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Neglecting non-bee pollinators may lead to substantial underestimation of competition risk among pollinators

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ABSTRACT

Due to the increasing pressures on bees, many beekeepers currently wish to move their managed livestock of *Apis mellifera* into little disturbed ecosystems such as protected natural areas. This may, however, exert detrimental competitive effects upon local wild pollinators. While it appears critical for land managers to get an adequate knowledge of this issue for effective wildlife conservation schemes, the frequency of this competition is not clear to date. Based on a systematic literature review of 96 studies, we assessed the frequency of exploitative competition between honey bees and wild pollinators. We found that 78% of the studies highlighted exploitative competition from honey bees to wild pollinators. Importantly, these studies have mostly explored competition with wild bees, while only 18% of them considered other pollinator taxa such as ants, beetles, bugs, butterflies, flies, moths, and wasps. The integration of non-bee pollinators into scientific studies and conservation plans is urgently required as they are critical for the pollination of many wild plants and crops. Interestingly, we found that a majority (88%) of these studies considering also non-bee pollinators report evidence of competition. Thus, neglecting non-bee pollinators could imply an underestimation of competition risks from honey bees. More inclusive work is needed to estimate the risks of competition in its entirety, but also to apprehend the context-dependency of competition so as to properly inform wildlife conservation schemes.

1. Introduction

Recent studies have highlighted a global decline in wild bee populations (Biesmeijer et al., 2006; Koh et al., 2016; Zattarra and Aizen, 2021) and increased mortality rates in the livestock of managed honey bees *Apis mellifera* (Requier et al., 2018; Gray et al., 2023; Bruckner et al., 2023; Requier et al., 2024). These colony losses force beekeepers to increase their livestock to compensate for the mortalities, resulting in a global increase in the number of managed honey bee colonies (Phiri et al., 2022). Threats to bee populations have alarmed scientists and public authorities given their ecological and economic importance

(Potts et al., 2016; Pérez-Méndez et al., 2020). The safeguard of wild and managed bees is essential for the maintenance of pollination services, food security and associated human well-being (Potts et al., 2016). Yet, this major ecosystem service is threatened by land use change, intensification and associated disturbances that strongly impact both wild and managed pollinators.

Land use changes and intensification have greatly modified many habitats including agricultural landscapes, confronting bees (and other pollinator insects) to disturbances in food resource availability (Requier et al., 2015, 2017, 2020; Timberlake et al., 2019) and exposure to pesticides (Henry et al., 2012, 2015; Prado et al., 2019; Barascou et al.,

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2022). Consequently, many agricultural dominated landscapes are today inhospitable for pollinators and beekeepers (Otto et al., 2016; Dixon et al., 2021). In contrast, due to their rich and diversified (floral) food resources and their lower exposure to pesticides, protected natural areas are of great interest to beekeepers seeking to minimize colony loss (Geldmann and González-Varo, 2018; Henry and Rodet, 2018; Valido et al., 2019). Thus, more and more beekeepers place or move their managed honey bee colonies to protected natural areas (Geldmann and González-Varo, 2018). However, these preserved areas are also considered as sanctuaries for the conservation of wild pollinators (Öckinger et al., 2007; Morandin and Kremen, 2013; Ropars et al., 2020a).

Recent studies have shown that the introduction of honey bee colonies into protected areas could deplete floral resources with detrimental effects on populations of wild pollinators (e.g., Magrach et al., 2017; Henry and Rodet, 2018; Valido et al., 2019; Ropars et al., 2020b, 2022; Page and Williams, 2023a, 2023b; MacInnis et al., 2023; Prendergast and Ollerton, 2022; Weaver et al., 2022; Casanelles-Abella et al., 2023; MacKell et al., 2023; Mouillard-Lample et al., 2023; Sponsler et al., 2024). In particular, studies suggest potential causal links between this exploitative competition and the fitness of wild pollinators (e.g., Cane and Tepedino, 2017; Fig. 1). Exploitative competition from honey bees can lead to local food limitation in nectar and pollen (Carneiro and Martins, 2012; Sponsler et al., 2024) with consequences for wild pollinator foraging, such as an increase foraging activity and energy expenditure by exploring more distant resources and longer flights (Thomson, 2004; Zurbuchen et al., 2010), an increase in predation risk (Sponsler et al., 2023), which can lead to a decrease in food acquisition (Carneiro and Martins, 2012; Cane and Tepedino, 2017), and a decrease in time spent caring for nest construction and offspring (Sponsler et al., 2023; Goodell, 2003; Fig. 1). In turn, these foraging disruptions can lead to detrimental effects on the fitness of wild pollinators (Cane and Tepedino, 2017), such as male-biased sex ratios (Peterson and Roitberg, 2006; Bosch, 2008), a decrease in the quantity of offspring due to predation and parasitism (Goodell, 2003), and a decrease in the quality of offspring with, for example, smaller body size (Tepedino and Torchio, 1982; Bosch, 2008; Fig. 1). There are also two other competition processes at play: apparent competition and interference competition (Zakardjian et al., 2022; Geslin et al., 2023). In the apparent competition, managed and wild pollinators may indirectly compete with each other due to the effect of shared pathogens that may spread among individuals through successive visits of the same flowers (Alger et al., 2019a, 2019b; Dalmon et al., 2021; Cilia et al., 2022). Finally, in interference competition, individuals may compete among each other through direct physical fight, while accessing the same flower, or through kleptoclept where by the largest or most aggressive individuals or the robber are generally favored (Cairns et al., 2005; Londei and

Marzi, 2024).

Of major importance, the competition issue is becoming more and more prominent in conservation science. While reviews exist on the potential risks and disturbances of introducing honey bee colonies on the ecology of wild pollinators (e.g., Geslin et al., 2017, 2023; Mallinger et al., 2017; Agüero et al., 2018; Wojcik et al., 2018; Iwasaki and Hogendoorn, 2022; Sponsler et al., 2023), most have focused on the potential impact of honey bees on other Anthophila (i.e., wild bees). Little is known about the proportion of studies reporting evidence of competition between honey bees and wild pollinators when considering a larger diversity of pollinator taxa, such as the inclusion of ants, beetles, bugs, butterflies, flies, moths, and wasps, whose contribution to plant pollination and crop yields is demonstrated in an increasing number of studies (e.g., Rader et al. 2016, Lucas et al., 2018a; Rader et al., 2020; Doyle et al., 2020, Page et al., 2021, 2023a, Travis and Kohn, 2023, Requier et al., 2023, Muinde and Katumo, 2024).

For that purpose, we performed an extensive literature search using the *Web of Science* section of the bibliographic database *ISI Web of Knowledge* (*Web of Knowledge*, 2022). We used the *TS* function to define the search strings (i.e. the criteria keywords) in order to separate articles that had studied the topic of interest from those which only mentioned it. We included all literature from 1945 until May 2020. The complete search string was "(TS=Apis mellifera OR TS=honeybee* OR TS=honey bee*) AND (TS=wild OR TS=ative) AND (TS=competit* OR (TS=pathogen* AND (TS=transmission* OR TS=spill-over* OR TS=spillover*)))". This search revealed 325 studies. Abstracts and full texts were reviewed for relevance, in order to select empirical studies using original data and to exclude review papers and simulation-based studies. Lastly, given that it is acknowledged that combining search methods improves the robustness and completeness of a systematic literature review (Booth et al., 2021), we included 29 additional studies not found in the automatic process described above, based on the authors' expertise (e.g. found in the references of selected publications). A total of 96 studies estimating the risk of exploitative competition between honey bees and wild pollinators was therefore selected for the review (see the complete list in **Supporting Information, Appendix A**). Response variables of wild pollinators commonly measured for quantifying competition were classified in five variables including number of pollinators, richness/diversity of pollinators, foraging behavior (e.g. time of flower visit and part of the flower that was visited), fitness (e.g. offspring quantity and quality) and other (i.e. different of the four other variables) (Fig. 2). The predictor variables often used to quantify the degree of honey bee competition pressure were classified in five variables including number of honey bees, foraging behavior (e.g. time of flower visit and part of the flower that was visited), density of colonies, distance to colonies and other (i.e. different of the four other variables)

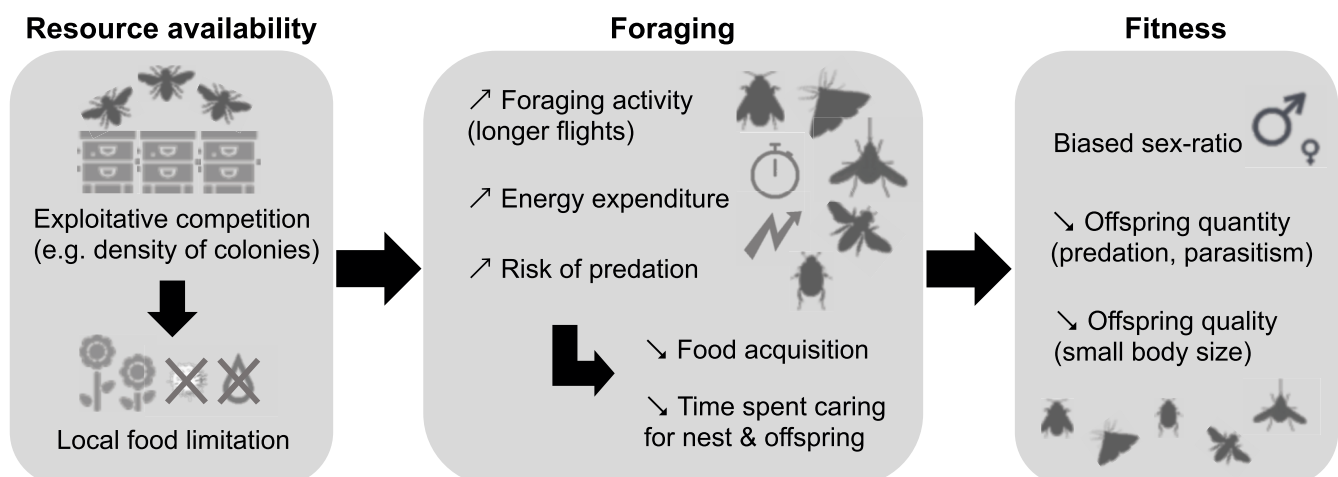


Fig. 1. Potential causal links between exploitative competition and the fitness of wild pollinators. Icons used from www.freepik.com.

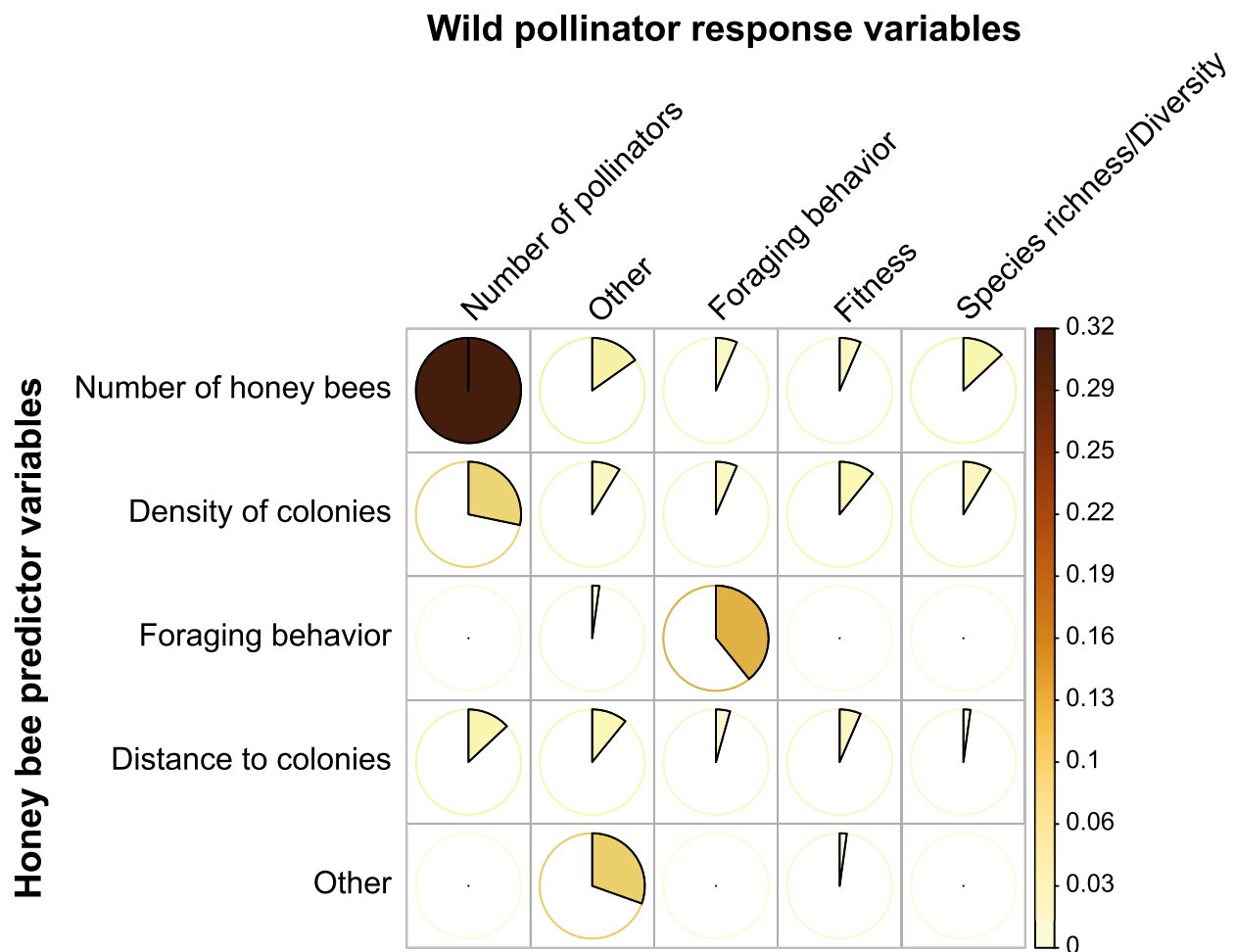


Fig. 2. Diversity of variables usually used to study the risk of competition between honey bee predictor variables (i.e. the predictor variables often used to quantify the degree of honey bee competition pressure) and wild pollinator response variables. Color gradient and pie charts represent the frequency of occurrence of variables based on the articles considered in this review ($n = 96$ articles).

(Fig. 2).

2. Frequency of the competition among pollinators

Among the 96 articles considered, only one study found a positive effect of honey bees on wild pollinators (Nielsen et al., 2012). This study analyzed whether the presence of honey bees affected the visitation rate of wild pollinators on plant species in European countries. The authors found a positive relationship between visitation frequencies of honey bees and bumble bees, suggesting that the presence of honey bees enhanced the bumble bee visitation rate in the study sites considered. However, they noted that this does not indicate a general absence of competition, as other relationships (positive, negative, and neutral) were found with hoverflies and solitary bees. The study highlighted the need to consider multiple factors such as flower abundance, diversity of pollinators, and climate when analyzing competition risk, indicating that it is a complex and potentially context-dependent phenomenon.

On the other hand, we found that 78% ($n = 75$ articles) of the articles identified an exploitative competition from honey bees to wild pollinators. This estimate confirms previous finding (66% in Iwasaki and Hogendoorn, 2022). These studies highlighted that honey bees could have a negative effect on pollination services driven by wild pollinators by reducing the diversity of wild pollinators and their foraging activity (e.g. Valido et al., 2019; Leguizamón et al., 2021). The other 22% ($n = 21$ articles) of the articles found no effect of honey bees on wild pollinators (e.g. Roubik et al., 1986; Steffan-Dewenter and Tschamtkke, 2000;

Roubik and Wolda, 2001). This result suggests that competition between honey bees and wild pollinators is frequently observed but is not systematic (see also Wojcik et al., 2018), and potentially context dependent. It is also possible that a part of those studies was carried out under conditions of low beekeeping density, below certain ecological threshold liable to trigger competition per se (e.g., Henry and Rodet, 2018; McCune et al., 2020).

It is important to note that there is currently no standardized method to study competition risk among pollinators. For instance, we found a wide diversity of honey bee variables and wild pollinators response variable used across the 96 studies considered in the review (Fig. 2). The main metric used is the number of honey bees observed visiting flowers (Hudewenz and Klein, 2015; Torné-Noguera et al., 2016), that may be further weighted by the distance to nearest honey bee colonies (Ropars et al. 2022). Other candidate metrics are the distance to honey bee colonies, the density of honey bee colonies in the surrounding landscape, and the foraging behavior (Steffan-Dewenter and Tschamtkke, 2000; Goras et al., 2016; Ropars et al. 2019; Fig. 2). Response variable used could either refer to the number, the foraging behavior, the species richness and diversity of wild pollinators or to bipartite network metrics (Torné-Noguera et al., 2016; Ropars et al., 2019, 2022; Fig. 2). The use of such a wide diversity of methods makes it difficult to robustly assess the frequency of competition risk among pollinators and may bias estimates of competition. Thus, methodological standardizations are urgently required (see also Henry and Rodet, 2018).

3. Beyond the risk of competition between *Apis* and non-*Apis* bees

One hypothesis of the context-dependency of the competition risk among pollinators could be the diversity of the pollinator community considered in the studies. Indeed, increasing number of studies demonstrates the critical role of Diptera, Lepidoptera, Coleoptera, Hemiptera and non-bee Hymenoptera in the pollination of wild plants and crops (Rader et al., 2016, 2020; Doyle et al., 2020; Requier et al., 2023). Pollinator diversity, including non-bee species such as ants, beetles, bugs, butterflies, flies, moths, and wasps, contributes to crop pollination even in the presence of honey bees (Garibaldi et al., 2013; Orford et al., 2015; Rader et al., 2016, 2020; Schurr et al. 2021). Overall, it is estimated that non-bee pollinators perform 25–50% of the flower visits in global important crops (Rader et al., 2016). Thus, we explored whether the competition studies actually considered this pollinator diversity. Importantly, we found that 82% ($n = 79$ articles) of the studies assessing the risk of competition among pollinators focused only on the impact of honey bees on wild bees, i.e. focused on the risk of competition between *Apis* and non-*Apis* bees. Among the 17 studies (18%) that extended their analyses to other insect groups (Table 1), we found that Diptera were systematically considered (see also Sladonja et al., 2023), followed by Lepidoptera and Coleoptera (Table 1). Other insect groups, such as Hemiptera and Neuroptera, were considered in an even more marginal way. Very interestingly, we found that 88% of these studies ($n = 15$ of the 17 articles) reported a negative effect of the presence of honey bees on these wild (non-bee) pollinators, instead of 76% ($n = 60$ of the 79 articles) for the articles considering only bees in the competition risk (Fig. 3). This result suggests that focusing on the effect of honey bees on wild bees could underestimate the risk of competition (Fig. 4).

4. Neglecting pollinator diversity would underestimate competition risk among pollinators

A large number of studies assessing the risk of competition among pollinators currently omit pollinator diversity in their entirety by solely focusing on the interaction between honey bees and wild bees. Although bees contribute critically to pollination in agriculture (Requier et al., 2023), the rest of the pollinators have an essential role in plant-pollinator interaction networks in nature. Diptera, for example, are the second most important pollinators and visit about 72% of crops (Rader et al., 2016, 2020). It is also not surprising to note that it is the most studied taxon within the 16 articles extending their fields of research to pollinators other than Apoidea. Among them, hoverflies are one of the main taxa visiting plants for floral rewards in nectar and pollen (Doyle et al., 2020). Adult hoverflies indeed require significant

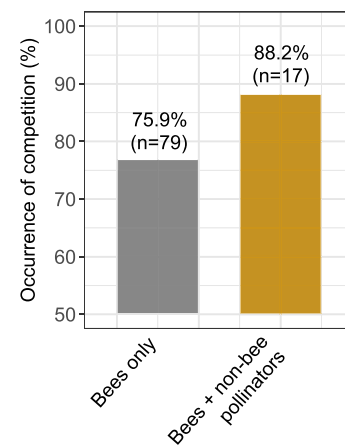


Fig. 3. Frequency of occurrence of competition (%) reported considering only wild bees ($n = 79$ articles) or wild bees + non-bee pollinators ($n = 17$ articles).

supplies of energy through nectar for flight or for laying eggs (Schneider, 1948). During their sexual maturation, females also need to consume large amounts of protein and amino acids, and thus consume substantial amounts of pollen. Lepidoptera (butterflies) are also a known example of a nectar-consuming pollinator. We found that 59% ($n = 10$) of the article considering non-bee pollinators in the competition risk from honey bees included Lepidoptera. Competition with honey bees for floral resources should therefore impact all wild pollinators and not considering them would underestimate this competition especially since some recent studies have shown that this impact differs from one species to another, probably related to their morphological characteristics (Henry and Rodet, 2018; Leguizamón et al., 2021; Lázaro et al., 2021; Ropars et al. 2022).

On the other hand, to improve our understanding of these risks of competition, taking into account the complex networks of interactions between plants and pollinators constitutes a significant path for improvement. While plant-bee networks are largely explored, there is a lack of knowledge about floral diet of Diptera, Lepidoptera and Coleoptera taxa (Orford et al., 2015; Klecka et al., 2018; Howlett et al., 2021). Therefore, specialization of these taxa on plant species is still unknown. Some bees, for example, are monolectic and specialize in pollen from specific plants, as opposed to oligolectic bees that forage on several genera of plants or polylectic bees that forage on several families of plant (Wojcik et al., 2018). This is also reported for hoverflies, which sometimes select their floral resources (Gilbert 1981; Lucas et al., 2018b). Competition risk is consequently stronger on specialist species which cannot modify their floral diet when honey bees focused on their

Table 1

Summary of the species studied in the articles resulting from the synthesis of the literature and taking wild pollinators into account more broadly ($n = 17$).

	Diptera	Lepidoptera	Coleoptera	Hymenoptera (other than bees)	Hemiptera	Other (e.g. Araneae, Neuroptera, Thysanopter)
Horskins and Turner (1999)	X	X	X	X	X	X
Kato and Kawakita (2004)	X	X	X	X		X
Levitt et al. (2013)	X	X	X	X	X	X
Polatto and Chaud-Netto (2013)	X	X	X	X		
Hung et al. (2019)	X	X	X	X		
Aizen and Feinsinger (1994)	X	X		X		
Alomar et al. (2018)	X	X	X	X		
Badano and Vergara (2011)	X		X	X		
Smith-Ramírez et al. (2014)	X		X	X		
Mallick and Driessen (2009)	X	X	X			
Ropars et al. (2019)	X	X	X			
Valido et al. (2019)	X	X	X			
Conner and Neumeier (1995)	X					
Jeavons et al. (2020)	X					
Lindstrom et al. (2016)	X					
Magrach et al. (2017)	X					
Tepedino et al. (2007)	X					

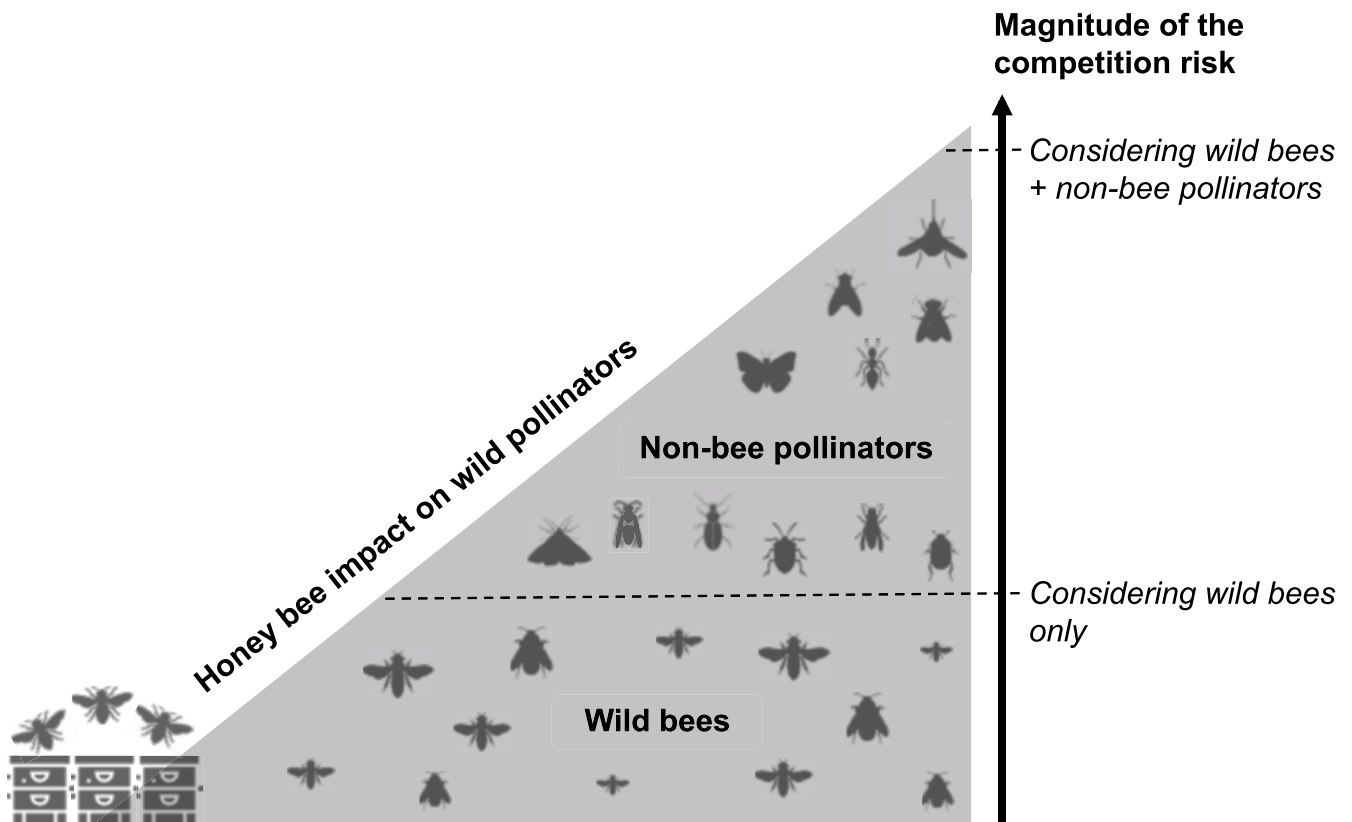


Fig. 4. Conceptual illustration of the potential underestimation of the competition risk among pollinators by neglecting non-bee pollinators. Icons used from www.freepik.com.

host plant species. Moreover, the dominance of certain pollinator species within network pollination strongly influences the access of floral resources for other pollinators (Hung et al., 2019; Weekers et al., 2022). The composition and diversity of pollinator communities are affected by the dominant species, increasing competition for non-dominant and rare species (see Kunte, 2008 among butterflies; Gilbert and Owen, 1990 among hoverflies and Morse, 1981 between bumblebees and hoverflies). Finally, aggressive or territorial behavior of some pollinator species could also increase the risk of competition and the partitioning of floral resources (e.g. Fitzpatrick and Wellington 1983). Thus, the higher abundance and diversity of wild pollinators with potentially more specialist species could explain why we observed a higher frequency of competition risk when considering together wild bees and other wild pollinator species (Fig. 4). Developing models taking these specificities into account would refine our understanding of these risks and inform more appropriate management practices.

5. The context-dependency of competition risks among pollinators

Although focusing on the risk of competition between honey bees and wild bees could underestimate the real risk of competition among pollinators, other factors should be considered as context-dependent variables. For instance, the landscape composition and configuration may directly affect the risk of competition and even explain the lack of competition in some studies (see Herbertsson et al., 2016; Leguizamón et al., 2021). First, landscape composition and configuration have direct effects on the availability of flower resources, and thus the intensity of the resource limitation that drives competition risk (Herbertsson et al., 2016; St. Clair et al., 2022). Moreover, some landscape characteristics critically affects on the abundance and diversity of wild pollinators, which may have restricted foraging range (e.g. for bees, Kendall et al., 2022). The presence of semi-natural habitats in the landscape drives the

availability of nesting sites for many wild pollinator species (Proesmans et al., 2019; Eeraerts et al., 2022), and thus directly affects the risk of competition.

In agricultural landscapes, food shortage may exacerbate competition and could occur early in the season when the demand for floral resources is high compared to their availability (Timberlake et al., 2019), between flowering periods of mass-flowering crops (Requier et al., 2015; Timberlake et al., 2019), or at the end of the season when flowers are scarce while floral resources demands is still high (Timberlake et al., 2019). These periods therefore appear to be particularly critical in the event of competition with honey bees. However, the amount of resources available to pollinators is not assessed in most of the studies, although it may constitute a context influencing competition and despite recent advances in the estimation of floral resources at the landscape scale (Timberlake et al., 2019; Alignier et al., 2023; Mouillard-Lample et al., 2023). Precisely, in order to estimate the amount of floral resources available to pollinators, databases on nectar and pollen production by plant species are currently being developed (Baude et al., 2016; Flo et al., 2018; Filipiak et al., 2022; Venjakob et al., 2022). These include measurements of nectar volume and sugar concentration from a single sample per day and the quantity of pollen grains as well as analysis of protein content. While the amount of pollen is more consistent per flower, nectar production is variable and recent studies emphasize the importance to consider the kinetic of nectar production. Frequent visits may stimulate the flower to replenish its nectar leading to potential current underestimation of nectar production in the studies with a high density of pollinators (Carisio et al., 2022).

6. Towards inclusive studies of the risk of competition among pollinators

Our review shows that the risk of competition between honey bees and wild pollinators is frequently observed. However, most of the

studies tend to underestimate the magnitude of the risk by focusing on the interaction between bees (*Apis* vs. non-*Apis*) rather than considering the full diversity of wild pollinators, which includes non-bee species such as ants, beetles, bugs, butterflies, flies, moths, and wasps (Rader et al., 2016, 2020; Doyle et al., 2020; Requier et al., 2023). Currently, some beekeepers are banished from natural areas due to suspicion of competition from their honey bee colonies on wild pollinators and recommendations of conservation plans foster this practice (Geldmann and González-Varo, 2018). Nevertheless, the magnitude of the risk of competition shows potential context-dependency due to the diversity of pollinators considered, the landscape and the methods used to assess the risk. A conflict is therefore crystallizing between beekeepers and managers of natural areas due to considerable uncertainty about the management measures to be recommended. Standardization of the assessment of the risk of competition and the integration of non-bee pollinators into scientific studies are urgently required. There is a critical need (i) to investigate the entire pollinator community in competition assessment, with the inclusion of non-bee pollinators; (ii) to set methodological standards and metrics to measure the impact of honey bees and the response of wild pollinators, especially for considering the number of colonies at a given site, (iii) to assess the flower resource availability in order to estimate the intensity of resource limitation; (iv) to consider the landscape composition and configuration that could modulate the risk of competition. Given the diversity of pollinators that are likely to be affected by this competition, it is important to remain vigilant in order to better adapt conservation practices, in collaboration with all the stakeholders involved.

CRedit authorship contribution statement

Fabrice Requier: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Myriam Abdelli:** Data curation, Formal analysis, Investigation. **Mathilde Baude:** Validation, Writing – review & editing. **David Genoud:** Validation, Writing – review & editing. **Hadrien Gens:** Validation, Writing – review & editing. **Benoît Geslin:** Validation, Writing – review & editing. **Mickaël Henry:** Validation, Writing – review & editing. **Lise Ropars:** Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.cris.2024.100093](https://doi.org/10.1016/j.cris.2024.100093).

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