Sociobiology 72(3): e11410 (September, 2025) DOI: 10.13102/sociobiology.v72i3.11410

Sociobiology
An international journal on social insects

REVIEW

Effect of Agricultural Matrices on the Biodiversity Metrics of Bees (Hymenoptera: Anthophila): A Review

José V. A. Ferreira[1*], Juliana M. de Almeida-Rocha[2], José C. Morante-Filho[1], Danielle Storck-Tonon[3], Maíra Benchimol[1]

1 - Applied Ecology and Conservation Lab, Universidade Estadual de Santa Cruz, Ilhéus-BA, Brazil
2 - The Nature Conservancy, São Paulo-SP, Brazil
3 - Programa de Pós-Graduação em Ambiente e Sistemas de Produção Agrícola (PPGASP), Universidade do Estado de Mato Grosso, Tangará da Serra-MT, Brazil

Article History

Edited by
Kleber Del-Claro, UFU, Brazil
Received 03 November 2024
Initial acceptance 31 December 2024
Final acceptance 06 February 2025
Publication date 15 July 2025

Keywords
Biodiversity conservation, biodiversity-friendly matrices, cropland, pollinators, species loss.

Corresponding author
José Victor Alves Ferreira
Applied Ecology and Conservation Lab
Universidade Estadual de Santa Cruz
Rodovia Jorge Amado Km 16
CEP: 45662-900 - Ilhéus-BA, Brasil.
E-Mail: ferreirajvabio@gmail.com

Abstract

Agriculture has been globally responsible for biodiversity decay. Since 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). We calculated the effect size from the standardized mean difference among agriculture-native habitats in the meta-analysis. We considered moderators that may influence this effect, including response type, flowering type, crop life cycle, and region. Based on the review, which mainly included studies conducted in the neotropical region, we identified that 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 (as such, cocoa agroforests with low or high diversity of native shade trees). Additionally, meta-analysis supports this finding by revealing an overall negative effect, especially for abundance. Negative effects were consistent for non-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.

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),

ISSN: 0361-6525

which directly contributes to reduced species diversity of several faunal groups, including terrestrial insects (van Klink et al., 2020; Raven & Wagner, 2021).

Agricultural expansion and intensification have driven many insect species to local extinctions, including species that could directly enhance productivity (Raven & Wagner, 2021). Since insects provide a wide range of ecological functions, such as pest control and pollination (Yang & 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 & 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; Rahimi et al., 2022; Ockermüller et al., 2023), 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 & 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 non 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 & 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 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). We used the abovementioned words in English, Portuguese, and Spanish for this. 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 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 recently published (Ferreira et al., 2024) and therefore was unavailable during the literature search, whereas the others comprise unpublished data. The first unpublished database 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 48 hours at each site sampled. The data was provided by the "Economia das Cabrucas" project (see Ferreira et al. (2024) for more details about the study area). The second unpublished dataset refers to surveys conducted in soybean monocultures and native Cerrado remnants, in the south-central region of Mato Grosso, Brazil. The data was provided by the project "Rede de Biotecnologia Aplicada aos Serviços e Desserviços da Biodiversidade à Agricultura no Cerrado e na Amazônia" (BIOAGRO; see Oliveira et al. (2022) for more details about the study area).

Screening process

As inclusion criteria for the studies to be included in the review and meta-analysis, 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 of this short distance makes it difficult to determine whether the bees found in this transitional area are 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 these 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; Table S1).

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 the agricultural matrix on bee's 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 exclude exotic species or provided a data set that allowed for this type of distinction. We classified and quantified all 32 studies according to the characteristics of the agricultural matrices, i.e., i) flowering type (mass flowering or non 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 Table S1.

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 agricultural matrix; and vi) 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

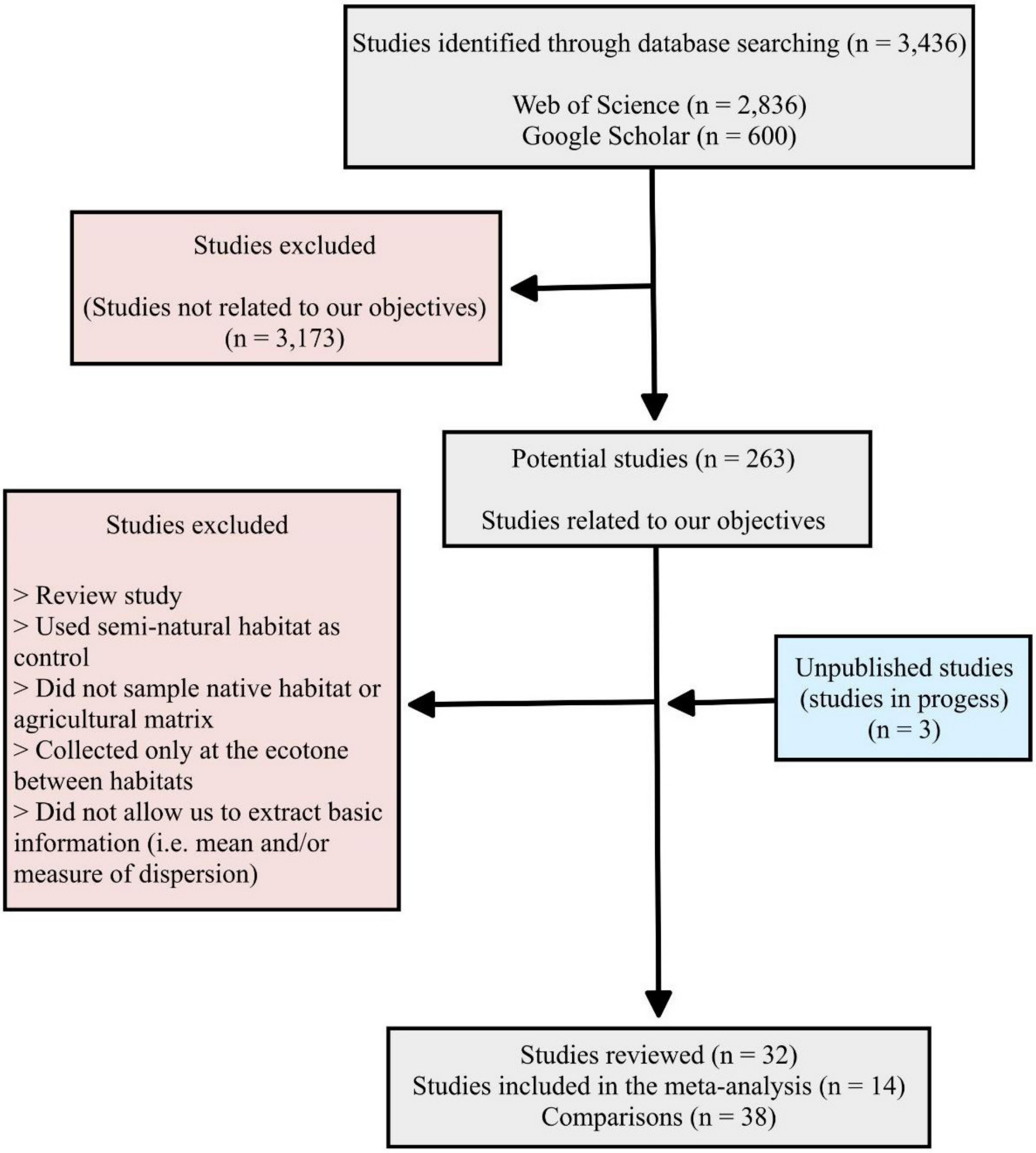

Fig 1. Diagram of the stages of selection and exclusion of studies used in our review (n = 32) and meta-analysis (n = 14) evaluating the effects of agricultural matrices on bee richness and/or abundance.

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 effects 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).

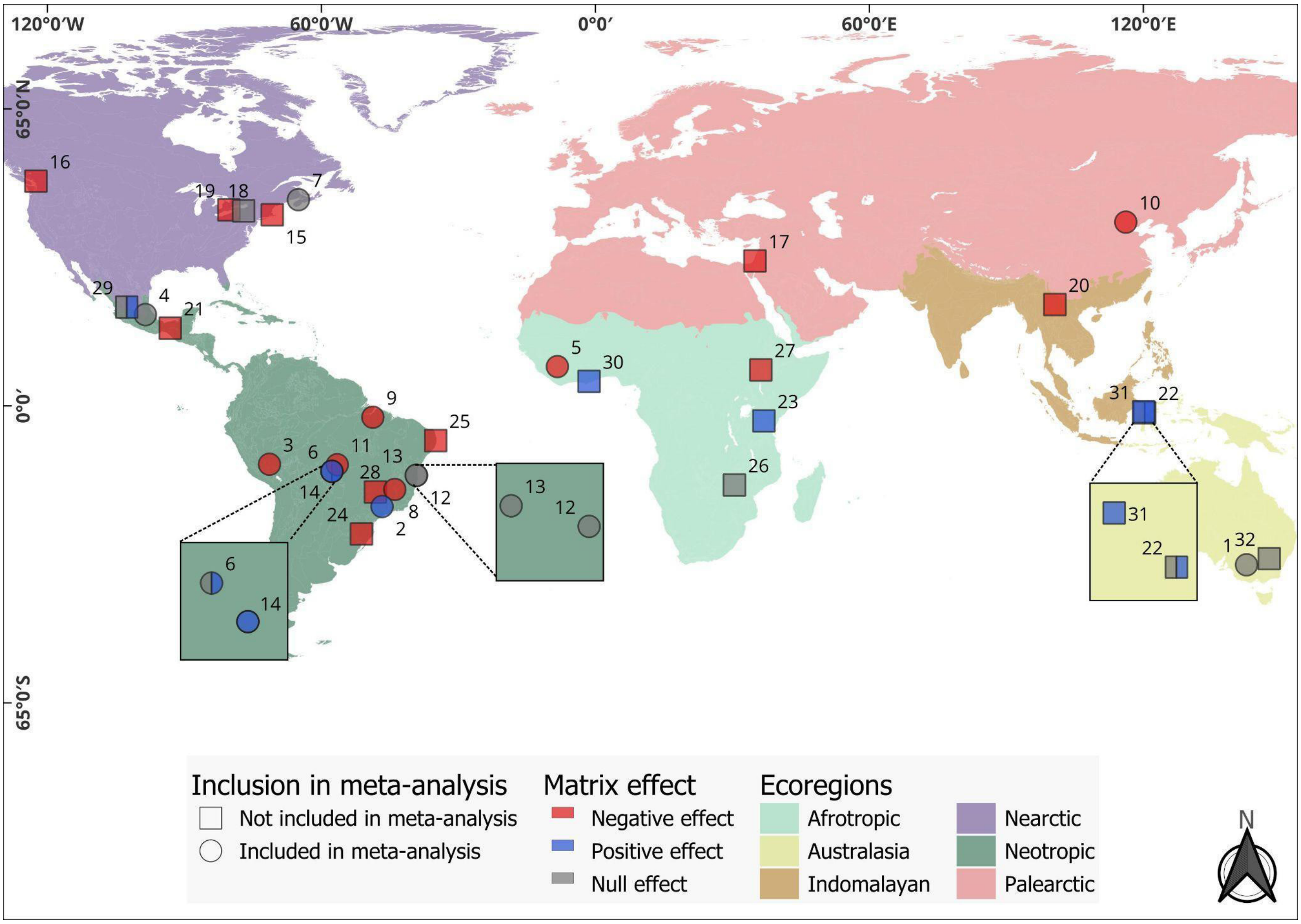

Fig 2. Global distribution of the 32 studies used in our review. Square and circle symbols represent, respectively, the 18 studies not included, and the 14 studies included in our meta-analysis. The effect of agricultural matrix on bee diversity, defined based on the main conclusions of the reviewed studies, is represented by the symbol colors – red = negative, blue = positive and gray = neutral. See Table S1 for details of each study.

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 non-mass-flowering), life-cycle of crops (perennial or annual crops), and region (tropical or temperate). We repeated the same general approach of random effects meta-analysis for each subgroup 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 & Tweedie, 2000) to estimate the number of missing studies 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 a non-significant effect that, if included in our meta-analysis, would render our results non-significant. We used the bootstrap approach for 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 the biodiversity metrics of bees (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, as cacao agroforests with a low diversity of planted shade trees, or positive when considering less intensive management, as cocoa agroforests with several natural shade trees).

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; 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 had two studies (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 (28.1%) 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; Table S2). We also observed a high heterogeneity among the studies' effect sizes (I2 = 78%). Regarding publication bias, despite the funnel plot suggesting an asymmetry (Fig S1), the Trim and Fill test indicated that only nine studies needed to be included in the dataset to complete a symmetric

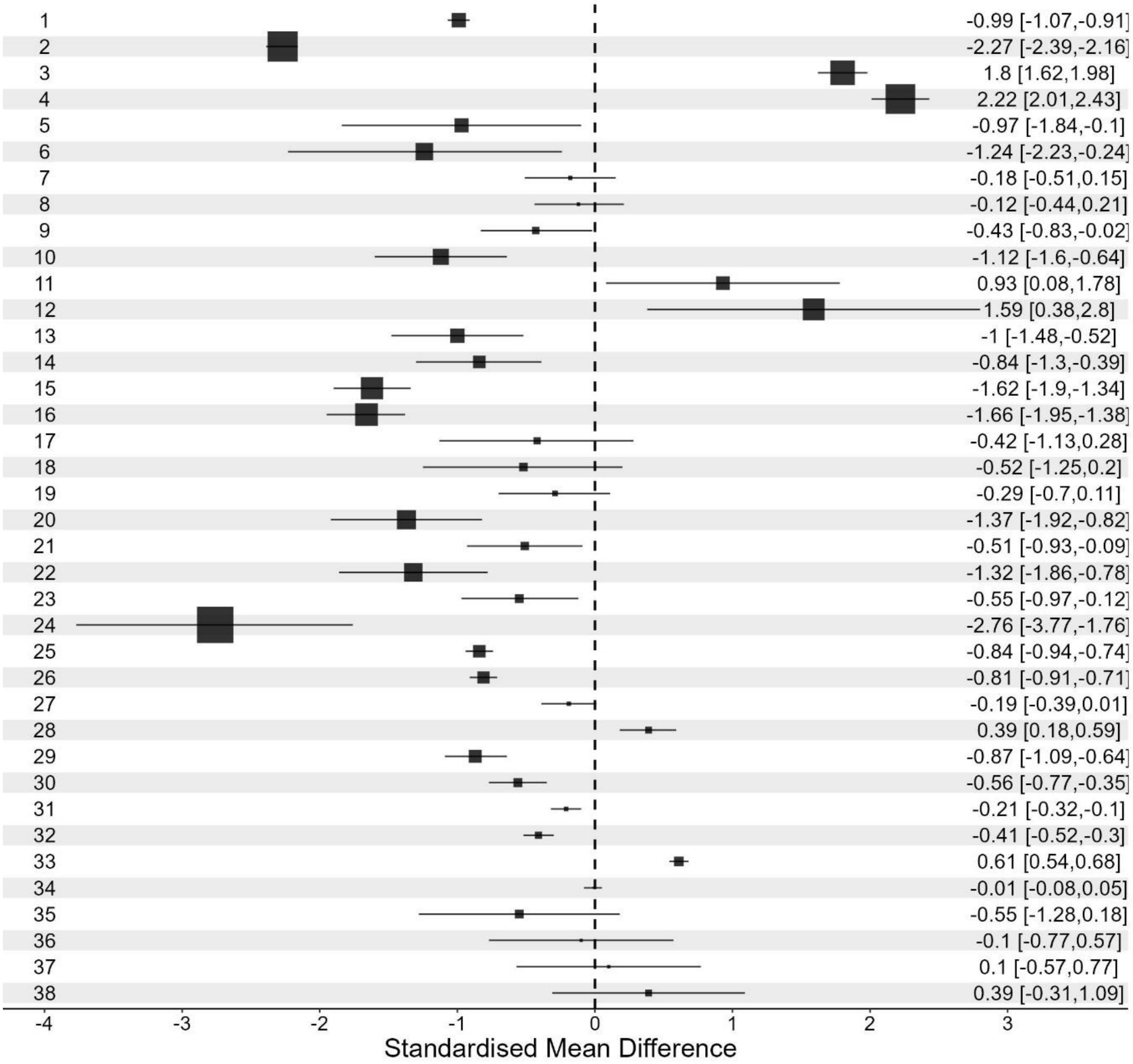

Fig 3. Effect size of the 38 pairwise from 14 studies investigated in meta-analysis. The horizontal bars indicate a 95% confidence interval. Black square indicates the individual effect (size is proportional to effect size). Negative and positive values indicate, respectively, a negative and positive 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.

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.

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 non 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 non-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 know, this is the first review investigating the effects of different agricultural matrices on the abundance and species richness of bees globally. Unlike 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 converting natural habitats to agricultural lands is consistently more detrimental to bee conservation than previously thought, driven mainly by monocultures in temperate regions.

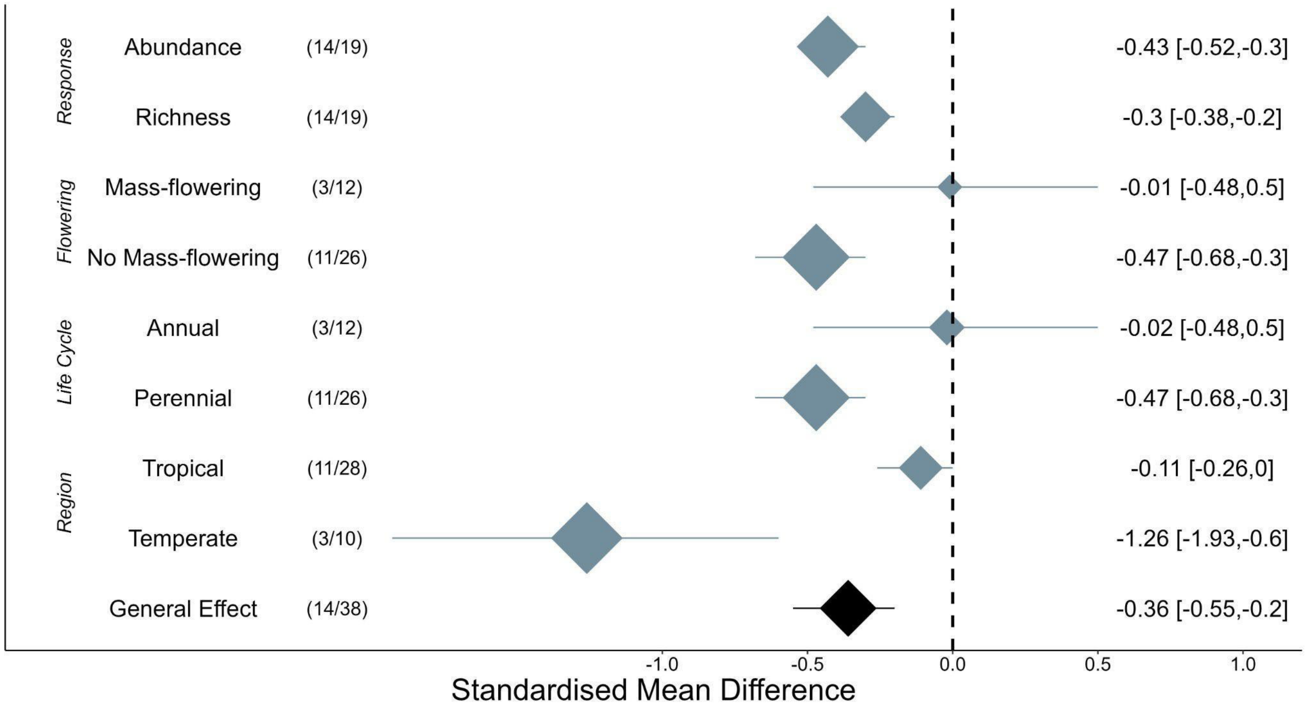

Fig 4. Effect size, calculated with the bootstrap approach, for the different subgroups: type of response (abundance or richness of bees), type of flowering (massive and no-mass flowering), life-cycle (annual or perennial), biogeographic region (tropical or temperate). The horizontal bars indicate a 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.

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, reinforcing that agricultural systems are 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), has serious impacts at a population and community level (Brittain & Potts, 2010; Belsky & 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 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 demonstrated that matrices composed of non-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 crops are associated with food resource availability and bee nesting site provision. We cannot overlook the fact that there was an 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 non-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 & Goodell, 2011). Besides the reduced diversity of food resources available in agricultural areas, the smaller amount of these resources in agricultural matrices without mass flowering negatively impacts the maintenance of bee populations. On the other hand, crops with mass flowering may provide an ample supply of food resources, such as nectar and pollen, and therefore favor 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 why we did not find a significant effect of these flowering type crops on bee diversity. However, this result should be cautiously observed, 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 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 crops. Therefore, this result supports the idea that even crops that could have reduced negative effects on bee diversity substantially affect these insects. Hence, these findings demonstrate that, although some perennial crops support high species richness, these environments are insufficient to harbor and retain high bee diversity.

Our findings also demonstrated 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 conserving 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 habitats as a control. Therefore, despite the more significant history of agricultural activities in temperate regions, bee assemblages remain sensitive to replacing native habitats with 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 shown a negative or neutral effect, we failed to detect 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 soybean 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 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 characteristic could reduce isolation and favour the access of bees to the agricultural matrix, which possibly contributed to explaining the lack of effect on species abundance and richness 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 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. Furthermore, 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 to 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 biodiversity maintenance.

Acknowledgements

We want to thank our funders: The Rufford Foundation (nº 36668-1 and 28847-1), Fundo Brasileiro para Biodiversidade (FUNBIO, nº 039/2022), along with the Humanize Institute and Eurofins, Idea Wild, and the Pró-Reitoria de Pesquisa e Pós-Graduação (PROPP nº 073.6764.2021.0013306-41) at the Universidade Estadual de Santa Cruz (UESC). We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) for the Doctoral Scholarship Grant awarded to José Victor Alves Ferreira (Grant ID 88887. 814823/2023-00) and the Technological Development for the productivity grant awarded to Maíra Benchimol (304189/2022-7) and José Carlos Morante-Filho (303302/2022-4). We also thank the authors to kindly sent the data to us, even not being included in the analysis due to data limitations: Ana Gabriela Armas Quiñonez, Ana Montero Castaño, Brianne Du Clos, Cory S. Sheffield, Derek W. Rosenberger, Dušanka Vujanović, Hugo Reis Medeiros, Jason M. Tylianakis, Manu E. Saunders, Marina P. Rosanigo, Paula María Montoya-Pfeiffer, Pia E. Lentini, Robert M. Ewers, Saul A. Cunningham, Thaline F. Brito and Gudryan J. Baronio for sending us the requested data, even though not all studies were included in our analyses. We also thank those responsible for the projects "Rede de Biotecnologia Aplicada aos Serviços e Desserviços da Biodiversidade à Agricultura no Cerrado e na Amazônia" (BIOAGRO) and "Eco-nomia das Cabrucas" for sharing data that have not yet been published. Finally, we thank Paloma S. Resende, Martín de Jesús Cervantes-López, Gabriela Alves-Ferreira, Leiza Aparecida Souza Serafim Soares, and members of the Applied Ecology and Conservation Lab (LEAC / UESC) for their discussions and contributions throughout the development of this study and the anonymous reviewers for their excellent suggestions, which helped improve the manuscript.

Authors' Contributions

J.V.A.F.: Conceptualization, methodology, formal analysis, writing-original draft, writing-review & editing.
J.C.M-F: Conceptualization, methodology, supervision, writing-review & editing.
JMA-R: Methodology, supervision, writing-review & editing.
DS-T: Methodology, supervision, writing-review & editing.
MB: Methodology, supervision, 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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