher in cocoa agroforests (25 species) than forests (17), and the number of exclusive species was two-times higher in cocoa agroforests sites (16 species) than in forests (8), with 9 species showing a shared distribution (Fig. 2).

The average number of species was higher in cocoa agroforests than in forests for bees, although this pattern is dependent on the region assessed (Fig. 3). We observed that the number of bee species is greater in agroforests located in the high ($\beta = -0.59$; $p = 0.03$) and intermediate deforested regions ($\beta = -0.58$; $p = 0.006$), and was similar in the region with low deforested ($\beta = -0.04$; $p = 0.89$). For social wasps, the number of species did not differ between habitats in the three regions (high: -0.54; $p = 0.07$; intermediate: -0.18; $p = 0.47$; low: -0.16; $p = 0.53$). Total beta diversity values between cocoa agroforests and forests were moderate in bees (βJAC = 0.66) and relatively high in social wasps (βJAC = 0.73). When assessing the relative contribution of species turnover (βJTU) and nestedness (βJNE) to total beta diversity (βJAC), we found that in both taxa, beta diversity was principally related to a high species turnover between land covers (bees: βJTU = 67%, βJNE = 33%; social wasps: βJTU = 88%; βJNE = 12%).

Regarding the relative effect of forest cover and region on bee assemblages (Table 1), the species number ratio differed significantly among regions ($\chi^2 = 7.43$, $p = 0.01$), being significantly higher in the intermediate deforested region than in the low deforested region (Fig. 4a). Yet, the species number ratio was weakly related to landscape forest cover, and such a weak relationship was independent of the region (i.e. see a non-significant interaction effect in Table 1). Furthermore, the inter-site distance did not affect the species number ratio of bees. Conversely, bee beta diversity (βJAC) decreased with increasing landscape forest cover ($\chi^2 = 3.96$, $p = 0.05$; Fig. 4b). However, the effect of forest cover depended on the region ($\chi^2 = 20.42$, $p < 0.01$), being negative only in the high and intermediate deforested regions (Fig. 4c). The turnover component (βJTU) of bee beta diversity was also negatively related to forest cover ($\chi^2 = 4.70$, $p = 0.03$; Fig. 4d), and differed among regions ($\chi^2 = 6.26$, $p = 0.04$; Fig. 4e), tending to be lower in the intermediate deforested region than in the low deforested region. The nestedness component (βJNE) of bee beta diversity was not related to the predictor variables (Table 1).

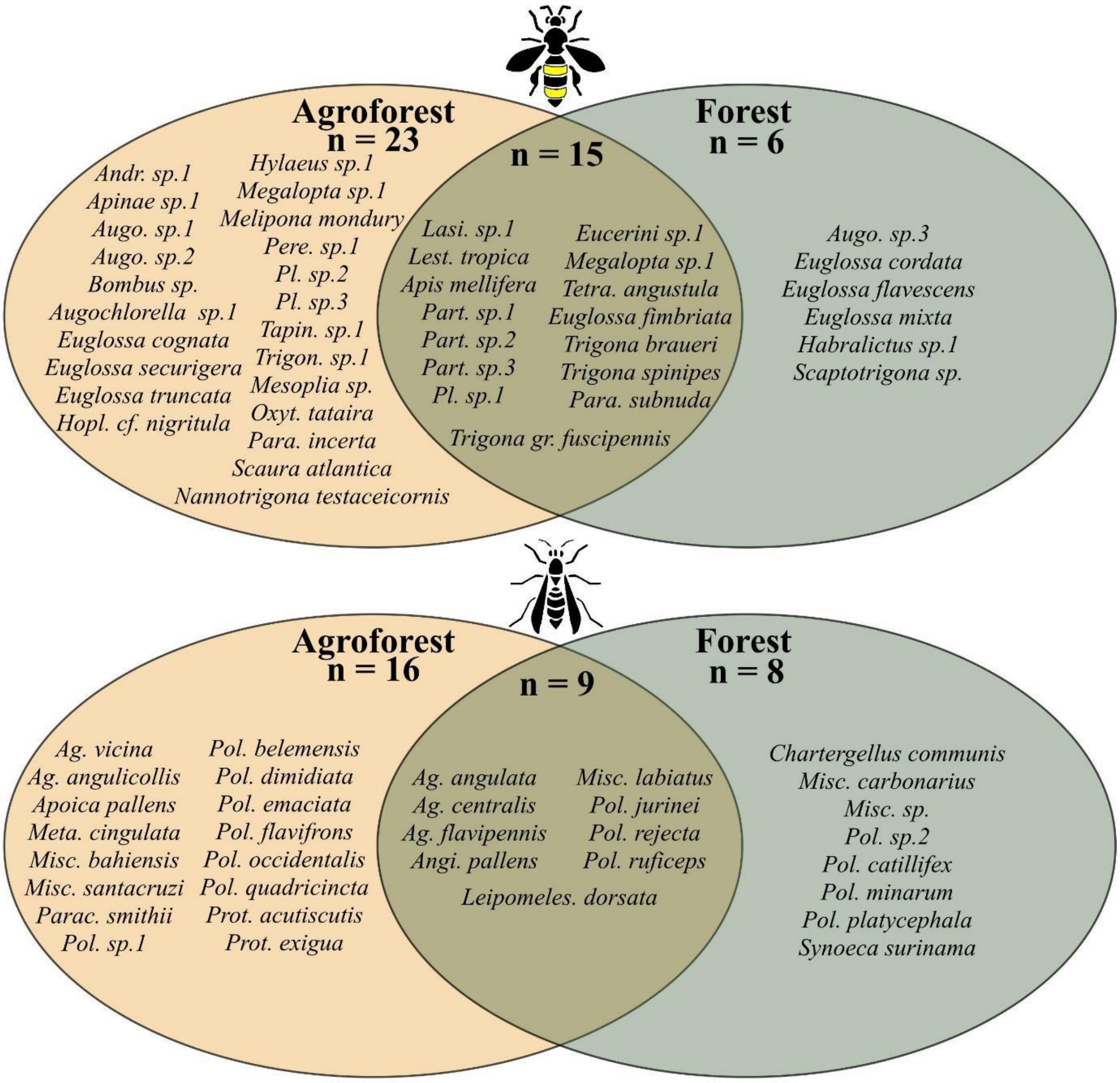

Figure 2 Venn diagram representing the occurrence of exclusive and shared species of bees (top) and social wasps (bottom) between shaded cocoa agroforestry (orange) and forests (green). Abbreviations of bee genera: Andr. = Andrenidae; Augo. = *Augochloropsis*; Hopl. = *Hoplostelis*; Pere. = *Pereirapis*; Pl. = *Plebeia*; Tapin. = Tapinotaspinini (tribe); Trigon. = *Trigonisca*; Oxyt. = *Oxytrigona*; Para. = *Paratrigona*; Lasi. = *Lasioglossum*; Lest. = *Lestrimelitta*; Part. = *Partamona*; Tetra. = *Tetragonisca*. Abbreviations of social wasp genera: Ag. = *Agelaia*; Ap; Meta. = *Metapolybia*; Misc. = *Mischocyttarus*; Parac. = *Parachartergus*. Pol. = *Polybia*; Prot. = *Portopolybia*; Angi. = *Angiopolybia*.

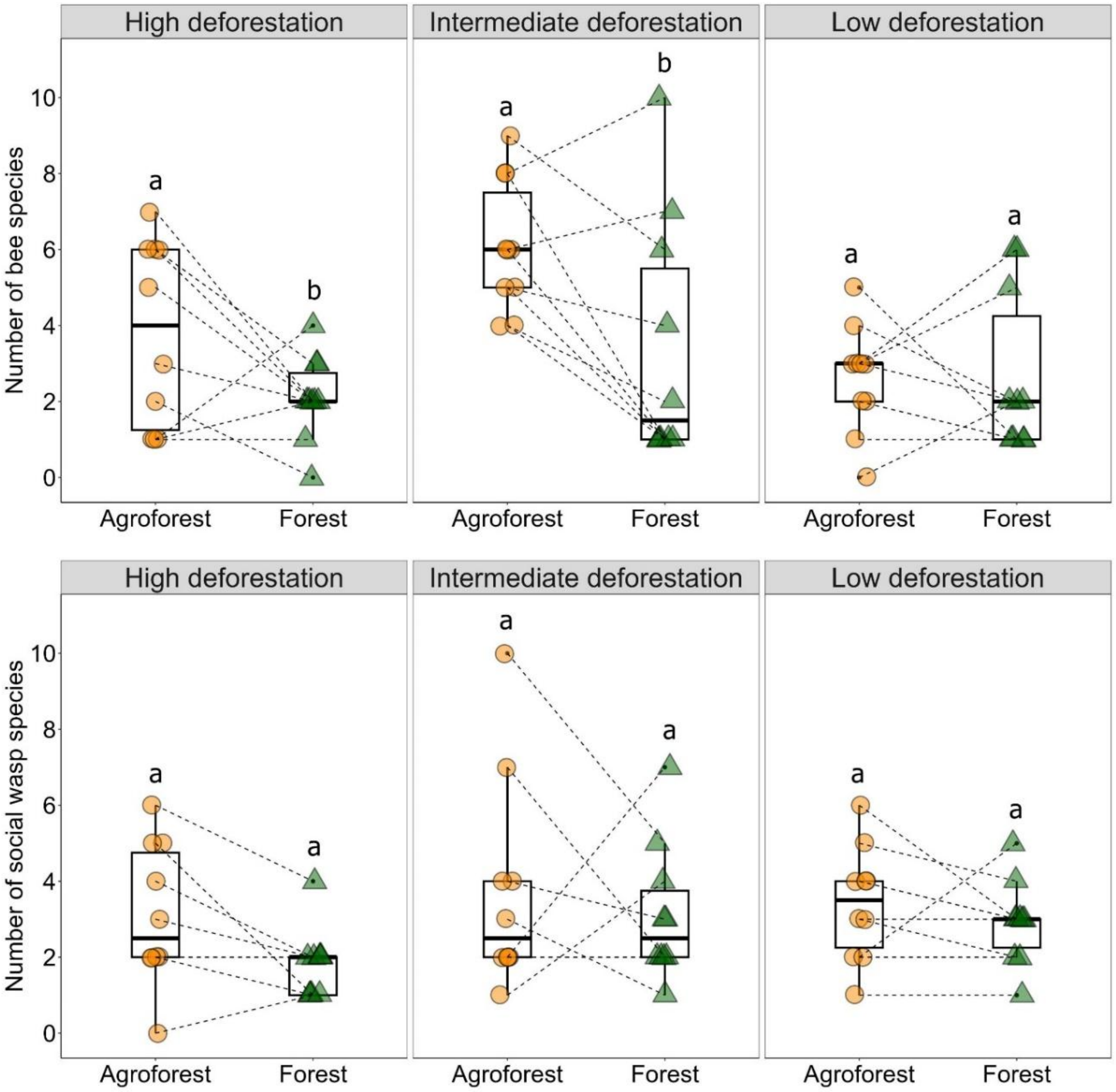

Figure 3 Species number of bees (a) and social wasps (b) sampled in 30 cocoa agroforests (orange) and 30 neighbouring forests (green), with dashed lines indicating each pairwise comparison (cocoa agroforest and forest) in the three regions with different levels of deforestation. Significant differences (p-value ≤ 0.05) in species richness between habitats within each region are indicated by different letters. The whiskers extend to the smallest and largest values within 1.5 times the interquartile range below the first quartile and above the third quartile, respectively. Values beyond these whiskers are considered outliers and are plotted as individual points. Dots and triangles are the data points.

Table 1. Additive and interacting effects of landscape forest cover and regional context on bees and social wasps sampled in shaded cocoa agroforests and nearby rainforests (paired design) in the Brazilian Atlantic Forest. We separately assessed the response of species number ratio, total beta diversity (βJAC), and its turnover (βJTU) and nestedness (βJNE) components. We included the inter-site distance between each pair of sites (cocoa agroforest to forest) to consider the potential confounding effect of this variable in the models. Significant terms ($p \leq 0.05$) are indicated in bold.

Taxon	Response	Independent variable	χ^2	p	R^2
Bees	Species number ratio	Forest cover	0.00	0.97	0.38
		Region	**10.34**	**0.01**	
		Forest cover * Region	3.17	0.21	
		Inter-site distance	2.75	0.10	
	Beta diversity (β_{JAC})	**Forest cover**	**3.96**	**0.05**	0.34
		Region	5.38	0.07	
		Forest cover * Region	**20.42**	**0.00**	
		Inter-site distance	0.37	0.54	
	Turnover (β_{JTU})	**Forest cover**	**4.70**	**0.03**	0.40
		Region	**6.26**	**0.04**	
		Forest cover * Region	4.89	0.09	
		Inter-site distance	0.29	0.59	
	Nestedness (β_{JNE})	Forest cover	3.36	0.07	0.37
		Region	2.87	0.24	
		Forest cover * Region	3.91	0.14	
		Inter-site distance	0.31	0.58	
Social wasps	Species number ratio	Forest cover	1.78	0.18	0.31
		Region	1.60	0.45	
		Forest cover * Region	0.40	0.82	
		Inter-site distance	**4.48**	**0.03**	
	Beta diversity (β_{JAC})	Forest cover	1.04	0.31	0.28
		Region	**7.43**	**0.02**	
		Forest cover * Region	0.83	0.66	
		Inter-site distance	**4.87**	**0.03**	
	Turnover (β_{JTU})	Forest cover	0.14	0.71	0.13
		Region	2.05	0.36	
		Forest cover * Region	0.65	0.72	
		Inter-site distance	0.00	0.95	
	Nestedness (β_{JNE})	Forest cover	1.04	0.31	0.17
		Region	7.43	0.02	
		Forest cover * Region	0.83	0.66	
		Inter-site distance	4.87	0.03	

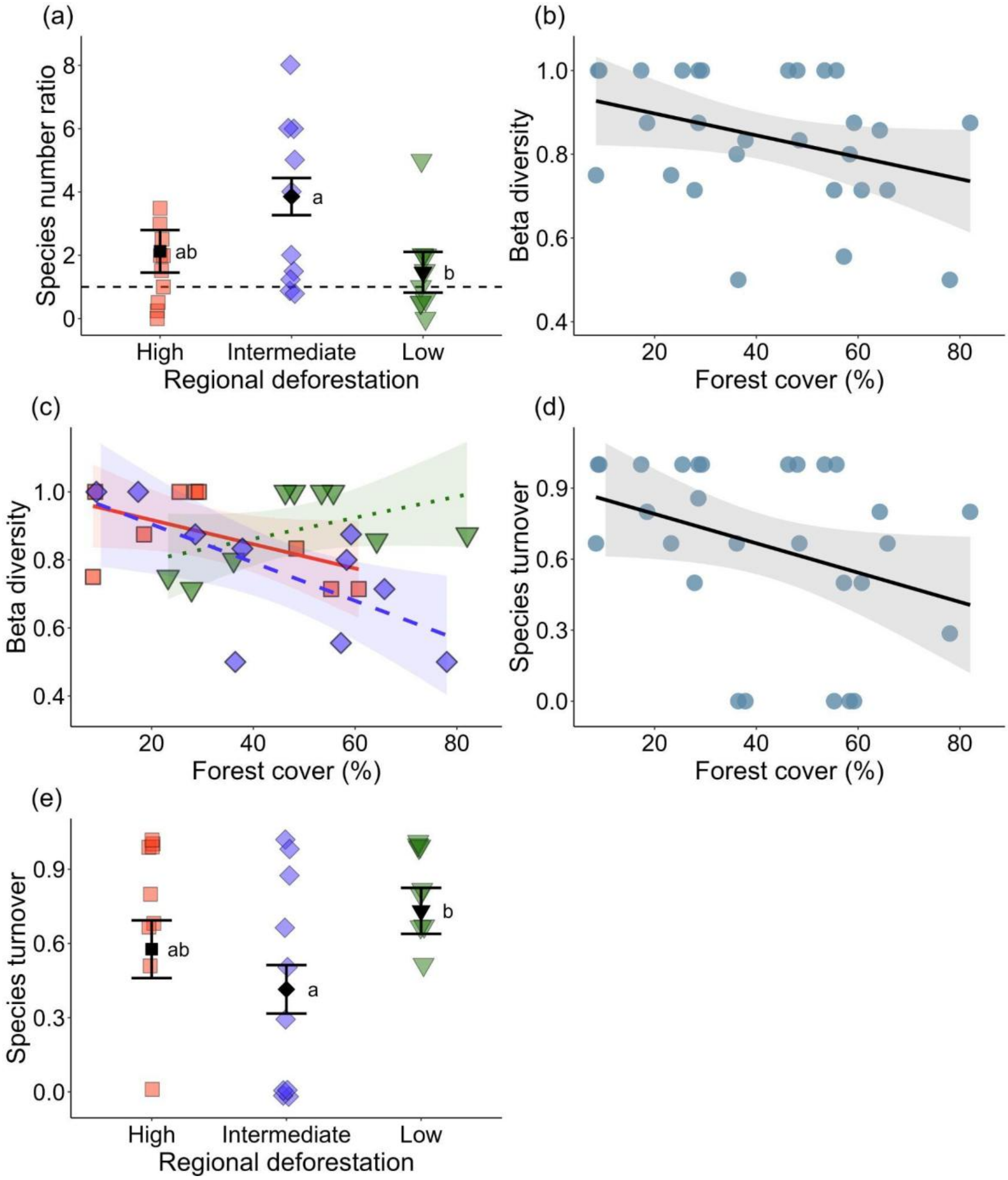

Figure 4 Effects of regional context and landscape forest cover on bee assemblages. We only show significant associations from the generalised linear models shown in Table 1. The regions that differed from each other are indicated with different letters. In panel a, values equal to or above one (dashed black line) represent landscapes in which cocoa agroforest had a number of bee species equal to or greater than neighbouring forest, respectively. The shading area represents the 95% confidence intervals. In panels a and e, the black symbols represent the estimated marginal means and the bars the standard error.

In contrast to bee assemblages, the species number ratio of social wasps was weakly related to all predictor variables, but it increased with increasing inter-site distance

($\chi^2 = 4.48$, p = 0.03; Fig. 5a). The total beta diversity of social wasps differed among regions ($\chi^2 = 7.43$, p = 0.02), being significantly higher in the high deforested region than in the low deforested region (Fig. 5b). Total beta diversity increased with increasing the distance between sites ($\chi^2 = 4.87$, p = 0.03; Fig 5c). Nevertheless, the turnover and nestedness components of beta diversity were not significantly associated with any of our predictor variables (Table 1).

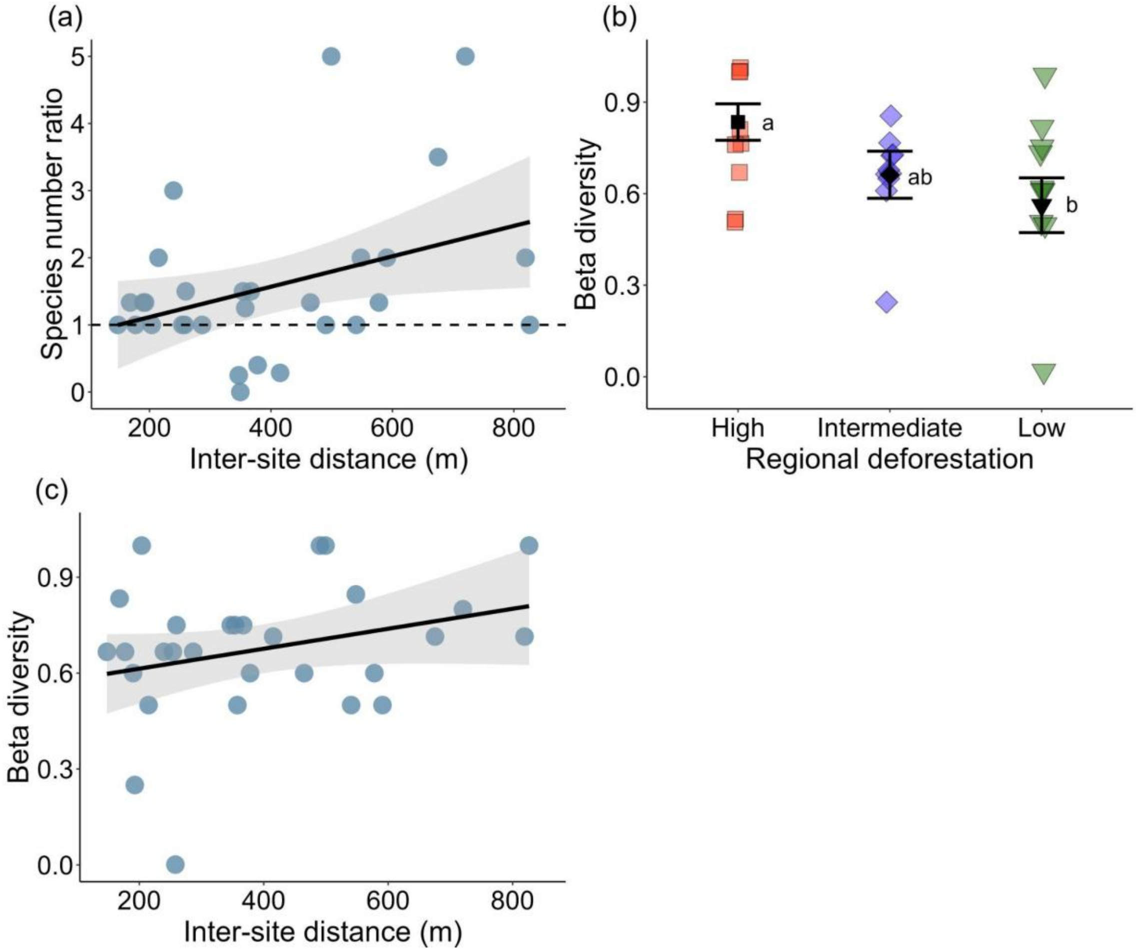

Figure 5 Effect of regional context and inter-site distance on social wasp assemblages. Only significant associations from generalised linear models (see Table 1) are shown. Regions that differ from each other are indicated by different letters. In panel a, values equal to or above one (dashed black line) represent landscapes in which cocoa agroforest had a number of social wasp species equal to or greater than neighbouring forest, respectively. The shading area represents the 95% confidence intervals. The black symbol in panel (b) represents the estimated marginal means and the bars the standard error.

DISCUSSION

This study provides several lines of evidence suggesting that, as expected, shaded cocoa agroforests are highly valuable for preserving bees and social wasps in the Brazilian Atlantic Forest. First, the number of species of bees was higher in cocoa agroforests than forest, although this pattern depends on the studied regions. Importantly, this pattern was evident at the site (alpha) and regional (gamma) scales, that is, considering each pair of sites (cocoa vs. forest) and the accumulated values by each habitat type in the entire region. Furthermore, 51% of species (52% of bee species and 48% of social wasp species) were unique to cocoa agroforests, indicating that these agricultural lands increase beta diversity, and thus, the total number of species in the entire region. However, the conservation value of cocoa agroforests for bee assemblages largely depends on forest cover at the landscape and regional scales. The species number ratio peaked in the intermediate-deforested region, and total beta diversity decreased with increasing forest cover, indicating that both habitats shared more bee species in more forested landscapes, especially in the high- and intermediate-deforested regions. For social wasps, however, only total beta diversity differed among regions, decreasing in more forested regions, probably because this regional context facilitates the species exchange between cocoa agroforests and neighbouring forests. Below we discuss the ecological and applied implications of these findings.

The high conservation value of shaded cocoa agroforests for bees and social wasps is consistent with previous works. In particular, several studies reported that these agroforestry systems can help maintain species diversity in agricultural landscapes (Cassano et al. 2009; Faria et al. 2009; Gama-Rodrigues et al. 2021). As cocoa trees are planted under the shade of canopy trees, including native species, shaded cocoa agroforests can provide resources (e.g. food, nesting sites, shelter) for a wide range of taxa, such as birds (Cabral et al. 2021), bats (Faria and Baumgarten 2007), small mammals (Silva et al. 2020), and ground mammals (Ferreira et al. 2020a). However, we expected cocoa agroforests to have a similar number of species as forests, not more, as we found for bees. So why can shaded cocoa agroforests hold more bee species than native forests? We suggest that, as argued by previous studies with similar results (Hoehn et al. 2010; Schüepp et al. 2012; Serralta-Batun et al. 2024), the high species number in cocoa agroforests can be explained by the fact that these agroecosystems are environments with intermediate levels of disturbance. Indeed, cocoa agroforests are spatially and structurally heterogeneous, as they combine resources from both native forests and anthropogenic lands. Such a combination can favour the coexistence of species with different ecological requirements (i.e. forest species, open area species, and generalist species), which may increase the total number of species in these agricultural lands (Hoehn et al. 2010; Schüepp et al. 2012; Niether et al. 2020; Serralta-Batun et al. 2024). Thus, it is also unsurprising that the species number ratio of bees was significantly higher in the intermediate deforested region, as this region showed the highest amount of cocoa plantations, covering approximately 33% of the territory. We can therefore conclude that shaded cocoa agroforests may contribute to the conservation of bee diversity.

Two important findings suggest, however, that bee assemblages in shaded cocoa agroforests are likely to depend on the source of individuals (and species) from neighbouring forests. On the one hand, we found the lowest species number ratio in the low-deforested region, probably because this regional context increases connectivity (Fahrig 2013), facilitating the exchange of individuals and species between cocoa agroforests and forest (see the cross-habitat spillover hypothesis; Tscarntke et al., 2012). Thus, both habitat types tend to converge in species number in more forested regions. Importantly, not only species number but also species composition converged with increasing forest cover, as total beta diversity and its species turnover component related negatively to landscape forest cover. In other words, the composition and structure of bee assemblages seem to depend on the remaining forest cover, so preserving forest cover is paramount, especially for bees.

This does not mean, however, that cocoa agroforests are 'sink' habitat (sensu Dunning et al., 1992) that depends on the source of individuals from the forest. Our findings suggest that these agroforestry systems may be suitable habitats for some bee species. Firstly, the number of species whose distribution was restricted to a single habitat type was three times higher in cocoa agroforests than forests. As argued above, this can be explained by the very high heterogeneity of shaded cocoa agroforests, which can provide important resources (e.g. food, nesting places) for bees (Jha and Vandermeer 2010). For example, eusocial bees particularly depend on this heterogeneity, as they build their nests in pre-existing cavities, such as those found in the hollows of older trees (Morato and Martins 2006; Visick and Ratnieks 2023), which tends to be more abundant and diverse in forests. However, managed habitats, such as agroforests, can offer a greater quantity of floral resources than forests (Hoehn et al. 2010), and provide valuable substrate for nest building. In fact, all but one (Scaptotrigona sp.) eusocial bee species were sampled in cocoa agroforests, and almost half were exclusively recorded in this agroecosystem. Although we cannot rule out that some of these species could have dispersed from the nearby forest, which was in average only 397 (±195.2 m) away, we observed Meliponini nests in cocoa agroforests, and sampled several small-sized species (e.g. Plebeia spp.) which are known to have low vagility (Greenleaf et al. 2007). Therefore, it is reasonable to hypothesise that cocoa agroforests are not only used as temporary habitat, but also permanently by some bee species, especially eusocial species.

Unlike bees, the conservation value of cocoa agroforests for social wasps was largely independent of the landscape and regional context. This finding may be explained by the generalist habit of social wasps, which are considered opportunistic predators that thrive in a range of habitats, including farmlands (Richter 2000; Schüepp et al. 2012; Michelutti et al. 2017; Ferreira et al. 2020b). In fact, they can feed on a wide variety of prey, especially insects, which can increase its abundance in anthropogenic landscapes (Prezoto et al. 2019). The shaded cocoa agroforests also offer large quantities of ripe fruit, such as jackfruit and cocoa, which are important sources of carbohydrates for this group of insects (Richter 2000; Prezoto 2021). Agroforests can also offer suitable nesting sites for these wasps, as suggested by our observation of three species (Angiopolybia pallens, Apoica pallens, and Polybia sp.) building nests in the studied cocoa agroforests. Therefore, cocoa agroforests can be suitable habitat for this group, making it less dependent on the remaining forest cover at the landscape and regional scales. This does not imply, however, that social wasp assemblages in cocoa agroforests are completely independent of the regional context. Indeed, total beta diversity decreased in more forested regions, probably because this regional context favours the cross-habitat spillover of species (Boesing et al. 2018). Although additional studies (e.g. with capture-recapture methods) are needed to accurately test this hypothes is, it was also supported by the significant positive effect of inter-site distance on total beta diversity and species number ratio, as these two associations imply that the closest pairs of sites tended to converge in species composition and number of species.

Taken together, our findings have critical applied implications, which can be used to design optimal landscape scenarios for biodiversity and humans (Melo et al. 2013; Arroyo-Rodríguez et al., 2020). First, our study underscores the high conservation value of shaded cocoa agroforests for both taxa in the Brazilian Atlantic Forest. These agroforestry systems seem to be suitable habitats for bees and social wasps, which can provide key ecosystem services to local communities, such as pollination (Ricketts et al. 2008; Toledo-Hernández et al. 2017) which, despite the need for more evidence, is possibly carried out mainly by small bees (Maia-Silva et al. 2024), and biological pest control (Landis et al. 2000). Thus, public policies should avoid the conversion of these agroforestry systems to more intensive production systems such as cocoa monocultures, which tend to be unfavourable for biodiversity (Niether et al. 2020). However, we also emphasise the importance and role of forest remnants for the conservation of bees and social wasps, since native habitats provide a greater diversity of the resources required by these taxa and are capable of retaining strictly forest species. In addition, the conservation value of shaded agroforestry systems may depend on the remaining forest cover at the landscape and regional scales, which can be important sources of species, especially for bees. Although there is no information on the minimum amount of forest cover that should be preserved in the entire region to preserve these two taxa, based on previous studies of other taxa (Banks-Leite et al. 2013; Rigueira et al. 2013; Morante-Filho et al. 2015; Arroyo-Rodríguez et al. 2020, 2021; Brindis-Badillo et al. 2022), we suggest that a conservative approach might be preserving ≥30-40% of forest cover. Our results support this approach, as we found that even the high-deforested region (≈27% of forest over) was highly valuable for preserving bees and social wasps.

Author contributions J.V.A.F. and M.B. developed the idea of the study, with support from V.A.R., J.C.M.F and D.S; J.V.A.F. and M.B. obtained financial support; J.V.A.F. collected and analysed the data with guidance from all coauthors; A.S., J.A.S., T.M. and M.L.O identified the species. All authors made substantial contributions to the intellectual content, interpretation and editing of the manuscript.

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Conflict of interest: None.

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SUPPLEMENTARY INFORMATION

Online Resource 1. Scale of effect of forest cover on each response variable and insect group. We assessed the effect of forest cover across different scales with generalised linear models, and selected the scale at which forest cover best predicted each response (lowest AIC, highlighted with boldface).

Response variables and insect groups	Landscape size (radius, m)	AIC	ΔAIC	p value
bee species density ratio	**2000**	**132.000**	**0.000**	**0.691**
	1750	132.074	0.074	0.764
	1500	132.154	0.154	0.898
	1250	132.172	0.172	0.988
	1000	132.172	0.172	0.990
bee beta diversity	2000	-1.385	2.318	0.269
	1750	-1.507	2.196	0.248
	1500	-1.923	1.780	0.191
	1250	-2.790	0.913	0.114
	1000	**-3.703**	**0.000**	**0.068**
social wasp species density ratio	2000	95.040	0.200	0.030
	1750	95.170	0.330	0.032
	1500	**94.840**	**0.000**	**0.027**
	1250	95.002	0.162	0.029
	1000	95.490	0.650	0.038
social wasp beta diversity	**2000**	**-2.215**	**0.000**	**0.181**
	1750	-2.172	0.043	0.186
	1500	-2.149	0.066	0.188
	1250	-1.944	0.271	0.214
	1000	-2.050	0.165	0.200

Online Resource 2 Presence of different bee and social wasp species in cocoa agroforest sites and forest sites in the southern region of Bahia state. Proportion of occupied sites in each land-use type is also indicated in parenthesis.

Species	**Cocoa agroforests**	**Forest**	**Occurrence**
Bees			
Andrenidae sp.1	1 (0.3)	-	Cocoa
Apinae sp.1	1 (0.3)	-	Cocoa
Apis mellifera	8 (2.4)	2 (0.6)	Cocoa / Forest
Augochlorella sp.1	1 (0.3)	-	Cocoa
Augochloropsis sp.1	1 (0.3)	-	Cocoa
Augochloropsis sp.2	1 (0.3)	-	Cocoa
Augochloropsis sp.3	-	2 (0.6)	Forest
Bombus sp.	1 (0.3)	-	Cocoa
Eucerini sp.1	1 (0.3)	1 (0.3)	Cocoa / Forest
Euglossa cognata	1 (0.3)	-	Cocoa
Euglossa cordata	-	1 (0.3)	Forest
Euglossa fimbriata	1 (0.3)	1 (0.3)	Cocoa / Forest
Euglossa flavescens	-	1 (0.3)	Forest
Euglossa mixta	-	1 (0.3)	Forest
Euglossa securigera	1 (0.3)	-	Cocoa
Euglossa truncata	1 (0.3)	-	Cocoa
Habralictus sp.1	-	2 (0.6)	Forest
Hoplostelis cf. *nigritula*	1 (0.3)	-	Cocoa
Hylaeus sp.1	1 (0.3)	-	Cocoa
Lasioglossum (*Dialictus*) sp.1	4 (1.2)	1 (0.3)	Cocoa / Forest
Lestrimelitta tropica	1 (0.3)	1 (0.3)	Cocoa / Forest
Megalopta sp.1	2 (0.6)	5 (1.5)	Cocoa / Forest
Megaloptina sp.1	1 (0.3)	-	Cocoa
Melipona mondury	1 (0.3)	-	Cocoa
Mesoplia sp.	1 (0.3)	-	Cocoa
Nannotrigona testaceicornis	2 (0.6)	-	Cocoa
Oxytrigona tataira	2 (0.6)	-	Cocoa
Paratrigona incerta	1 (0.3)	-	Cocoa
Paratrigona subnuda	4 (1.2)	2 (0.6)	Cocoa / Forest
Partamona sp.1	22 (6.6)	16 (4.8)	Cocoa / Forest
Partamona sp.2	7 (2.1)	6 (1.8)	Cocoa / Forest
Partamona sp.3	12 (3.6)	8 (2.4)	Cocoa / Forest
Pereirapis sp.1	2 (0.6)	-	Cocoa
Plebeia sp.1	3 (0.9)	10 (3)	Cocoa / Forest
Plebeia sp.2	5 (1.5)	-	Cocoa
Plebeia sp.3	1 (0.3)	-	Cocoa
Scaptotrigona sp.	-	1 (0.3)	Forest
Scaura atlantica	1 (0.3)	-	Cocoa
Tapinotaspinini sp.1	2 (0.6)	-	Cocoa
Tetragonisca angustula	1 (0.3)	2 (0.6)	Cocoa / Forest

Trigona braueri	10 (3)	15 (4.5)	Cocoa / Forest
Trigona gr. *fuscipennis*	8 (2.4)	1 (0.3)	Cocoa / Forest
Trigona spinipes	10 (3)	3 (0.9)	Cocoa / Forest
Trigonisca sp.1	1 (0.3)	-	Cocoa
Social wasps			
Agelaia angulata	12 (3.6)	13 (3.9)	Cocoa / Forest
Agelaia angulicollis	1 (0.3)	-	Cocoa
Agelaia centralis	16 (4.8)	17 (5.1)	Cocoa / Forest
Agelaia flavipennis	1 (0.3)	4 (1.2)	Cocoa / Forest
Agelaia vicina	2 (0.6)	-	Cocoa
Angiopolybia pallens	25 (7.5)	23 (6.9)	Cocoa / Forest
Apoica pallens	1 (0.3)	-	Cocoa
Chartergellus communis	-	2 (0.6)	Forest
Leipomeles dorsata	5 (1.5)	2 (0.6)	Cocoa / Forest
Metapolybia cingulata	1 (0.3)	-	Cocoa
Mischocyttarus bahiensis	1 (0.3)	-	Cocoa
Mischocyttarus carbonarius	-	3 (0.9)	Forest
Mischocyttarus labiatus	1 (0.3)	3 (0.9)	Cocoa / Forest
Mischocyttarus santacruzi	1 (0.3)	-	Cocoa
Mischocyttarus sp.	-	1 (0.3)	Forest
Parachartegus smithii	1 (0.3)	-	Cocoa
Polybia (*Myraptera*) sp.1	1 (0.3)	-	Cocoa
Polybia (*Myraptera*) sp.2	-	1 (0.3)	Forest
Polybia belemensis	1 (0.3)	-	Cocoa
Polybia catillifex	-	1 (0.3)	Forest
Polybia dimidiata	1 (0.3)	-	Cocoa
Polybia emaciata	1 (0.3)	-	Cocoa
Polybia flavifrons	4 (1.2)	-	Cocoa
Polybia jurinei	3 (0.9)	1 (0.3)	Cocoa / Forest
Polybia minarum	-	1 (0.3)	Forest
Polybia occidentalis	4 (1.2)	-	Cocoa
Polybia platycephala	-	2 (0.6)	Forest
Polybia quadricincta	1 (0.3)	-	Cocoa
Polybia rejecta	13 (3.9)	2 (0.6)	Cocoa / Forest
Polybia ruficeps	2 (0.6)	1 (0.3)	Cocoa / Forest
Protopolybia acutiscutis	2 (0.6)	-	Cocoa
Protopolybia exigua	1 (0.3)	-	Cocoa
Synoeca surinama	-	1 (0.3)	Forest

Capítulo 4

Multiscale drivers of bee and wasp species richness and composition in shaded cocoa agroforests

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Multiscale drivers of bee and wasp species richness and composition in shaded cocoa agroforests

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Abstract: Understanding the main factors determining the maintenance of native species in agroecosystems is of great importance to promote biodiversity-friendly practices. Here, we assessed the relative importance of local (management intensity, tree basal area, and tree diversity) and landscape (forest cover) predictors of the diversity of bees and social wasps in shaded cocoa agroforests located in three regions with contrasting land-use contexts in the Brazilian Atlantic Forest. Using Malaise and attractant traps to survey these insects on 29 agroforests, we revealed that bee richness was negatively associated with management intensity in the high deforestation region and positively associated with forest cover, but only in the high and intermediate deforested regions, whereas none of the assessed variables influenced bee species composition. In contrast, wasp richness enhanced with increasing management intensity, but only at the intermediate deforested region. Wasp species composition was influenced by management intensity in the intermediated region and forest cover in the high-deforested region, but the effect of forest cover depended on the basal area of shade trees. We recommend that increasing the surrounding native forest cover, even under more intensive management practices, can ensure the high conservation value of these insects in cocoa agroforests in this unique biodiversity hotspot.

Key-words: Agroecosystem, Atlantic Forest, Biodiversity-friendly matrix, habitat amount hypothesis, pollinators, predators.

Introduction

The global biodiversity crisis is mainly caused by agriculture-driven forest loss (Ramankutty et al., 2018; Watling et al., 2020). Consequently, preventing forest loss and increasing forest cover are considered essential principles to enhance biodiversity conservation (Riva et al., 2024). However, species conservation can also be achieved by improving matrix quality (Perfecto and Vandermeer, 2010, Arroyo-Rodríguez et al., 2020). For instance, agroecosystems that maintain native tree species can exhibit a vegetation structure similar to that of native habitats, therefore prone to support greater biodiversity and consequently preserving a wide range of forest species (Niether et al., 2020; Ferreira et al., 2020). However, each agroforestry system can have different local environmental conditions (e.g., vegetation structure and management intensity) and be embedded in different landscape scenarios (e.g., remaining forest cover), which can determine its conservation value (de la Mora et al., 2013; Ferreira et al., 2024a). Therefore, understanding the relative importance of local and landscape predictors for preserving species diversity in agroforestry systems becomes crucial to promote biodiversity-friendly agricultural practices in human-modified landscapes (Arroyo-Rodríguez et al., 2020).

In tropical countries, shaded cocoa plantations are important agroforestry systems in terms of socio-economic-environmental benefits. This is the case of traditional cocoa (*Theobroma cacao*) plantations (hereafter, shaded cocoa agroforest) in southern Bahia, Brazil, which combine cocoa cultivation with emergent native species from the Atlantic Forest biome, a global biodiversity hotspot (Myers et al., 2000). Such a combination of native and cocoa trees increases the heterogeneity of vegetation structure, providing resources for several animal species (Cassano et al., 2009). In fact, these agroforests are recognized for their high conservation value, as they are used as temporary or permanent habitats by different terrestrial and flying mammals (Faria and Baumgarten 2007; Ferreira et al., 2020, 2025), reptiles, and amphibians (Cervantes-López et al., 2025).

Shaded cocoa agroforests can also be highly valuable for insect conservation, such as bees and social wasps (Bos et al., 2007; Ferreira et al., 2024a). However, as cocoa plantations exhibit different vegetation structure mostly driven by contrasted management practices, the local condition can differ among agroecosystems, with subsequent influence on species persistence. For example, in Indonesian cocoa agroforests, management intensification, which resulted in the reduction of shade trees and local changes (temperature, humidity, canopy openness and herbaceous extract), significantly reduced the diversity of bees and wasps (Bos et al., 2007). As the availability of nesting substrate is important for determining the occurrence of bees and wasps (Araújo et al., 2021; Morato and Martins 2006), especially for species that nest above ground, the structural vegetation complexity can also predict the diversity of these insects in agroforests. Finally, the landscape forest loss can also limit the availability of resources for bees and social wasps (Ferreira et al., 2024a), and therefore the effect of management intensity may depend on the remaining forest cover (i.e., an interacting effect). However, to our knowledge, no study to date has assessed this hypothesis on agroecosystems.

Here, we investigated the effect of local (i.e., vegetation structure and management intensity) and landscape (i.e., forest cover) predictors on the number and composition of bee and social wasp species across 29 shaded cocoa agroforests from the northeastern Brazilian Atlantic Forest. In addition, we considered the land use context at a regional scale (i.e., with low, intermediate and high levels of deforestation) as a modulator of the effects of local and landscape predictors. Overall, we expected a more pronounced effect on bees than wasps, since bees tend to be more specialized with food and nesting resources (Reis et al., 2019; de Araújo et al., 2021). Specifically, we predicted that farms under greater management intensity would retain lower species number, since such practices will imperil the persistence of more sensitive species. In addition, shaded cocoa agroforest presenting greater tree diversity, higher basal area of shading trees and inserted in landscapes with higher forest cover would retain a greater number of species for both groups (Medeiros et al., 2019), given their relation to floral resources, nesting sites and habitat availability, respectively (Basset et al., 2012; Flores et al., 2018; Medeiros et al., 2019). We also predicted that agroforests with high management intensity, tree diversity, basal area of shading trees and inserted in landscapes with lower forest cover would show high species composition dissimilarity, due to the loss of sensitive species typically associated with native forests and the dominance of generalist species commonly found in degraded environments (Souza et al., 2010). Finally, we expected that the effects of management intensity, diversity and basal area of shade trees will be less evident with increasing landscape forest cover, especially in more deforested regions.

Methods

Study area

We conducted the study in the southern Bahia state, Brazil (Fig. 1) – where the economy has been based on cocoa production through shade agroecosystems, and other land cover types comprise native forests (i.e., Atlantic Forest), cattle pastures, eucalyptus monocultures, and urban areas (Mapbiomas 2024). As the cocoa agroforests are distributed in three regions exhibiting different levels of deforestation and main land use types (i.e., low deforested region = 54.1% of remaining forest cover, intermediate deforested = 43%, high deforested = 26.7%), we carefully selected 29 shaded cocoa agroforests distributed in those regions (Fig. 1). The region with high deforestation (~4203 km^2) is mainly dominated by cattle pastures (36.3%), following by forest remnants (26.7%), shaded cocoa agroforest (15.4%) and eucalyptus monoculture (4.6%); while the region with intermediate deforestation (~2181 km^2) is dominated by forest remnants (43%) and shaded cocoa agroforest (33%). Finally, the region with low deforestation (~2301 km^2) is dominated by forest remnants (54.1%) and includes the most extensive areas of Atlantic Forest in southern Bahia.

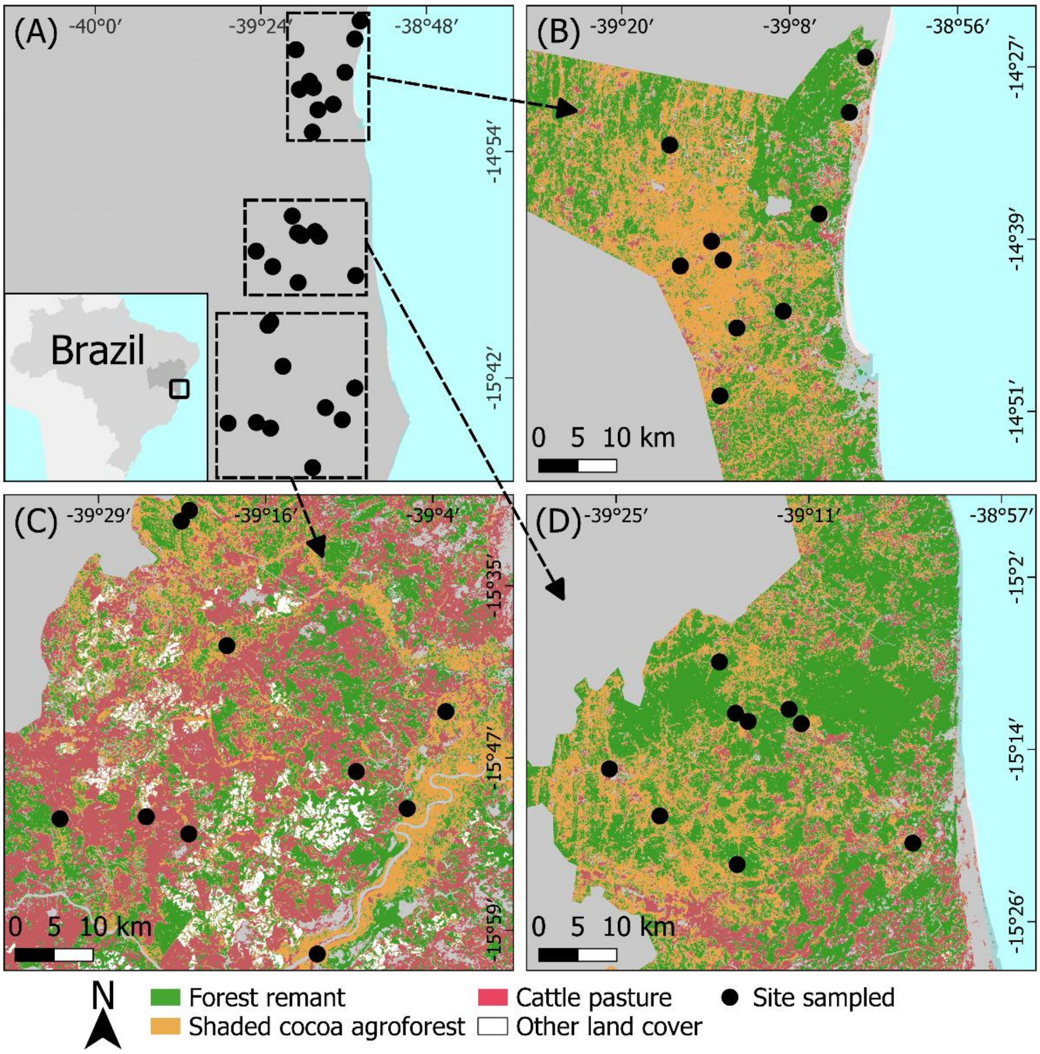

Figure 1. Location of the study regions and shaded cocoa agroforests in southern Bahia state, Brazil (A). We surveyed 10, 9, and 10 agroforests in regions with intermediate (B) high (C) and low (D) levels of deforestation, respectively.

Insect sampling

The sampling protocol is detailed elsewhere (Ferreira et al., 2024a), but a brief overview is given here. In each agroforest, we deployed three Malaise traps and six attractant traps: two with water and sardine attractant, two with artificial orange juice and two with artificial guava juice (adapted from Souza et al., 2015). Traps remained active for an uninterrupted period of ~72 hours, and collections were conducted from December 2022 to February 2024. The material was collected under license issued by the responsible Brazilian agency (ICMBIO license n° 83493-1) and specimens were deposited in the Entomological Collection of the National Institute for Amazonian Research (INPA).

Local and landscape predictors

To quantify the vegetation structure variables, we established four 50 x 50 m plots in each agroforest, separated by a minimum distance of 30 m. In these plots, we quantified, identified and measured the diameter at breast height (DBH) of all trees ≥ 10 cm (native and non-native species, including palm trees). Tree identifications were made at the lowest possible taxonomic level, with the assistance of an experienced botanist. Plant individuals not identified in the field were collected to be identified in the Herbarium of the Cocoa Research Centre at the Executive Commission of the Cocoa Farming Plan (CEPEC/CEPLAC), and the Herbarium of the Universidade Estadual de Santa Cruz (UESC). We then quantified two variables: the effective number of common tree species (i.e., Hill number in order 1, q1) using the iNEXT package (Jost 2006; Hsieh et al., 2016), and the total basal area of native trees (m^2/ha).

To quantify management intensity in each agroforest, we interviewed farmers, obtaining information on four management practices: (i) frequency of weed control (per year); (ii) frequency of fertilization (organic or chemical) and/or liming (per year); (iii) frequency of pruning cocoa trees (per year), in which they often remove excess shoots and rarely carry out heavy pruning of larger branches and stems; and (iv) the total number of cocoa trees in the established vegetation plot. The observed values were normalized by dividing each value by the highest observed value (separately for each variable) among all agroforests. The resulting values of the four variables for each agroforest were summed so that values equal to zero and four represent minimum and maximum management intensities, respectively (adapted from Mas and Dietsch 2003).

Finally, we calculated landscape forest cover in multiple buffers (500, 750 and 1000 m) from each sampling site. To do this, we used a combination of two mappings: Mapbiomas collection 7 (Mapbiomas 2024), which contains land cover but does not separate forest remnants from shaded cocoa agroforest, and Mapbiomas cocoa (Mapbiomas Cacau 2023), which contains land cover from shaded cocoa agroforest but does not separate forest remnants from silviculture. Therefore, we used the combination of both mappings to only obtain the native forest cover in each landscape (i.e., forest cover). To determine the scale of forest cover effect (Jackson and Fahrig, 2015), we constructed Generalized Linear Models (GLM) relating the response variable with forest cover measured at each scale. We then used the Akaike information criterion corrected for small samples (AICc) to select the best scale (Burnham and Anderson 2002). For more details, see Appendices A, B and C in the Supplementary Material 1.

Data analysis

We used GLMs to assess the effect of local and landscape predictors on the number and composition of bee and social wasp species. Considering that bees and wasps can respond differently to habitat modification and that these effects can vary between regions (Ferreira et al., 2024a), we conducted the analyses separately for each taxon (bee and wasp) and region (i.e., with different levels of deforestation). Changes in species composition across cocoa agroforests were quantified with the first axis of a Principal Coordinate Analysis (PCoA), calculated from a dissimilarity matrix using the *vegdist* function from the *vegan* package (Oksanen et al., 2022), constructed with a presence-absence matrix and Jaccard's index. To generate the dissimilarity matrix, we excluded one site where no individuals were collected, resulting in 28 agroforests. The first axis of the PCoA captured 32%, 28% and 40% of the variation in bee species composition, and 38%, 37% and 39% of social wasps in the high, intermediate and low deforested regions, respectively. Our GLMs were built with a Poisson distribution for count data (number of species) or a Gaussian distribution for continuous values (first axis of the PCoA). We evaluated the correlation between our predictors and, given the low correlation observed (< 29% between any two variables; Appendix D in Supplementary Material), we retained all variables in our analyses. We constructed models considering each predictor separately, in addition to the interaction of each local variable with forest cover, and the null model, which resulted in eight models for each taxon in each region. The predictor variables were standardized (subtracted by the mean and divided by the standard deviation) to zero mean and unit variance, ensuring that the coefficients represent changes in response per unit standard deviation of the predictor variable. We used the *simulateResiduals* function of the *DHARMa* package to ensure that the residuals of our models did not violate the assumptions of homoscedasticity, over- or under-dispersion and outliers. Finally, we used the AICc to select the best models, i.e., $\Delta\text{AICc} \leq 2$ (Burnham and Anderson 2002), and selected the null model when it was among the most parsimonious models.

Results

We collected 254 bees belonging to 38 species, and 346 wasps from 24 species (Supplementary Material 2). The mean number of bee species was 4.3 ±2.3 (range = 0 to 9 species), and the number of wasp species averaged 3.4 ±2.1 (range = 0 to 10 species). Our model selection approach revealed that the number of bee species was best predicted by landscape forest cover alone, with a positive influence, but this effect was only significant in the intermediate ($\beta = 1.37$; $p = 0.01$; Figure 2A) and high ($\beta = 0.37$; $p = 0.01$; Figure 2B) deforested regions. Furthermore, the number of bee species was also negatively associated with management intensity, but only in the region with high deforestation ($\beta = -0.35$; $p = 0.05$; Figure 2C). In contrast, the null model best explained the variation in bee species composition (Table 1).

Regarding the social wasps, the number of species was best explained by management intensity, with a positive influence, but only in the intermediate deforested region ($\beta = 0.45$; $p = 0.002$; Figure 2D). In addition, three models best explained the composition of wasp species. Specifically, we detected that: (i) management intensity, in the intermediate deforested region ($\beta = 0.25$; $p = 0.003$; Figure 2E); (ii) and forest cover, in the high deforested region ($\beta = 0.26$; $p = 0.01$; Figure 2F), increased the dissimilarity of species composition. However, iii) the effect of forest cover increased dissimilarity only in agroforests with a moderate and high basal area of shaded trees ($\beta = 0.27$; $p = 0.001$; Figure 2G; Table 1). See Appendix E in Supplementary Material for details of all models.

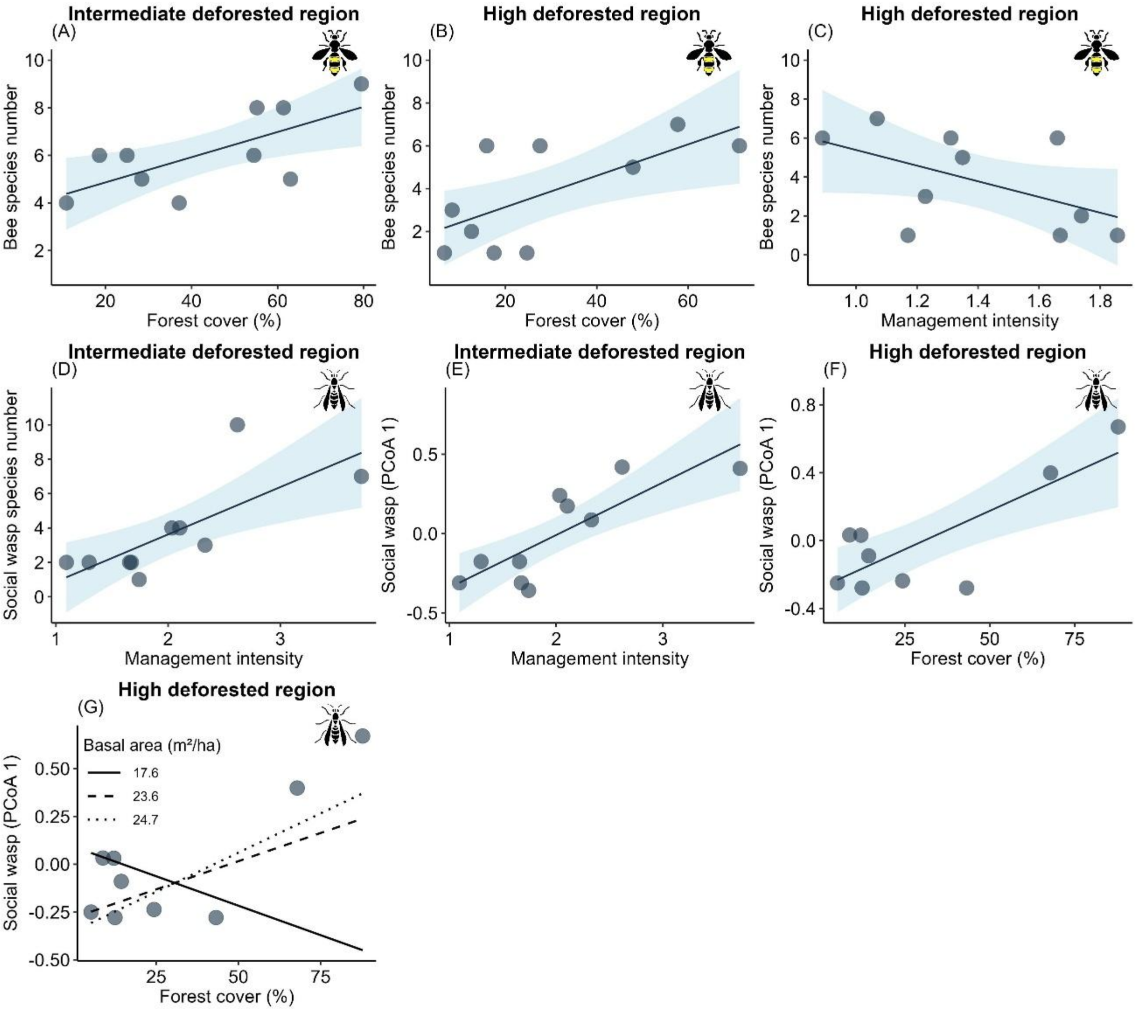

Figure 2. Significant effects of landscape forest cover and local management intensity on the number of bee (panels A, B and C) and wasp species (panel D), and on the composition of social wasps (panels E to G) in southern Bahia state, Brazil, according to the regional level of deforestation. Note that the effect of forest cover on the composition of wasp species in the high deforested region depended on local tree basal area. The solid, dashed and dotted lines correspond, respectively, to the first, second and third percentile of the basal area of shade trees. Only the selected model results (parsimonious models) are shown.

Table 1 - Result of model selection. Only the most plausible models (i.e., ΔAICc < 2) are shown in the table. We only presented the null model when it was present among the parsimonious models. All numerical predictors were scaled to zero mean and unit variance. Weight = evidence weight of the model.

Taxon	Response	Region	Model	ΔAICc	Weight	Estimate	P
Bee 	Number of species	Low deforested	Null	0	0.43	0	-
		Intermediate deforested	y ~ forest cover	0	0.82	1.37	0.01
		High deforested	y ~ forest cover	0	0.46	0.37	0.01
		High deforested	y ~ management intensity	1.9	0.18	-0.35	0.05
	Species composition	Low deforested	Null	0	0.47	0	-
		Intermediate deforested	Null	0	0.31	0	-
		High deforested	Null	0	0.33	0	-
 Social wasp	Number of species	Low deforested	Null	0	0.40	0	-
		Intermediate deforested	y ~ management intensity	0	0.66	0.45	0.002
		High deforested	Null	0	0.25	0.48	-
	Species composition	Low deforested	Null	0	0.40	0	-
		Intermediate deforested	y ~ management intensity	0	0.92	0.25	0.004
		High deforested	y ~ forest cover: basal area	0	0.48	0.3	0.01
		High deforested	y ~ forest cover	0.2	0.43	0.27	0.01

Discussion

As far as we are aware, this is the first study that assessed the combined effects of local and landscape predictors on bee and social wasp richness and composition in agroforests. In particular, we unveiled that the effects of local characteristics are dependent on the context of land cover on a landscape and regional scales. The landscape forest cover and management intensity were the main factors explaining the number of bee species, whereas management intensity best predicted both the number and composition of wasp species. Finally, forest cover also affected the composition of social wasps, but this effect was dependent on the basal area of shading trees. Considering that we are facing a global diversity and pollinator crisis (Betts et al., 2017; Levy, 2011), which calls for urgent management measures in human-modified landscapes (Arroyo-Rodríguez et al., 2020), our results demonstrate that both landscape context and local management practices should be considered to maximize bee and wasp species in cocoa agroforests.

According to our expectations, the intensity of management negatively affected the number of bee species, but this effect was only observed in the region with high deforestation. This result contrasts with previous findings in which bee species richness was positively associated with management intensification in cocoa agroforests (Hoehn et al., 2010). This association was possibly explained by the higher density of herbaceous plants present in more managed agroforests. However, our management index is positively associated with the frequency of weed control and the density of cocoa trees. Consequently, an increase in the management intensity is influenced by a lower supply of floral resources (herbaceous plants) and a higher density of plants with flowers that are unattractive to bees, i.e., cocoa trees (Jordão et al., 2024). Furthermore, it is important to note that the intensification of common management practices in these agroforests reduces bee species richness only in conditions of low forest cover on a regional scale. In fact, landscape composition proved to be important in determining the number of bee species in these agroforests. For example, according to our predictions, landscape forest cover positively explained the increase in bee species number in surveyed agroforests, but only in regions with high and intermediate deforestation, which can be explained by the habitat amount hypothesis (Fahrig 2013). Landscapes composed of a high forest amount may offer a greater availability of resources, which can be accessed mainly by organisms that have a high vagility, as in the case of bees (Zurbuchen et al., 2010). Indeed, habitat loss has been one of the main causes of the decline of pollinators (Potts et al., 2010), including bees in agricultural landscapes (Saturni et al., 2016; Reis et al., 2019). Therefore, our results support the idea that maintaining or restoring forest remnants, especially in deforested landscapes, is an essential and priority measure to ensure the conservation of bee diversity in agricultural landscapes (Arroyo-Rodríguez et al., 2020; Riva et al., 2024), even in biodiversity-friendly systems.

Unlike bees, we observed that the number of wasp species responded positively to the management intensity, which consequently induced to changes in species composition (Appendix F). Our management intensity index includes practices such as pruning and thinning cocoa trees, which possibly contribute to increase solar incidence in agroforests and is positively associated with the activity rate of social wasps (da Silva et al., 2022). In addition, environments with more sunlight, such as edges and clearings, can present high density of prey individuals for social wasps (Barbosa et al., 2005; Pereira et al., 2017). In fact, we observed that the agroforest with the highest number of wasp species (10 species) also had the lowest shading value (31% shading, almost half the overall average of the other agroforests, which was 59 (±8.4%). Therefore, because they are opportunistic predators, social wasps can benefit from intensified management in agroforests in regions with moderate amounts of forest cover.

We also identified that landscape forest cover, either alone or interacting with tree basal area, modulates patterns of wasp species composition, but only in highly deforested region. Both forest cover and the basal area of pioneer trees independently determined the composition of wasps in a context of more intensive land use, such as coffee monocultures and aquatic matrices (Medeiros et al., 2019; Ferreira et al., 2024b). As discussed above, increasing forest cover in the landscape tends to enhance biodiversity by providing resources and conditions for a higher number of species, especially for those more sensitive species to habitat loss. In fact, greater amount of forest cover tends to increase the compositional similarity of wasp species between cocoa agroforests and forest remnants (Ferreira et al., 2024a). Nevertheless, we observed that this pattern depends on the local structure of the vegetation, in this case represented by the basal area of shade trees. Structural complexity in agroforests can modulate the occurrence of social wasp species, since more complex environments can create more favorable conditions for the establishment of more species, including those more selective in terms of the type of nesting substrate (Corbara et al., 2009). However, despite the significant relationship between basal area and species composition, this response needs to be interpreted with caution. The observed pattern was not very clear and was a consequence of the presence of exclusive species (Appendix F). For example, three (*Polybia ruficeps*, *Apoica pallens* and *Agelaia flavipennis*) and two species (*Agelaia vicina* and *Agelaia angulata*) occurred exclusively in the agroforest with the lowest basal area of shade trees and in two forests with the highest value of forest cover, respectively (Appendix F). Since these five species, which occurred exclusively at the extremes of both variables, represent almost half of the species sampled in the region with high deforestation (i.e., five out of twelve species), it is expected that they will have a greater weight influencing compositional changes. Furthermore, this effect was only observed in the region with the lowest forest cover and, since conditions at a regional level are less favourable, with a high amount of cattle pasture and eucalyptus monocultures, the effects of local vegetation structure and forest cover on the landscape may be even more evident.

Interesting, our study did not detect an effect of landscape forest cover on wasp species number. We suggest that this result is likely explained by the compensatory role of shaded cocoa agroforests, possibly acting as a supplementary habitat for these insects.

Previous studies have shown that these agroforests tend to have a high species richness of social wasps (Ferreira et al., 2024c), even compared to neighbouring forest remnants (Ferreira et al., 2024a). Therefore, the fact that the study area, in general, has extensive potential habitat cover (i.e., agroforests and forest remnants; ~61%), combined with the generalist characteristics of these insects, could explain the absence of native forest cover effect on the species number of social wasps.

The sustainability of agricultural practices depends on the adoption of strategies that minimize the trade-off between biodiversity conservation and agricultural yields. Despite the high conservation value of the shaded cocoa agroforests in the southern Bahia, this system has low productivity, considering the average production in other regions (Gama-Rodrigues et al., 2021). This lower economic gain can drive producers to adopt more intensive production methods with potential damage to biodiversity, like full-sun cocoa plantations or coffee monocultures, as previously observed in our region. However, studies suggest that the maintenance of shade trees associated with less invasive management practices (i.e., changes in the structural characteristics of agroforests such as the density of cocoa trees and associated trees), which is possibly the main bottleneck to greater productivity (Jagoret et al., 2017), can provide win-win scenarios for productivity and biodiversity conservation by enhancing the economic gains ensure the maintenance of high species number in these systems. In this context, our results indicate that agroforests inserted in landscapes or regions with high forest cover can favour insect conservation, especially of bees, even under more intensive management. Additionally, these agroforests could experience greater productivity due to ecosystem services and ecological intensification associated, while maintaining local biodiversity (Araújo et al., 2025).

Finally, considering that pollination deficit is an important factor associated with low cocoa productivity (Toledo-Hernández et al., 2017), maintaining a suitable habitat for bees (such as shaded cocoa agroforests), which can be potential cocoa pollinators (Maia-Silva et al., 2024), could also reflect in a favourable habitat for the maintenance of more effective cocoa pollinators (Toledo-Hernández et al., 2017; Jordão et al., 2024). These benefits could be extended to include the biological control offered by wasps and insectivorous vertebrates (Aycart-Lazo et al., 2025). Therefore, we suggest that restoration (in landscapes with low forest cover) or the maintenance of forest remnants (in landscapes with moderate or high forest cover), which could reduce the possible negative effects of intensified management on bee species richness, should be priority efforts to safeguard the taxonomic diversity of bees and social wasps in shaded cocoa agroforests.

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Appendix A. Mean, minimum, maximum and standard deviation (SD) values for all the predictor variables (at the different scales, in the case of forest cover - 500, 750 and 1000 m) observed in each of the three regions investigated: high, intermediate and low deforestation.

Variable	Metric	High	Intermediate	Low
FC (500 m)	Mean	28.48	43.35	44.81
FC (500 m)	Min.	5.15	10.90	27.22
FC (500 m)	Max.	87.80	79.46	66.84
FC (500 m)	SD	28.58	22.46	12.87
FC (750 m)	Mean	29.01	44.17	48.25
FC (750 m)	Min.	6.63	10.20	25.79
FC (750 m)	Max.	71.23	80.29	72.86
FC (750 m)	SD	22.33	21.99	14.38
FC (1000 m)	Mean	28.50	44.04	49.57
FC (1000 m)	Min.	7.85	9.74	22.93
FC (1000 m)	Max.	59.05	77.91	74.54
FC (1000 m)	SD	17.98	22.02	17.16
Shade tree diversity (q1)	Mean	14.04	14.34	12.29
Shade tree diversity (q1)	Min.	14.04	14.34	12.29
Shade tree diversity (q1)	Max.	10.45	4.88	8.27
Shade tree diversity (q1)	SD	19.22	26.47	19.78
Basal area (m²/ha)	Mean	20.65	16.06	18.34
Basal area (m²/ha)	Min.	11.30	7.52	7.84
Basal area (m²/ha)	Max.	25.83	23.24	31.19
Basal area (m²/ha)	SD	4.79	5.38	6.65
Management intensity	Mean	1.48	2.14	1.79
Management intensity	Min.	0.94	1.09	1.15
Management intensity	Max.	1.86	3.97	3.09
Management intensity	SD	0.32	0.81	0.56

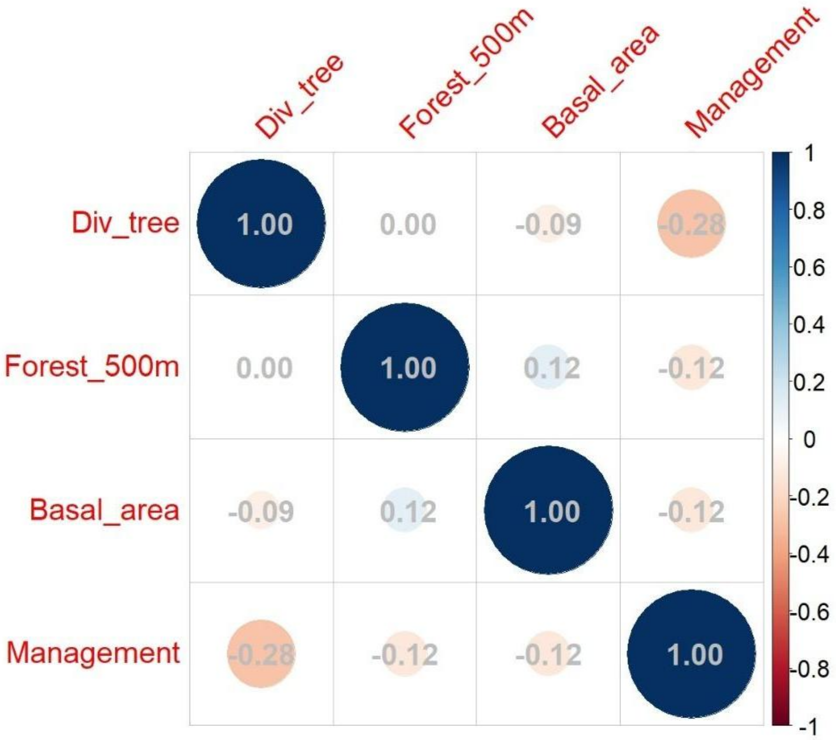
Appendix B. Geographical location (longitude and latitude); site code/identification (ID); values of the predictor variables (FC = percentage of forest cover at radii of 500, 750 and 1000 m; tree diversity of shade trees (Hill number of order q1); sum of basal area of shade trees (m²/ha) and management intensity); and number of bee and social wasp species observed in each of the 29 shaded cocoa agroforests sampled in regions with different levels of deforestation (high, intermediate and low).

Region	**ID**	**Long.**	**Lat.**	**FC 500 m**	**FC 750 m**	**FC 1000 m**	**Shade tree diversity**	**Basal area (m²/ha)**	**Management intensity**	**Bee species number**	**Wasp species number**
High	B13	-39.322	-15.659	14.34	24.71	24.1	19.22	17.57	1.27	1	3
High	B14	-39.167	-15.806	24.32	27.58	30.1	11.77	15.98	1.78	6	5
High	B15	-39.214	-16.018	5.15	6.63	7.85	14.83	23.59	1.77	1	4
High	B16	-39.376	-15.515	67.89	57.72	51.3	15.59	23.89	1.12	7	6
High	B18	-39.366	-15.502	87.8	71.23	59.1	10.45	25.83	1.41	6	2
High	B19	-39.059	-15.736	12.08	15.89	18.8	11.94	24.75	0.94	6	2
High	B20	-39.106	-15.849	12.43	17.5	25.5	10.65	24.87	1.86	1	2
High	B21	-39.368	-15.878	8.75	12.57	13.2	18.45	11.3	1.84	2	5
High	B7	-39.419	-15.858	8.88	8.31	9.23	14.71	20.66	1.33	3	0
High	B9	-39.522	-15.860	43.18	47.92	45.9	12.75	18.04	1.5	5	2
Intermediate	I10	-39.095	-14.621	79.46	80.29	77.9	13.2	23.24	1.84	9	1
Intermediate	I11	-39.260	-14.681	10.9	10.2	9.74	13.85	7.52	1.09	4	2
Intermediate	I12	-39.209	-14.674	25.01	21.75	18.7	11.62	20.94	3.97	6	7
Intermediate	I13	-39.273	-14.541	18.59	30.55	38.2	7.1	9.56	2.72	6	10
Intermediate	I14	-39.193	-14.753	37.11	36.18	37	4.88	15.03	2.53	4	3
Intermediate	I15	-39.059	-14.503	54.48	45.91	45.6	12.31	21.33	1.35	6	2
Intermediate	I16	-39.040	-14.439	61.35	69.3	67.4	18.15	12.66	2.23	8	4
Intermediate	I17	-39.213	-14.832	55.18	58.53	60	14.54	17.23	2.15	8	4
Intermediate	I4	-39.223	-14.652	28.43	32.24	27	21.32	20.25	1.72	5	2
Intermediate	I8	-39.138	-14.734	62.99	56.72	58.9	26.47	12.86	1.81	5	2
Low	U1	-39.056	-15.339	44.04	45.77	43.8	9.5	23.34	1.73	4	6
Low	U11	-39.253	-15.197	37.34	47.34	52.7	8.27	22.57	1.98	2	2
Low	U13	-39.419	-15.252	30.56	25.79	22.9	19.78	16.56	1.23	3	3
Low	U14	-39.287	-15.128	66.84	72.86	74.5	9.84	16.24	1.56	3	4
Low	U15	-39.266	-15.364	44.46	54.52	61.2	11.34	17.71	1.8	0	2
Low	U16	-39.189	-15.200	27.22	30.57	28.5	10.26	13.65	3.09	3	4
Low	U17	-39.358	-15.307	47.6	44.1	40.1	15.66	15.92	1.76	5	1
Low	U3	-39.268	-15.188	44.2	52.89	56.5	15.04	31.19	1.77	2	3
Low	U7	-39.204	-15.183	61.01	60.39	65.9	10.93	7.84	1.15	3	5

Appendix C. Effect scale selection results. We considered parsimonious all models with ΔAICc ≤2. When more than one model was considered parsimonious, we opted for the model with the smallest radius. (*) The scale used in the models.

Region	Buffer size (m)	Response variable	Taxon	ΔAICc
High	500*	Species number	Bee	0.2
High	750	Species number	Bee	0.2
High	1000	Species number	Bee	0
Intermediate	500	Species number	Bee	3.4
Intermediate	750*	Species number	Bee	0
Intermediate	1000	Species number	Bee	0.7
Low	500*	Species number	Bee	0.7
Low	750	Species number	Bee	0.5
Low	1000	Species number	Bee	0
High	500*	Species composition (PCoA 1)	Bee	0
High	750	Species composition (PCoA 1)	Bee	0.6
High	1000	Species composition (PCoA 1)	Bee	1.3
Intermediate	500*	Species composition (PCoA 1)	Bee	0
Intermediate	750	Species composition (PCoA 1)	Bee	1.1
Intermediate	1000	Species composition (PCoA 1)	Bee	0.7
Low	500*	Species composition (PCoA 1)	Bee	0
Low	750	Species composition (PCoA 1)	Bee	0.3
Low	1000	Species composition (PCoA 1)	Bee	0.2
High	500*	Species number	Social wasp	0
High	750	Species number	Social wasp	0
High	1000	Species number	Social wasp	0
Intermediate	500*	Species number	Social wasp	0
Intermediate	750	Species number	Social wasp	2.3
Intermediate	1000	Species number	Social wasp	3.4
Low	500*	Species number	Social wasp	0
Low	750	Species number	Social wasp	0.2
Low	1000	Species number	Social wasp	0.2
High	500*	Species composition (PCoA 1)	Social wasp	0
High	750	Species composition (PCoA 1)	Social wasp	2.6
High	1000	Species composition (PCoA 1)	Social wasp	4.5
Intermediate	500*	Species composition (PCoA 1)	Social wasp	0
Intermediate	750	Species composition (PCoA 1)	Social wasp	0.5
Intermediate	1000	Species composition (PCoA 1)	Social wasp	0.6
Low	500*	Species composition (PCoA 1)	Social wasp	0
Low	750	Species composition (PCoA 1)	Social wasp	0.1
Low	1000	Species composition (PCoA 1)	Social wasp	0

Appendix D – Pearson's correlation values between four predictor variables: diversity of shade trees (Div_tree), forest cover at a radius of 500 m (Forest_500m), basal area of shade trees (Basal_area) and management intensity (Management).



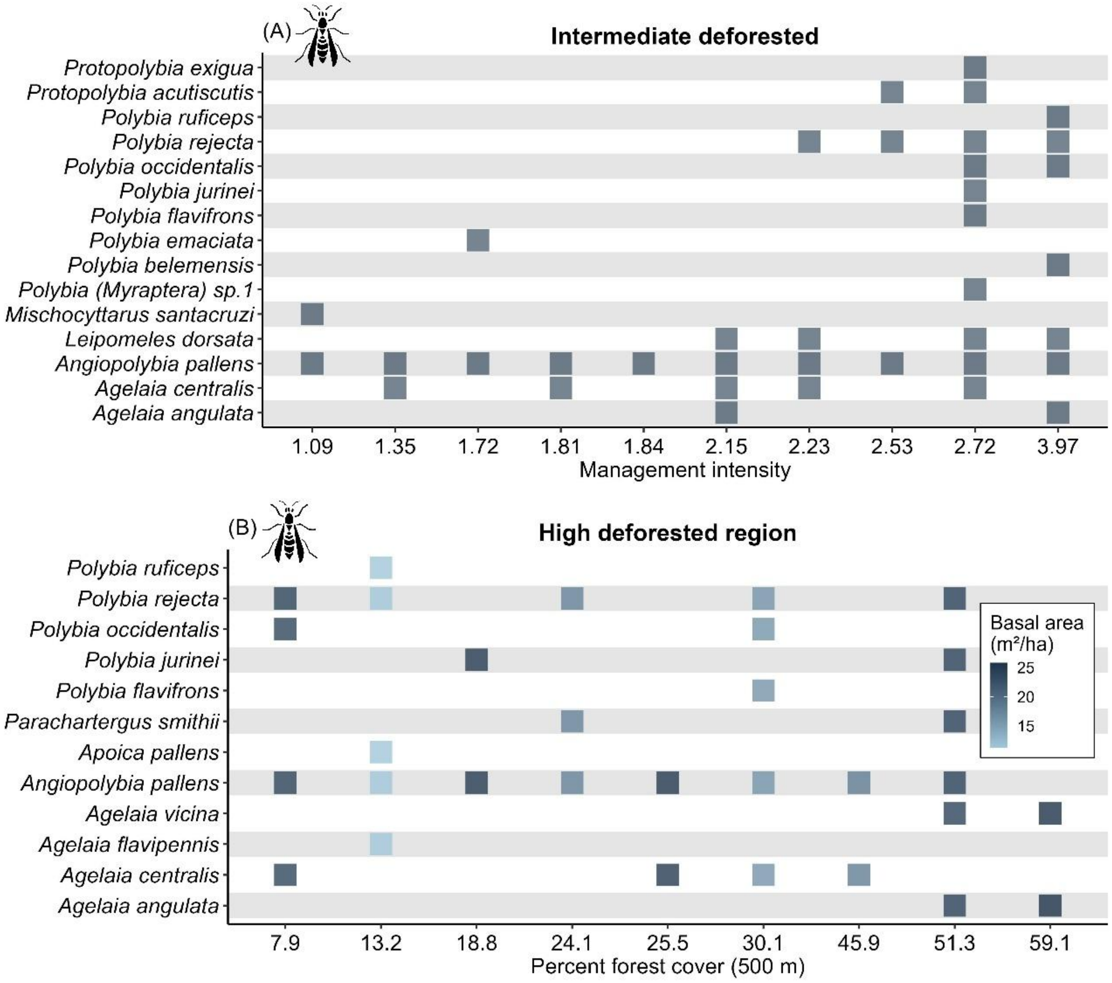
Appendix E. Values of ΔAICc and weights of all the models built and used in model selection. We always select the null model when it is present among the parsimonious models. Parsimonious models (ΔAICc ≤2) are highlighted in bold. All numerical predictors were scaled to zero mean and unit variance.

Region	Response variable	Taxon	Model	ΔAICc	Weight	Estimate
Low	**Species number**	**bee**	**null**	**0**	**0.43**	**0**
Low	Species number	bee	y ~ basal area of shade trees	3.2	0.09	-0.1
Low	Species number	bee	y ~ shade tree diversity	3.22	0.09	0.09
Low	Species number	bee	y ~ forest cover	3.38	0.08	0.05
Low	Species number	bee	y ~ shade tree diversity: forest cover	3.41	0.08	-0.04
Low	Species number	bee	y ~ management intensity: forest cover	3.41	0.08	-0.03
Low	Species number	bee	y ~ management intensity	3.42	0.08	0.09
Low	Species number	bee	y ~ basal area of shade trees: forest cover	3.43	0.08	-0.01
Intermediate	**Species number**	**bee**	**y ~ forest cover**	**0**	**0.82**	**1.37**
Intermediate	Species number	bee	null	4.8	0.07	0
Intermediate	Species number	bee	y ~ basal area of shade trees	7.23	0.02	0.12
Intermediate	Species number	bee	y ~ management intensity: forest cover	7.58	0.02	-0.09
Intermediate	Species number	bee	y ~ shade tree diversity: forest cover	7.85	0.02	-0.11
Intermediate	Species number	bee	y ~ management intensity	7.96	0.02	0.03
Intermediate	Species number	bee	y ~ shade tree diversity	8.01	0.02	0.02
Intermediate	Species number	bee	y ~ basal area of shade trees: forest cover	8.01	0.02	0.01
High	**Species number**	**bee**	**y ~ forest cover**	**0**	**0.46**	**0.37**
High	**Species number**	**bee**	**y ~ management intensity**	**1.85**	**0.18**	**-0.35**
High	Species number	bee	null	2.63	0.12	0
High	Species number	bee	y ~ shade tree diversity	2.95	0.1	-0.31
High	Species number	bee	y ~ basal area of shade trees: forest cover	4.55	0.05	0.2
High	Species number	bee	y ~ basal area of shade trees	5.16	0.03	0.15
High	Species number	bee	y ~ shade tree diversity: forest cover	5.82	0.03	0.03
High	Species number	bee	y ~ management intensity: forest cover	5.84	0.02	0.02
Low	**PCoA 1**	**bee**	**null**	**0**	**0.47**	**0**
Low	PCoA 1	bee	y ~ management intensity	1.99	0.18	0.12
Low	PCoA 1	bee	y ~ basal area of shade trees: forest cover	3.47	0.08	0.23
Low	PCoA 1	bee	y ~ shade tree diversity	3.58	0.08	-0.17
Low	PCoA 1	bee	y ~ basal area of shade trees	4.27	0.06	0.14
Low	PCoA 1	bee	y ~ management intensity: forest cover	4.42	0.05	-0.12
Low	PCoA 1	bee	y ~ shade tree diversity: forest cover	4.54	0.05	0.14
Low	PCoA 1	bee	y ~ forest cover	5.25	0.03	-0.07
Intermediate	**PCoA 1**	**bee**	**null**	**0**	**0.31**	**0**
Intermediate	PCoA 1	bee	y ~ forest cover	0.26	0.28	0.16
Intermediate	PCoA 1	bee	y ~ management intensity	1.49	0.15	0.14
Intermediate	PCoA 1	bee	y ~ shade tree diversity: forest cover	2.66	0.08	0.15
Intermediate	PCoA 1	bee	y ~ basal area of shade trees	3.68	0.05	-0.07
Intermediate	PCoA 1	bee	y ~ management intensity: forest cover	3.81	0.05	0.06
Intermediate	PCoA 1	bee	y ~ basal area of shade trees: forest cover	3.91	0.04	0.05
Intermediate	PCoA 1	bee	y ~ shade tree diversity	4.05	0.04	0.04
High	**PCoA 1**	**bee**	**null**	**0**	**0.33**	**0**
High	PCoA 1	bee	y ~ forest cover	0.01	0.33	0.17

High	PCoA 1	bee	y ~ basal area of shade trees: forest cover	2.03	0.12	0.14
High	PCoA 1	bee	y ~ shade tree diversity: forest cover	3.82	0.05	-0.07
High	PCoA 1	bee	y ~ basal area of shade trees	3.84	0.05	-0.06
High	PCoA 1	bee	y ~ management intensity: forest cover	3.91	0.05	-0.08
High	PCoA 1	bee	y ~ management intensity	4.05	0.04	0.1
High	PCoA 1	bee	y ~ shade tree diversity	4.13	0.04	-0.04
Low	**Species number**	**wasp**	**null**	**0**	**0.4**	**0**
Low	Species number	wasp	y ~ shade tree diversity	2.57	0.11	-0.19
Low	Species number	wasp	y ~ management intensity: forest cover	2.86	0.1	-0.11
Low	Species number	wasp	y ~ basal area of shade trees: forest cover	3.06	0.09	-0.14
Low	Species number	wasp	y ~ forest cover	3.13	0.08	0.11
Low	Species number	wasp	y ~ basal area of shade trees	3.31	0.08	-0.07
Low	Species number	wasp	y ~ shade tree diversity: forest cover	3.34	0.08	-0.06
Low	Species number	wasp	y ~ management intensity	3.41	0.07	-0.02
Intermediate	**Species number**	**wasp**	**y ~ management intensity**	**0**	**0.66**	**0.45**
Intermediate	Species number	wasp	y ~ management intensity: forest cover	3.81	0.1	-0.45
Intermediate	Species number	wasp	y ~ forest cover	4.46	0.07	-0.38
Intermediate	Species number	wasp	y ~ shade tree diversity	4.93	0.06	-0.37
Intermediate	Species number	wasp	y ~ shade tree diversity: forest cover	5.2	0.05	0.45
Intermediate	Species number	wasp	null	5.74	0.04	0
Intermediate	Species number	wasp	y ~ basal area of shade trees	7.29	0.02	-0.22
Intermediate	Species number	wasp	y ~ basal area of shade trees: forest cover	8.75	0.01	-0.07
High	Species number	wasp	y ~ management intensity: forest cover	0	0.32	-0.55
High	**Species number**	**wasp**	**null**	**0**	**0.25**	**0.48**
High	Species number	wasp	y ~ shade tree diversity	2.49	0.09	0.2
High	Species number	wasp	y ~ basal area of shade trees	2.65	0.09	-0.19
High	Species number	wasp	y ~ basal area of shade trees: forest cover	3.05	0.07	0.16
High	Species number	wasp	y ~ management intensity	3.2	0.06	0.13
High	Species number	wasp	y ~ shade tree diversity: forest cover	3.43	0.06	0.11
High	Species number	wasp	y ~ forest cover	3.52	0.06	0.08
Low	**PCoA 1**	**wasp**	**null**	**0**	**0.40**	**0**
Low	PCoA 1	wasp	y ~ shade tree diversity	0.14	0.37	0.19
Low	PCoA 1	wasp	y ~ management intensity: forest cover	4.46	0.04	0.05
Low	PCoA 1	wasp	y ~ basal area of shade trees: forest cover	4.6	0.04	0.05
Low	PCoA 1	wasp	y ~ shade tree diversity: forest cover	4.7	0.04	-0.03
Low	PCoA 1	wasp	y ~ management intensity	4.71	0.04	-0.03
Low	PCoA 1	wasp	y ~ basal area of shade trees	4.71	0.04	-0.03
Low	PCoA 1	wasp	y ~ forest cover	4.77	0.04	0.02
Intermediate	**PCoA 1**	**wasp**	**y ~ management intensity**	**0**	**0.92**	**0.25**
Intermediate	PCoA 1	wasp	null	7.01	0.03	0
Intermediate	PCoA 1	wasp	y ~ management intensity: forest cover	7.69	0.02	-0.18
Intermediate	PCoA 1	wasp	y ~ shade tree diversity: forest cover	9.13	0.01	0.19
Intermediate	PCoA 1	wasp	y ~ shade tree diversity	9.28	0.01	-0.13
Intermediate	PCoA 1	wasp	y ~ basal area of shade trees: forest cover	9.78	0.01	-0.1
Intermediate	PCoA 1	wasp	y ~ forest cover	10.61	0	-0.08
Intermediate	PCoA 1	wasp	y ~ basal area of shade trees	10.86	0	-0.06
High	**PCoA 1**	**wasp**	**y ~ basal area of shade trees: forest cover**	**0**	**0.48**	**0.3**

High	**PCoA 1**	**wasp**	**y ~ forest cover**	**0.22**	**0.43**	**0.27**
High	PCoA 1	wasp	null	4.56	0.05	0
High	PCoA 1	wasp	y ~ shade tree diversity: forest cover	6.81	0.02	-0.18
High	PCoA 1	wasp	y ~ management intensity	7.14	0.01	-0.16
High	PCoA 1	wasp	y ~ basal area of shade trees	8.16	0.01	0.12
High	PCoA 1	wasp	y ~ management intensity: forest cover	8.72	0.01	-0.13
High	PCoA 1	wasp	y ~ shade tree diversity	9.33	0	-0.02

Appendix F. Ordination of social wasp species according to (A) the management intensity in 10 shaded cocoa agroforests, located in the region with intermediate deforestation, and to (B) forest cover in the landscape and basal area of shade trees in 10 shaded cocoa agroforests, located in the region with intermediate deforestation, in southern Bahia, Brazil.



CONCLUSÃO GERAL

A conversão de habitats nativos em áreas agrícolas representa uma ameaça às múltiplas facetas da biodiversidade, e mitigar tais efeitos é um dos principais desafios a serem enfrentados, especialmente por conservacionistas e formuladores de políticas públicas. Aqui nós demonstramos que matrizes agrícolas representam, de modo geral, uma ameaça para a manutenção da diversidade de abelhas em paisagens agrícolas. Mas também demonstramos que um modelo alternativo de produção, as agroflorestas de cacau sombreado, pode desempenhar um papel determinante na retenção não apenas da diversidade de abelhas, mas também de vespas sociais. Além disso, nós demonstramos que, apesar destas agroflorestas representarem uma oportunidade de conciliar conservação com a produção agrícola, o valor de conservação destes sistemas depende, sobretudo, da manutenção de uma alta cobertura florestal em múltiplas escalas.

Estes resultados possuem importantes implicações para a conservação da biodiversidade principalmente se considerarmos a atual situação de mudanças no uso do solo na região sul da Bahia, em que produtores têm optado por substituir o sistema de produção cacau-cabruca por sistemas mais intensivos e de maior rentabilidade a curto e médio prazo. Tais sistemas, que incluem principalmente monoculturas de cacau, café, eucalipto e pastagens destinadas a criação de gado, são reconhecidos por impactarem negativamente a biodiversidade. Portanto, um cenário de intensificação de uso do solo representa uma grave ameaça para a conservação em um ponto especialmente importante da Mata Atlântica. Sendo assim, nós recomendamos que políticas públicas que objetivam favorecer a conservação da biodiversidade e dos serviços ecossistêmicos promovam o apoio a produtores de cacau que optarem pela manutenção do sistema tradicional de cultivo cacau-cabruca. Tais incentivos podem incluir, por exemplo, medidas capazes de aumentar a produtividade destes sistemas, como o acesso facilitado a tecnologias, assistência técnica e insumos para adubação do solo – que tem sido um dos principais determinantes da produtividade de cacau na região - e, principalmente, incentivos econômicos, como o Pagamento por Serviços Ambientais. Finalmente, sugerimos que os esforços de conservação da biodiversidade também sejam destinados à restauração de habitats nativos que, além de contribuir para retenção de espécies nativas em paisagens agrícolas, pode garantir a continuidade e viabilidade da produção de cacau em países tropicais - ameaçada sobretudo pelo atual cenário de mudanças climáticas e crise da biodiversidade.