



The evidence for and against competition between the European honeybee and Australian native bees

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ABSTRACT

In Australia, the European honeybee (*Apis mellifera*) is an exotic, abundant, super-generalist species. Introduced two centuries ago, it thrives in the absence of many diseases adversely impacting honeybees elsewhere. Australia's native bees may be vulnerable to competition with honeybees, leading to reduced abundances, reproductive output or even loss of bee species. We review the literature concerning competition between honeybees and Australian native bees in order to: (1) identify the valence and strength of honeybee associations with native bees, and how this varies according to the response variable measured; (2) assess potential research biases; (3) use ecological theory to explain variation in results; and (4) identify key knowledge gaps. We found honeybees typically comprised the majority of individuals in surveys of Australian bee communities. Data on whether honeybees outcompete native bees is equivocal: there were no associations with native bee abundance, species richness, or reproductive output in most cases. However, there were more negative than positive associations. Data indicate effects of honeybees are species-specific, and more detailed investigations regarding how different species and life-history traits affect interactions with honeybees is needed. We propose the following investigations to address deficiencies in the current literature: greater geographic and landscape representation; trait-based investigations; quantifying resource availability and overlap; disease and predator interactions; experimental feral colony removals; and studies spanning multiple seasons and years. Identifying conditions under which honeybees have negative, neutral or positive effects on native bees, and how the ecological traits of native bees are affected by honeybee competition can guide conservation and management.

Keywords: Australian pollinators, conservation, exotic pollinators, interspecific competition, introduced species, pollinators, resource overlap, wild bees.

Introduction

Invasive species are one of the leading causes of species endangerment (Clavero and García-Berthou 2005; Aizen *et al.* 2008; González-Varo *et al.* 2013; Bellard *et al.* 2016). The European or western honeybee (*Apis mellifera*) is one such invasive species that is posited to cause native bee declines in its non-native range (Geslin *et al.* 2017). The European honeybee has a broad native range covering Africa, western Asia and south-east Europe, and now occurs on all inhabited continents, having been introduced for honey production and pollination services, especially for agricultural crops (Moritz *et al.* 2005; Geslin *et al.* 2017). The vigorous swarming behaviour of honeybees means they now occur as feral colonies in their introduced range (Manning *et al.* 2006).

Honeybees have been particularly successful in Australia following their introduction in the 1820s (Paton 1996; Goulson 2003) where they are important generalist pollinators, especially of introduced crops (New 1997; Rural Industries Research & Development Corporation (RIRDC) 2010). Honeybees occur in every state and territory of Australia, with high densities in the south-west, east coast and Tasmania (ALA (Atlas of Living Australia) 2021). Domesticated honeybees occur in managed hives, with beekeepers operating at scales from small local hobby beekeeping ventures, through to commercial ventures

involving hundreds of hives at single locations during ‘honey flow’ periods when mass flowering occurs or during crop flowering periods. Honeybees also occur in ‘un-managed’ feral colonies in regions of moderate climate with hollow-bearing trees, where they represent an invasive introduced species (Moritz *et al.* 2005). Both managed and feral colonies are thriving in Australia due to the lack of pathogens and diseases such as *Varroa destructor* mite and Deformed Wing Virus that cause colony losses on other continents, and appear to be less exposed or susceptible to lethal levels of pesticides (Goulson 2003; De la Rúa *et al.* 2009; vanEngelsdorp and Meixner 2010; Manning 2018).

The Australian honey bee industry consists of approximately 12 400 registered beekeepers, with about 520 000 hives, producing 25 000–30 000 tonnes of honey annually (Karasinski 2018a). In 2019, Australia was 44th in the world out of 340 countries in honey yield (FAO Food & Agriculture Organization of the United Nations, 2021). This industry has an overall estimated gross value of production of AUD1.75 billion/year in direct hive products, with an additional AUD14.2 billion/year through pollination services (BeeAware 2014; Karasinski 2018b). In Australia, honeybees are not only transported at high densities into areas to provide crop pollination services (where native bees tend to be in relatively low numbers due to unfavourable forage conditions, especially for oligolectic bees (Batley and Hogendoorn 2009; Prendergast *et al.* 2021b), but major influxes of honeybees also occur in natural areas such as parks and reserves in order for beekeepers to capitalise on flowering of major honey-source species; key species of high value in terms of production and honey quality include Jarrah (*Eucalyptus marginata*), Yellow Box (*Eucalyptus melliodora*), Leatherwood (*Eucalyptus lucida*), Marri (*Corymbia calophylla*), and tea tree (*Leptospermum* spp.).

There are concerns that this massively introduced managed species (*sensu* Geslin *et al.* 2017) exerts negative impacts on flower-visiting native fauna. Given that native bees rely on nectar and pollen as both adults and larvae, they can be expected to be in competition for these resources, through interspecific interference (contest) and/or resource (scramble) competition. Heterospecific interference competition, where one species physically interferes with another species’ ability to use a resource, tends to be strongly asymmetric, with aggressive, larger or group-foraging bees displacing less-aggressive, smaller, solitary bees, respectively (Johnson and Hubbell 1975; Lichtenberg *et al.* 2010) (but see Ali *et al.* 2015). Interference competition may exclude inferior competitors from accessing preferred, high-quality resources (Thomson 1989), and even the presence of honeybees has been observed to disrupt visitation to shared resources and inhibit co-existence (Chen 1993). The primary means by which honeybees appear to compete with native bees is via resource competition, monopolising limiting resources (nectar and/or pollen)

(Roubik 1978; Torné-Noguera *et al.* 2016). Negative effects on biological fitness (an organism’s success at surviving and reproducing, thereby passing on its genes) through resource competition will only occur if there is high niche overlap and if resources are limiting (Tilman 2004).

Honeybees are potentially able to monopolise and consume a large fraction of floral resources at a site (Geslin *et al.* 2017), especially under conditions when resources may be limiting, and may therefore exert a negative effect on the fitness of native bees; however, whether honeybees outcompete native bees for floral resources (nectar and/or pollen) such that they negatively affect populations of native bees, or under what conditions this might occur, remains unresolved (Eickwort and Ginsberg 1980). Global studies have reported both negative (Goulson 2004; Thomson 2004; Shavit *et al.* 2009; Torné-Noguera *et al.* 2016), as well as no effects of honeybees on native bee diversity and abundance (Forup and Memmott 2005; Steffan-Dewenter and Tscharnkte 2000; Roubik and Wolda 2001; Mallinger *et al.* 2017). A recent global review of literature concerning the impact of managed bees (both exotic and native) on wild bees (which included only nine studies from Australia) also found mixed effects, with 53% reporting negative effects on wild bees, while 28% reported no effects and 19% reported mixed effects (varying with the bee species or variables examined) (Mallinger *et al.* 2017). Our study goes further than previous analyses in a number of ways, through:

- (1) Importantly, distinguishing between abundance vs richness effects, as well as effects on reproduction.
- (2) Considering the ‘strength’ of the evidence.
- (3) Considering management status (managed vs feral), which may be especially pertinent.
- (4) Including studies that allow honeybee–native bee relationships to be assessed yet were not explicitly focused on competition, thereby discerning if there may be biases; and
- (5) Identifying major knowledge gaps, with recommendations on how to address these.

With an Australian focus, we may expect competition to be particularly severe in an Australian context due to contrasting evolutionary histories of Australian native bees and *A. mellifera* (Mallinger *et al.* 2017), and with other Australian taxonomic groups appearing to be highly vulnerable to the effect of introduced species (Jackson *et al.* 2016). In Europe, where honeybees have co-evolved with the flora and fauna, even high densities of managed honeybees that overlap in resource use with other bees by almost 50% have no adverse impact on bee species richness or abundance, or reproductive success (Steffan-Dewenter and Tscharnkte 2000). In contrast, honeybees have been present in Australia for some 200 years. These different histories over which wild bee assemblages have interacted with honeybees suggest we are unlikely to be able to

extrapolate findings from Europe to Australia (Strauss *et al.* 2006).

Within Australia, as is the case in other regions of the world, there is no scientific consensus on whether honeybees are negatively impacting native bees (Manning 1997). Australia has a high and distinctive diversity of mostly endemic native bees, with an estimated >2000 species, many of which are undescribed (Houston 2018). The Australian native bee fauna also has a unique taxonomic composition (Batley and Hogendoorn 2009). Large-bodied social *Bombus*, a major component in Eurasian and American ecosystems, and members of the family Melittidae and Andrenidae are absent. The family Stenotritidae is endemic to Australia, and unlike in most regions in the world, Colletidae is the most species-rich family, of which the most species-rich subfamily in Australia, the Euryglossinae, are endemic (Michener 2007). Only 11 species in two genera (*Austroplebia* and *Tetragonula*) are highly eusocial (Heard 2016). Australia's bee fauna is diverse compared with other continents, and the absence of honeybees as competitors may be a contributing factor (Michener 1965; Michener 1979). Given the economic importance of the Australian honeybee industry, if Australia's unique diversity of native bees is to be preserved, it is crucial to understand whether honeybees are exerting a negative impact. In this review, we focus on negative impacts that may arise through resource competition, which can lead to reduced fitness, translating to population declines and extirpation of a native bee species. In the literature assessed, proxies for such negative impacts are negative associations between honeybees and native bees in terms of abundance of a species or assemblage, number of species, or reproductive output. Here, we review the current known information on the impact of honeybees on native bee communities and outline key knowledge gaps and future research priorities. The aims of this review are to: (1) summarise the state of the literature to date; (2) identify the strength and direction of honeybee influences on native bee abundance, species richness and reproductive output, and how this varies according to the response variable measured; (3) discern potential biases; (4) provide explanations for variation in results, including how these may relate to ecological theory; and (5) identify key areas requiring investigation and make recommendations for future studies.

Materials and methods

Studies reviewed

To review evidence for competitive effects of honeybees on native bees in Australia, publications were sourced (Google Scholar and ProQuest) using combinations of the search terms 'honey bees, competition, *Apis mellifera*, honeybees, interactions, introduced bee, exotic bee, feral bee, invasive

species, pollination, Australia*' (search fields are connected by the Boolean search term 'and') published up to 29 June 2021. Other references were found in citation lists and relevant papers on Australian bees. Therefore, publications included in this review are not biased towards those explicitly looking for competition.

Fifty four cases evaluating the impact of honeybees on Australian native bees in 46 publications were found, published between 1977 and 2021. Eleven were reviews or opinion papers, leaving 43 empirical cases that form our review of the evidence for and against honeybee competition (Table 1; see Supplementary Material).

Twenty three of these cases were explicitly aimed at addressing competition between honeybees and native bees. It should be noted that of these, most failed to define or indicate how competition was measured.

Assessing the relationship between honeybees and native bees

In our systematic review on the relationship between honeybees and Australian native bees, we used a vote counting analysis to quantify the direction and 'strength' of evidence for the relationship between the introduced honeybee and Australian native bees. For this analysis, we only used original data papers, thus excluded reviews and opinion papers. Some publications evaluated more than one response variable, or contained results from more than one study or experiment; hence, there were a greater number of cases than publications. Publications included were those where there was a quantitative measure of both honeybees (presence/absence of colonies in space or time; abundance or density of colonies; visitation rates; distance from hives or apiaries) which could be related to that of native bees (abundance; visitation rates; species richness; reproductive rates). Publications were excluded that did not measure these metrics (e.g. if a study measured only pathogen transmission it would not be included), or if they were not in English. The limited number of publications overall, and the limited number of publications that provided quantifiable outcomes on the effect of honeybees on native bees (such as publications that did not explicitly analyse the effect of honeybees on native bees, or publications in which no statistical analyses were performed) precluded us from being able to perform a meta-analysis. Therefore, we indexed the effect of honeybees on native bee parameters according to a three-point scale, similar to that of Hoffmann and Andersen (2003): 1, weak apparent response, possibly representing background noise ($P < 0.1$), or no statistical tests performed; 2, apparently clear response, statistically tested ($P < 0.05$); and 3, very strong response, statistically tested ($P < 0.01$). The valence was recorded as negative (–) or positive (+). We also included a category for n.s. (no significant difference, $P > 0.05$), or unknown (? – not mentioned/addressed). We looked at three main parameters:

Table 1. Scoring of publications reviewed on the effect of the European honeybee on native bees in Australia.

Reference	Habitat type Native veg/ agricultural/ urbanised	Native bee species vs community study	Effect on native bee N	Effect on native bee reproductive output	Effect on native bee R	Resource competition Y/N/ inferred/ ambiguous	Floral resource type Native/exotic	HB dominant
Douglas (1977) ^A	Native veg	Review	—	?	—	Inferred		Y
Holm (1988) ^A	Native veg	Review	—	?	—	Inferred		Y
Hopper (1985) ^A	Native veg	Review	—/+	?	n.s.	Inferred		
Manning (1997) ^A	Native veg	Review	n.s.	?	n.s.	N		
Paini (2004) ^A	Native veg	Review	—/n.s./+	—/+	?	Inferred		
Paton (1993) ^A	Native veg	Review	—	?	?	Inferred		
Paton (1996) ^A	Native veg	Review	—/n.s.	?	n.s.	Ambiguous		
Paton (1997) ^A	Native veg	Review	—	?	?	Y		Y
Pyke (1999) ^A	Native veg	Review	n.s./—	?	?	Y/N		
Schwarz and Hurst (1997) ^A	Native veg	Review	n.s.	?	n.s.	Ambiguous		
Chapman and Oldroyd (2020) ^A	Native veg	Review	—/n.s./+	—/n.s./+	—/n.s./+	Inferred		
Arthur et al. (2010) ^B	Agricultural	Community	+++	?	?	N	Exotic	Y
Bailey (1994) ^{A,C}	Urbanised	Species: <i>Nomia</i> sp. (Halictidae)	---	?	?	Y	Native	Y
Gilpin et al. (2019a) ^B	Native veg	Community	n.s.	?	n.s.	Ambiguous	Native	Y
Gilpin et al. (2019b) ^{B,C}	Agricultural	Community	n.s.	?	?	N	Native + exotic	Y
Bernhardt (1987) ^B	Native veg	Community	—	?	—	Inferred	Native	Y + N
Gross and Mackay (1998) ^A	Native veg	Community	n.s.	?	n.s.	Inferred	Native	N
Gross (2001) ^A	Native veg	Community	---	?	—	Y	Native	Y (1 out of 2 sites)
Heard (1994) ^{B,C}	Agricultural	Species: <i>Tetragonula</i> (syn. <i>Trigona</i>) <i>carbonaria</i> (Apidae)	—/n.s.	?	n.s.	Y	Native	Y
Heard et al. (1990) ^B	Agricultural	Community	+	?	?	Ambiguous	Native	Y
Hermansen et al. (2014) ^A	Native veg	Species: <i>Lipotriches</i> <i>excellens</i> (Halictidae) (only native bee visitor out of 37 total wild insect visitors)	+	?	?	Inferred	Native	Y
Hingston et al. (2004a) ^{B,C}	Native veg	Community	—	?	—	Y	Native	Y
Hingston et al. (2004b) ^B	Native veg	Community	—	?	—	Ambiguous	Native	Y
Rymer et al. (2005) ^B	Native veg	Community	n.s.	?	n.s.	Ambiguous	Native	Y
Williams and Adam (1997) ^B	Native veg	Community	— (Hylainae) /n.s. (Tetragonula)	?	—	Inferred	Native	Y + N
Ettershank and Ettershank (1990) ^A	Native veg	Community	—	?	?	Inferred	Native	Y
Ettershank and Ettershank (1993) ^A	Native veg	Community	n.s.	?	?	N	Native	Y
Horskins and Turner (1999) ^B	Native veg	Community	n.s.	?	?	N/ambiguous	Native	

(Continued on next page)

Table 1. (Continued).

Reference	Habitat type Native veg/ agricultural/ urbanised	Native bee species vs community study	Effect on native bee N	Effect on native bee reproductive output	Effect on native bee R	Resource competition Y/N/ inferred/ ambiguous	Floral resource type Native/exotic	HB dominant
Ladd <i>et al.</i> (2019) ^B	Native veg	Community	?	?	+	N	Native	
Lomov <i>et al.</i> (2010) ^B	Native veg + Urbanised	Community	+/n.s.	?	n.s.	N	Native	Y
Mallick and Driessen (2009) ^A	Native veg	Community	n.s.	?	?	Inferred	Native	Y
Paini and Roberts (2005) ^A	Native veg	Species: <i>Hylaeus</i> <i>alcyoneus</i> (Colletidae)	?	—	na	Y	Native	
Paini <i>et al.</i> (2005) ^{A,C}	Native veg	Species: <i>Megachile</i> sp. 323 (Megachilidae)	?	n.s.	na	N	Native	
Paton (1990) ^A	Native veg	Community	?	?	?	Inferred	Native	Y
Pyke and Balzer (1985) ^A (Section 3 and 3)	Native veg	Community	?	?	?	N	Native	Y
Pyke and Balzer (1985) ^{A,C} (Section 5 and 6)	Native veg	Community	— — —	?	?	Y	Native	Y
Pyke and Balzer (1985) ^C (Section 6)	Native veg	Community	+	?	?	N	Native	Y
Pyke and Balzer (1985) ^{A,C} (Section 6)	Native veg	Community	— — —/n.s.	?	?	Inferred	Native	
Pyke and Balzer (1985) ^{A,C} (Section 6)	Native veg	Community	— — —	?	?	Inferred	Native	
Pyke and Balzer (1985) ^A (Section 7)	Native veg	Community	n.s./+ + +	?	?	Inferred	Native	
Pyke and Balzer (1985) ^A (Section 8)	Native veg	Community	n.s.	?	?	N	Native	
Pyke and Balzer (1985) ^A (Section 9)	Native veg	Community	n.s.	?	—	Inferred	Native	Y
Pyke and Balzer (1985) ^A (Section 10)	Native veg	Community	?	?	?	Ambiguous	Native	
Spessa (1999) ^{A,C}	Native veg	Species: <i>Amphylaeus</i> <i>morosus</i> (Colletidae)	n.s./+ +	n.s.	na	N	Native	
Sugden and Pyke (1991) ^{A,C}	Native veg	Species: <i>Exoneura</i> <i>asimillima</i> (Apidae)	— — —	+ + +	na	Ambiguous	Native	
Threlfall <i>et al.</i> (2015) ^B	Urbanised	Community	n.s.	?	?	Ambiguous	Native + exotic	N
Wills <i>et al.</i> (1990) ^B	Native veg	Community	?	?	?	Ambiguous	Native	
Yates <i>et al.</i> (2005) ^B	Native veg	Community	—/n.s.	?	?	Ambiguous	Native	Y
Prendergast <i>et al.</i> (2021b) ^B	Agricultural	Community	n.s.	?	n.s.	Ambiguous	Exotic	Y
Prendergast and Ollerton (2022) ^A	Urbanised	Community	?	?	?	Y	Native + exotic	Y

(Continued on next page)

Table 1. (Continued).

Reference	Habitat type Native veg/ agricultural/ urbanised	Native bee species vs community study	Effect on native bee N	Effect on native bee reproductive output	Effect on native bee R	Resource competition Y/N/ inferred/ ambiguous	Floral resource type Native/exotic	HB dominant
Prendergast et al. (2021a) ^A	Urbanised	Community	n.s. (overall) /n.s. (small, year 1)/+ + (small, year 2) / n.s. (medium, year 1) /n.s. (medium, year 2) /n.s. (large, year 1)/– (large, year 2)/– – (high PAC, year 1)/– (high PAC, year 2)	?	+ + + (year 1)/– – – (year 2) /n.s. (previous year)/+ + + (small, year 1) /n.s. (small, year 2)/n.s. (medium, year 1)/– – – (medium, year 2)/+ (large, year 1)/n.s. (large, year 2)	Y	Native + exotic	Y
Elliott et al. (2021) ^A	Native veg	Community	?	?	?	Inferred	Native	Y
Evans et al. (2021) ^{B,C}	Agricultural	Species: <i>Tetragonula carbonaria</i>	?	?		Inferred	native	Y
Johanson et al. (2019) ^A	Native veg	Community	?	?	?	Inferred	Native + exotic	Y

Effect of honeybees on native bee scores: following a scheme similar to that of Hoffmann and Andersen (2003): 1, weak apparent response, possibly represents background noise ($P < 0.1$), or no statistical tests performed; 2, apparently clear response, statistically tested ($P < 0.05$); and 3, very strong response, statistically tested ($P < 0.01$), with a negative (–) or positive (+) relationship, as well as n.s. (no significant difference, $P > 0.05$), or unknown (? – not mentioned/addressed). Refer to Supplementary Material to a summary of each article and further information.

^AReferences are those that explicitly were looking for competition.

^BReferences that reported honeybee and native bee parameters but were not explicitly looking at competition.

^CStudies that involved experimental manipulations of honeybee numbers.

native bee abundance, species richness, and reproductive output. Some studies measured more than one parameter (e.g. both abundance and species richness), and there were also studies where, when conducted over more than 1 year, or looking at different native bee guilds, the response metric varied (e.g. the strength or valence differed from 1 year to the next), and thus some studies had more than one response for a given parameter (see Supplementary Material).

Results

Honeybees are a dominant component of Australian ecosystems, with 93.3% of studies (out of $n = 30$) reporting that honeybees numerically dominated the assemblage. When abundance data was available ($n = 20$), honeybees represented on average $65 \pm 6\%$ of total bees recorded. None of the previous honeybee reviews unequivocally supported or refuted the hypothesis that honeybees had a negative effect on native bees, all concluding that the evidence was ambiguous or insufficient, emphasising the need for the current review to evaluate the strength of the evidence across all studies to date, and what factors may cause this variation in the relationship between honeybees and native bees in Australian ecosystems. We found only one early opinion piece that asserted that honeybees caused the extirpation of native bees, but was based on anecdotal evidence (Douglas 1977) (see summary in Supplementary Material).

Quantitative studies

Abundance was the most commonly measured metric of native bees (42 responses), followed by species richness (22 responses); only three studies measured reproductive output (Table 1). Of studies with data for assessing the relationship between honeybees and native bee response variables, 19 were conducted in New South Wales, 10 in Western Australia, six in Tasmania, four in Victoria, only one each in South Australia and the Northern Territory, with none in the Australian Capital Territory (Fig. 1). Regarding landscape type, 75% were from natural landscapes, 15.9% in agricultural landscapes, and 9.1% in urbanised landscapes (Table 1). The majority of studies measured the response of the native bee community, with only eight studies focusing on measuring the response of a particular species. These species-focused studies were further taxonomically restricted (Table 1). Despite Meliponini comprising a minority of Australian species (AFD (Australian Fauna Directory) 2021), one-quarter of species-level studies were with *Tetragonula carbonaria*. In contrast, no studies on the impact of honeybees have involved species in the subfamilies Euryglossinae and Neopasiphaeinae, Callomelittinae and Diphaglossinae (previously grouped together as Colletinae in Michener (2007; Almeida et al. 2012, 2019), which represent together over half of the native bee fauna and include many oligolectic species (Houston 2018; AFD (Australian Fauna Directory) 2021).

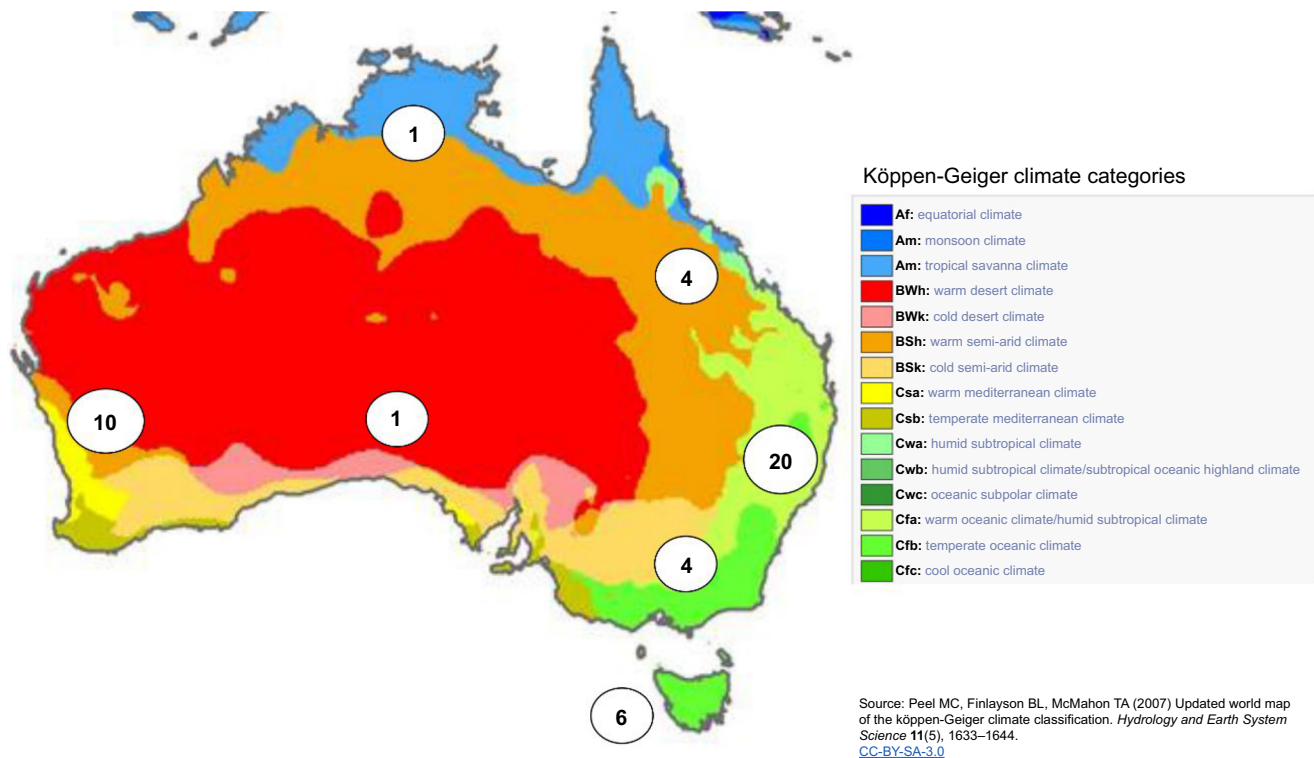


Fig. 1. Geographic and climatic bias in publications. Refer to Supplementary Material for studies associated with each state. Map source modified from: [Peel et al. 2007](#). Climate classifications follow those of the Köppen–Geiger Climate Classification ([Peel et al. 2007](#)).

Only a single study involved an oligolege (*Hylaeus alcyoneus*) ([Paini et al. 2005](#)).

Across all studies presenting data reviewed here, we found scant conclusive evidence that resource competition occurs between honeybees and native bees. Only eight cases (17.4%) concluded or provided evidence for resource competition between the taxa; however, resource competition was inferred, but not demonstrated in 14 cases (30.4%). Ten cases (21.7%) concluded or provided evidence that did not support asserting that resource competition was occurring ([Table 1](#)), and in 14 cases (30.4%) it was ambiguous ([Table 1](#)). Only two studies reported interference competition ([Williams and Adam 1997](#); [Gross and Mackay 1998](#)) (see Supplementary Material). These results describing resource competition will, however, be influenced by the particular resources under study (some studies looked at a single plant species, others a plant community; see Supplementary Material). Studies were also dominated by investigating native flora (87.8% of studies), with little research into managed horticultural or crop species, or exotic plant species.

Mensurative and manipulative studies

Mensurative studies (also known as observational studies) involve taking advantage of natural variation and making measurements of uncontrolled events, with space and/or

time being the only experimental variable, whereas manipulative studies involve two or more treatments, where experimental units in each treatment receive controlled manipulations ([Hulbert 1984](#)). Of the 43 cases involving data on relationships between honeybees and native bees, one quarter (12) involved manipulating honeybees, and the remainder (31) were mensurative ([Table 1](#)). Of manipulative studies, there were seven cases where no association was found, five negative associations, and only two positive associations. Moreover, two of the negative associations were highly statistically significant ([Fig. 2](#)). Of mensurative studies, 27 cases of no associations were found, and similar to manipulative studies, more negative than positive associations were found (16 vs 9). However, there were fewer highly statistically significant associations ([Fig. 2](#)). Proportions of cases finding negative, positive and no associations were similar between mensurative and manipulative studies, but mensurative studies appeared to have a slightly higher proportion of findings of no association.

Studies investigating honeybee competition compared with those that do not

Of all studies, 24 explicitly looked at the effect of honeybees on native bees; the remaining 19 provided information on honeybees and native bees but were not conducted with

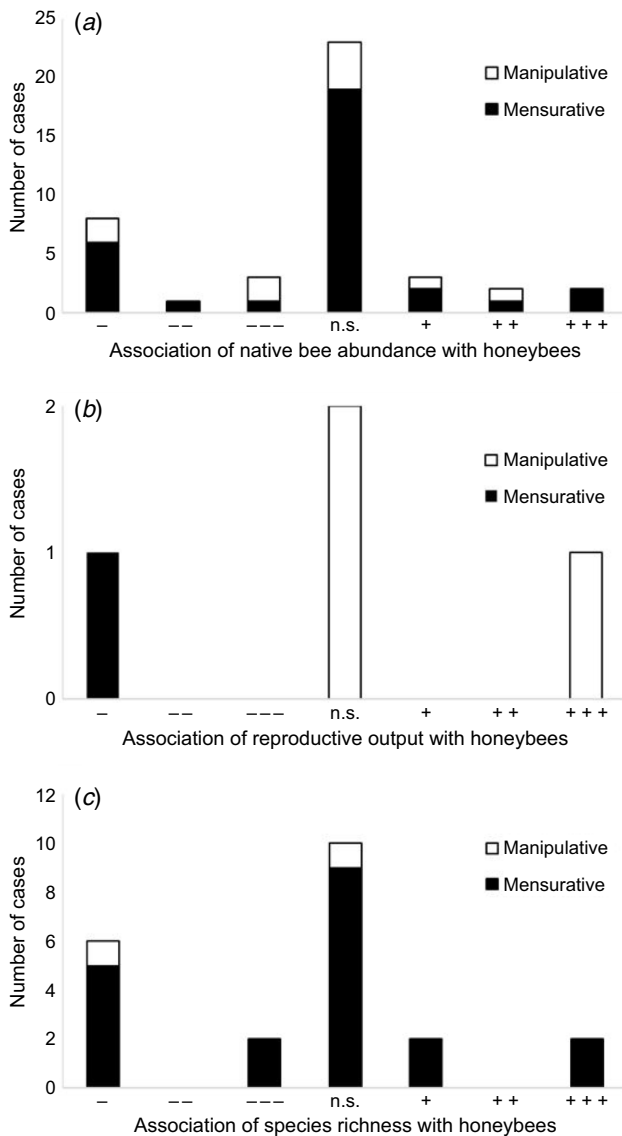


Fig. 2. Tabulation across studies on the outcome of the impact of honeybees on native bees in terms of (a) abundance; (b) reproduction; and (c) species richness, showing the relative number of cases for studies that were manipulative vs mensurative (observational). Impacts were assigned as negative (–) or positive (+) relationships, and quantified as: 1, weak apparent response, possibly represents background noise ($P < 0.1$), or no statistical tests performed; 2, apparently clear response, statistically tested ($P < 0.05$); and 3, very strong response, statistically tested ($P < 0.01$), as well as n.s. (no significant different, $P > 0.05$), or unknown (? – not mentioned/addressed).

the aim of investigating honeybee impact on native bees (Table 1). All highly significant instances of negative impacts on native bee abundance (three out of 24) were from studies that explicitly investigated the impact of honeybees (Fig. 3). In contrast, all negative associations reported by studies not specifically investigating honeybee competition were non-significant or were not statistically

analysed (Fig. 3). However, whilst this may suggest a bias towards detecting negative impacts of honeybees on native bees, the majority of positive associations (nine out of 12) also came from studies investigating honeybee impacts on native bees. A similar proportion of cases for no association between honeybees and native bees being reported occurred for both types of studies (50% and 53.6%, respectively). Contrary to the potential for researchers who were investigating competition to report negative associations, there was a greater proportion of positive associations from these studies than those not focused on looking at the impact of honeybees.

Response of native bee abundance

Non-significant associations between honeybees and native bee abundance dominated, making up just over 50% of responses (Figs 2a, 3a). There were more negative than positive associations (12 vs 7) (Figs 2a, 3a), although when excluding those cases where no tests were performed or there was a trend ($P = 0.05$ – 0.1), there was an equal number of statistically significant positive and negative associations (Figs 2a, 3a).

Response of native bee reproductive output

Only four studies measured reproductive output, with two showing no association with honeybees, one showing a statistically negative association, and one a highly significant positive association. With such a low sample size, it is difficult to draw any conclusions. All of these were studies explicitly investigating competition (Fig. 2b).

Response of native bee species richness

Responses in terms of species richness appeared to show the greatest support that honeybees may be exerting negative impacts on some species: eight studies had negative associations, with half of this number showing positive associations (Figs 2c, 3b). An equal number of studies had responses that were statistically significant (two each), and ten studies exhibited no association of honeybees with native bee species richness (Figs 2c, 3b).

Overall impact of honeybees on native bees

Combining all response parameters, non-significant effects dominated (Figs 2, 3). Overall, from studies where an outcome could be evaluated, non-significant responses comprised over 50%. However, almost twice as many negative associations were reported than positive (21 vs 11).

Discussion

Based on the surveyed literature there is limited *strong* evidence to support or to reject the hypothesis that

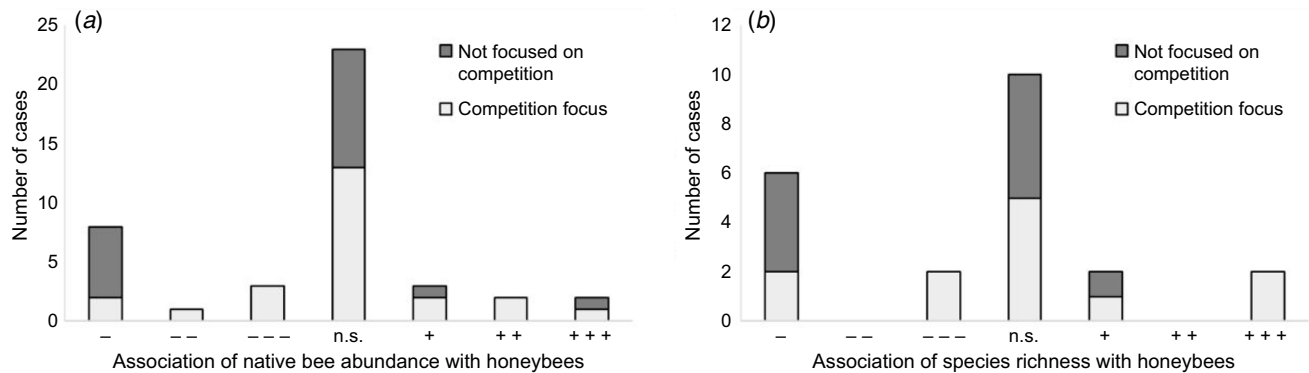


Fig. 3. Tabulation across studies on the outcome of the impact of honeybees on native bees in terms of (a) abundance; and (b) species richness, showing the relative number of cases for studies that that were explicitly had a honeybee competition focus vs those that were not evaluating the impact of honeybees on native bees. Impacts were assigned as negative (–) or positive (+) relationships, and quantified as: 1, weak apparent response, possibly represents background noise ($P < 0.1$), or no statistical tests performed; 2, apparently clear response, statistically tested ($P < 0.05$); and 3, very strong response, statistically tested ($P < 0.01$), as well as n.s. (no significant different, $P > 0.05$), or unknown (? – not mentioned/addressed).

honeybees have a deleterious impact on Australian native bees (Table 1; see Supplementary Material).

Abundant resources and unsaturated niches

Why might there be such variation in reported results? The impact of an introduced competitive species on native communities through resource competition will depend upon resource overlap between the introduced and resident species, resource availability and whether communities are 'saturated' (Stachowicz and Tilman 2005). The ease with which honeybees have spread and established throughout Australia implies that communities were not saturated, and there existed 'open niches' for honeybees.

The diversity and abundance of floral resources in most Australian ecosystems (ABRS (Australian Biological Resources Study) 2015) may explain both the ease of honeybee invasion, and why this introduced species has had minimal conclusive competitive effects on endemic bees (Simberloff 1981). In addition, honeybee foragers exhibit short-term flower constancy (Leonhardt and Blüthgen 2012), but undergo shifts throughout the day or season as the cost–benefit value of remaining in a patch changes. This behaviour is likely to leave resources incompletely diminished, such that nectar remains for native bees. Moreover, many native bees are small and solitary, with consequently lower nectar requirements (Eickwort and Ginsberg 1980; Goulson 1994; Manning 1997). This is supported by findings of substantial quantities of nectar remaining unexploited by honeybees, even near apiaries (Corbet and Delfosse 1984; Paton 1996; Horskins and Turner 1999). In Western Australian forests, short-term agistments of commercial apiarists on registered apiary sites results in only 40% of the available nectar crop being harvested (Manning 1997). Many Australian

flowering plant species that are highly visited by both honeybees and native pollinators are mass flowering, with easily accessed open-faced flowers, and produce a seasonal superabundance of nectar; e.g. Myrtaceae (Williams and Adam 1994). This suggests that nectar is seldom fully depleted and nectar resources are therefore not limiting. This reduces the potential for honeybees to adversely affect native bees through resource competition, even those species with overlapping niches (Manning 1989; Schwarz and Hurst 1997).

However, resources are not always at surplus levels (Zimmerman and Pleasants 1982; Dupont *et al.* 2004), and honeybees are documented to remove up to 97.2% of the nectar and 99.0% of pollen produced by some native Australian flora (Paton 1990). A study on Tasmanian leatherwood (*Eucryphia lucida*), a nectar resource highly sought after by commercial honey producers, found that honeybees rapidly removed pollen, and standing crops of nectar sugar were significantly depressed at apiary sites compared with control sites (situated 2 km away from apiaries), where pollen remained in flowers until the female phase (Mallick and Driessen 2009). However, despite this thorough resource use by honeybees, no competitive effects on native insect visitors, in terms of numbers of visits to leatherwood trees, were observed and visiting rates by native insects did not differ between control and apiary sites. It should be noted that the control sites still had a high abundance of feral honeybees (73% of that recorded at commercial apiary sites), which may explain the lack of difference in native bees since feral honeybees may have usurped resources to an extent that larger native bee populations could not be supported (Mallick and Driessen 2009). This study also found that across all sites honeybees were the dominant visitors, and carried significantly more pollen than did native bees.

Differences in life-history traits

Divergences in ecological and life-history traits leading to differences in foraging behaviour, floral preferences, or habitat preferences may also result in negative correlations between honeybees and native bees (Williams *et al.* 2010). Honeybees tend to be more abundant in agricultural areas or regions with high abundances of introduced plants, whereas native bees are more abundant and species-rich in areas with larger amounts of native vegetation (Martins *et al.* 2018). In Australia, differences in habitat use and flower species have been found in studies comparing native bee and honeybee abundance between habitat types (Heard *et al.* 1990; Threlfall *et al.* 2015; Prendergast *et al.* 2022) and flower species (Hingston 2002; Prendergast and Ollerton 2022). Unlike most native bees, honeybees can achieve their highest densities in communities with extensive human-induced ecosystem disturbance (Cairns *et al.* 2005). Stored resources in the hive may make honeybees better-equipped to persist in such landscapes, whereas native bees must constantly forage over a brief active season such that costs of foraging in impoverished landscapes are prohibitively high (Tomlinson *et al.* 2017). The large flight range of honeybees also allows them to be more resilient to landscape fragmentation, allowing them to more easily cross the matrix to reach forage resources. Honeybees are also highly polylectic, and will forage on a wide diversity of flora, including exotic crops, whereas many of Australia's native bees have co-evolved with the flora and have preferences for, or are specialised on, a more narrow range of native flora (Houston 2000).

Interactions with shared predators and flora

Honeybees may have a beneficial impact on native bees because as an abundant, energy-rich food source, bee-eating birds and spiders may reduce their per capita predation rate upon native bees (a 'dilution' or 'satiation' effect) (Schwarz *et al.* 1991; Schwarz *et al.* 1992; Manning 1997; Schwarz and Hurst 1997; DEC 2012). Honeybees may also indirectly have a beneficial effect on native bees by enhancing reproductive success of plants on which native bees depend (Heard *et al.* 1990). If native pollinators decline owing to anthropogenic disturbances, they may be at insufficient densities to effect maximal pollination, leading to pollination deficits. Because managed honeybees can be at least partly buffered against erratic periods of low bloom when beekeepers provide supplemental feeding, their ongoing pollination services in such conditions may halt otherwise cascading extinctions and breakdown of mutualist networks through occupying key nodes in invaded communities (Harrison and Winfree 2015). Nevertheless, it cannot be assumed that honeybees have positive influences on pollination networks, and indeed recent evidence has demonstrated honeybees not only are

not ecologically equivalent to native bees in their roles in pollination networks, but they also have disruptive influences on pollination networks, dominate interactions, and are associated with lower network stability and high indices of competition (Prendergast and Ollerton 2022).

Honeybees may also reduce plant reproductive success, as has been found both in Australia (Gross 1993; Gross and Mackay 1998; Delnevo *et al.* 2020; Prendergast and Ollerton 2022), and elsewhere on the globe (Hargreaves *et al.* 2010; Magrach *et al.* 2017; Valido *et al.* 2019; Agüero *et al.* 2020). They may also indirectly harm native bees by favouring spread of weeds (Goulson and Derwent 2004; Simpson *et al.* 2005).

Caveats to the literature and potential biases

The lack of consistent agreement between studies may be influenced by the nature of the studies themselves. The limited number of sites (median of 6) and duration of studies also has implications for interpreting results: it is likely that many of the studies reporting non-significant associations lacked the power to detect significant negative associations (James-Pirri *et al.* 2007). All studies have been of limited durations, some spanning only a few days, with a median of 3 months; most were conducted in just 1 year (median number of years: 1, mean 2.3 ± 0.2), over one, rarely two, seasons. The few long-term studies on honeybee interactions with native bee assemblages in other countries have found that negative effects of honeybees on other bees are transitory (Roubik 1983; Schaffer *et al.* 1983). Limitations in sample size and variability means that the scoring system used here also has caveats: a large mean difference yet with much variation may not have the power to be statistically significant, whereas a statistically significant difference may represent a small 'biologically meaningful' difference.

Many of the studies examined here ($n = 9$) came from a single set of experiments that were published as part of a report (Pyke and Balzer 1985). As such, a large proportion of the literature has not undergone the scrutiny of peer-review. Many studies also fail to consider confounding factors, spatial or temporal scale and levels of shared or alternative resources. Competition is often inferred by looking at resource overlap or changes in foraging patterns (e.g. visiting rates) which are indirect measures of competition, rather than assessing whether honeybees affect fitness, as measured by changes in native bee survival, fecundity, and population density. In addition, negative associations between honeybees and native bees can only be found if there is variation in these two parameters (see Prendergast *et al.* 2021a); and indeed, consistent high numbers of honeybees in relation to native bees was a common feature of studies in this review.

Another factor to consider is biases in expectations for finding competition. A novel aspect of this review was including data from studies where associations between

honeybees and native bees were presented, but the researchers did not set out to examine competition. The limited sample size means no strong conclusions can be drawn; however, we can see that negative effects are represented to a greater extent in studies looking at competition, with non-significant effects being represented to a greater extent in studies not looking for competition. Although this difference in the representation and strength of negative associations may be due to the experimental design in studies investigating honeybee competition, it may also be due to bias in looking for evidence of honeybees competing with native bees, and a bias against publishing non-significant results.

Our review has assessed the relationship between honeybees and Australian native bees reported in the literature, but we acknowledge that it remains contentious for what determines a competitive effect: a negative correlation or association is a necessary but not sufficient attribute but does not necessarily mean competition.

Response metrics

Our review emphasises the importance of the response metric being used to measure the impact of competition, and they may not necessarily be congruent, even within a study. Consider honeybee competition exerting negative impacts on the bee assemblages through resource competition (Fig. 4), a number of scenarios are possible:

- both abundance and species richness may decline;
- abundance of each species may decline, but not to a level where any species becomes locally extinct such that the number of species remains the same;

- the abundance of vulnerable species may decline to such an extent that they become locally extinct; these species however may have been in competition with other native bee species that are not in competition with honeybees, leading to a release from competition. Consequently populations of these remaining species would increase, leading to no net decrease in abundance at the community level (Dale 2017).

With a greater proportion of studies finding honeybees were negatively associated with native bee species richness rather than abundance, this third, complex diffuse competition scenario may be operating. This has yet to be investigated in the context of honeybee competition, but has been investigated in the context of plant communities which may serve as a model for such studies in the context of direct and indirect interactions between pollinator assemblages (Brooker *et al.* 2008; Xiao and Michalet 2013; Aschehoug and Callaway 2015; Godoy *et al.* 2017).

Determining whether competition with honeybees exerts negative impacts on native bee populations requires measuring their survival and reproduction (Begon *et al.* 2005). Yet only four studies have measured this response metric, with no consistent result. Furthermore, these studies all involved cavity-nesting bee species. Given that over 50% of native bee species are ground-nesting (Houston 2018), and some of these ground-nesting bees are pollen specialists (e.g. the ground-nesting Euryglossinae (Michener 2007), *Trichocolletes* (Batley and Houston 2012), some species of *Leioproctus* (e.g. Houston 1989)), this is an under-researched topic. It is challenging to measure reproductive output of ground-nesting bees; however, there are studies that have successfully estimated reproductive success of this nesting guild, e.g. Willis Chan and Raine (2021).

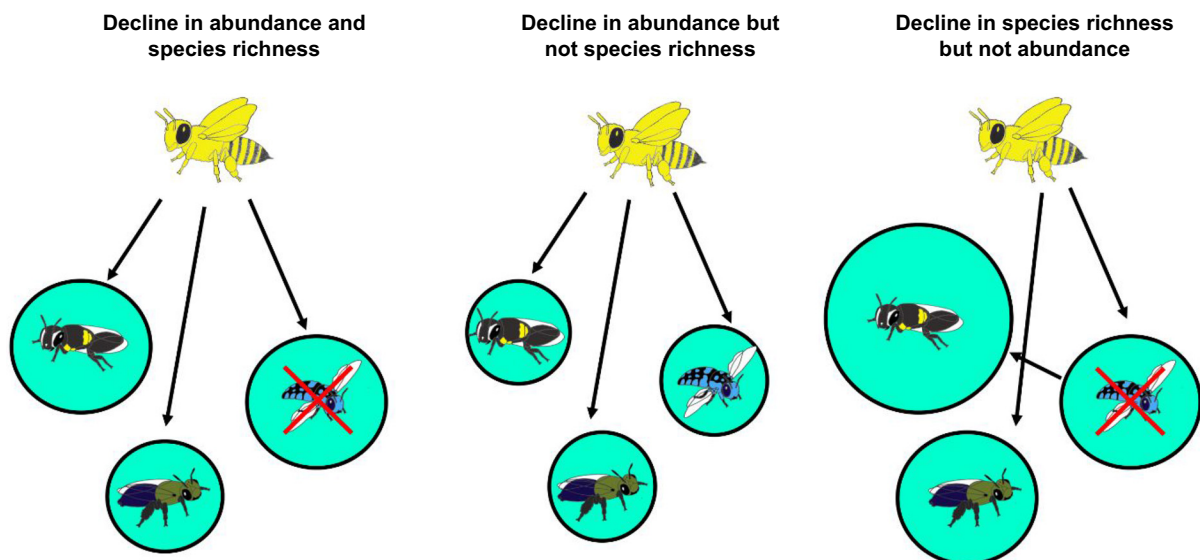


Fig. 4. Possible outcomes on native bee assemblages from honeybee competition in terms of abundance and species richness.

Key knowledge gaps

We identified seven key knowledge gaps (or biases), and areas of further research to help elucidate relationships between honeybees and native Australian bees.

Geographic biases

There is a geographic bias in studies, with a third of studies reviewed conducted in just one state (NSW) (Fig. 1). Australia is a large continent, possessing a diversity of environments. As such, studies on honeybees in a bioregion may not be valid for other regions. For example, in Australia's arid regions (Smith 2008), native bees are likely to have a competitive edge over honeybees through greater drought tolerance. Organisms adapted to Australia's arid environments characterised by environmental unpredictability often have evolved broad niches and high plasticity, which should reduce competitive exclusion (Levins 1968; Halcroft 2012). No studies on honeybee competition have been conducted in such regions.

Landscape type biases

A major knowledge gap is honeybee impacts on native bees in environments other than natural habitats. Three-quarters of studies were conducted in natural landscapes, 15.9% in agricultural, and only 9% were conducted in more urbanised landscapes (see Supplementary Material). The potential for competition may differ greatly in disturbed habitats compared with natural habitats. Firstly, because native bees tend to be at reduced population sizes in landscapes with fragmented native vegetation (Kremen et al. 2002a, 2002b; Steffan-Dewenter et al. 2005), whereas honeybees tend to do better in more disturbed landscapes, especially those with mass flowering crops (Steffan-Dewenter et al. 2002; Carré et al. 2009; Threlfall et al. 2015). Secondly, with the loss of native flowering plants, resources will be more limiting, exacerbating the potential for resource competition. Thirdly, given that islands are particularly vulnerable to invasive species (Kato et al. 1999; Traveset and Richardson 2011), habitat fragments, within inhospitable matrices, may be more conducive to native bees being displaced by honeybees. Conversely, it is possible that when presented with mass flowering crops in agricultural landscapes (Martins et al. 2018), or a diversity of exotics in urban landscapes (McKinney 2008), honeybees will preferentially forage on these non-native flowers, reducing niche overlap and competition with native bees. However, recent research has indicated that this is not the case, and instead honeybee competition is more intense in more urbanised habitats because there is a reduced amount of native flora available for native bees resulting in resource limitation, and a greater diversity of primarily exotic flora, favouring honeybees (Prendergast et al. 2021a; Prendergast and Ollerton 2022).

In Australia, honeybees attain high densities in urban areas (Prendergast and Ollerton 2022), which contrasts with most

urban bee fauna surveys in the northern hemisphere where overall abundance is dominated by native bees (Cane et al. 2005). This disparity may stem from a higher density of urban beekeepers in Australia. It may also be because *V. destructor* mites, and associated viruses and hive disorders, that have caused colony losses of honeybees in Europe and the USA, are absent in Australia, allowing healthier colonies and a greater densities of feral colonies (vanEngelsdorp and Meixner 2010). There have been proposals to intensively use urban lands for communal apiaries in order to reduce commercial honeybee impacts in supposedly superior natural habitats (Sugden et al. 1996). Yet, urban habitats may be a refuge for native bees, that may be eliminated if honeybee densities are allowed to rise (McFrederick and LeBuhn 2006; Ropars et al. 2019). With urban beekeeping and urban crop cultivation increasing (Moore and Kosut 2013; Saggin 2013; Lorenz and Stark 2015), it is important to identify opportunities for supporting both wild native bees as well as managed honeybees in urban contexts (MacIvor and Packer 2016).

Evaluating how species' traits influence competitive interactions

Predicting situations where honeybees will have adverse effects on native bees will be improved by information about the autoecology of native bees and factors limiting their populations, yet such data is poor for most of Australia's native bees (Batley and Hogendoorn 2009), and many studies suffer from poor taxonomic practices (Prendergast and Hogendoorn 2021). Morphological, ecological and behavioural similarities between native and alien pollinators are important in predicting competitive interaction intensities (Dohzono and Yokoyama 2010) and therefore, the traits of a bee species – body size (and associated energetic requirements and flight range), tongue length, floral preferences and lecty (extent of specialisation on pollen hosts), phenology – will influence the intensity and outcome of competition (Lancaster et al. 2017). However, the majority of studies have analysed changes in native bee abundance at the aggregate community level, and moreover have not distinguished between taxonomic groups. Testing to see if native bee taxonomic or trait-based guilds show variation in their vulnerability to honeybee competition should be a focus of further investigations. Importantly, recent research has revealed the importance of species' traits in their susceptibility to honeybee competition and how aggregate responses can mask vulnerability to competitive impacts (Prendergast et al. 2021a). Importance of a species' autoecology is underscored in two studies conducted in the same location investigating honeybee competition on two divergent species: a summer-active long-tongued megachilid, and a winter-active short-tongued *Hylaeus*, which arrived at opposing conclusions (Paini and Roberts 2005; Paini et al. 2005). Research into honeybee impacts across a far greater

diversity of native bee species is needed given only seven species have been investigated. For example, there have been no studies on Euryglossinae species, which is the most species-rich subfamily of Australian bees, the majority of which are oligolectic (Houston 2018).

Even if honeybees do not affect native bee abundance or species richness, they nevertheless may cause shifts in species composition, which are masked by these aggregate measures. This may occur where sensitive species are replaced by species that are unaffected by honeybee competition.

The greater the niche similarity between species, the greater the harm invaders are predicted to cause for native communities (Traveset and Richardson 2011). This may explain the susceptibility of *Bombus* to honeybee competition, as this genus comprises 'long-tongued', mainly large, social species. Australia lacks native taxa with a similar niche, but we may expect that the large-bodied, long-tongued *Amegilla* and *Xylocopa* may be most susceptible based on their niche similarity with honeybees in these life-history traits. Phylogeny has been proposed as a predictor for competition (Moritz *et al.* 2005; Violle *et al.* 2011; Rohr and Bascompte 2014), based on the premise that species that are phylogenetically closely-related have similar fundamental niches (Cahill *et al.* 2008). Indeed, studies have demonstrated negative competitive effects of honeybees on *Bombus* (Thomson 2004, 2006, 2016; Goulson *et al.* 2008; Elbgami *et al.* 2014; Torné-Noguera *et al.* 2016): a well-studied genus, phylogenetically close to *Apis* – both Apinae, Corbiculata (Bossert *et al.* 2019). Under this assumption, it can be predicted that competition will be relatively weak for most Australian species, but will be strongest between native apid genera (e.g. *Xylocopa*, *Tetragonula*, *Austroplebeia*, *Amegilla*) (Bossert *et al.* 2019).

Quantifying resource overlap and resource levels

To understand and predict competition, a measurement of resource overlap in terms of nectar and pollen plants, taking into account resource levels, should be quantified. In conjunction resource requirements of honeybees and native bees needs to be determined. This is crucial because even under low resource levels, resources may not be limiting for solitary native bees due to their relatively low per capita resource requirements, whereas the health of a honeybee colony relies on a flow of comparatively high amounts of nectar and pollen. However, the resources required to sustain solitary or social bee populations, and what represents a sustainable population size, are not known for many bee species (but see Franzén and Nilsson (2010) for the non-Australian bee, *Andrena hattorfiana*).

Feral honeybees

Feral honeybees have been present in Australia since the introduction of honeybees in the 1820s (Gibbs and Muirhead 1998). Feral and managed honeybees generate different predictions on the level of competitive threat they represent to native bees (Table 2). For example, feral honeybees represent chronic levels of competition and would be present when resources are limiting, whereas beekeepers tend to only place hives in areas where there is adequate, or at least greater amounts, of forage. Managed hives can however, be more vigorous due to beekeeping husbandry, and occur at higher densities. No feral hive removal experiments have been conducted in Australia, yet this may represent a more harmonious solution to honeybee management, being favourable to both commercial beekeepers and conservationists particularly as density or reproduction of inferior competitor species increases following removal of the superior competitor (Palmer *et al.* 2003).

Table 2. Differences in feral and managed European honeybee colonies and how this can affect the potential to compete and negatively interact with native bees in Australia.

Colony status	Feral	Managed
Duration of competition	Chronic	Acute
Density	Uncontrolled, fluctuate with the environment, but are more likely to swarm	Can reach very high densities
Spatio-temporal presence	Ubiquitous	May only be at high densities during crop bloom or peak nectar flow
Colony health	Subject to vagaries of the environment	Buffered against adverse conditions by beekeeping husbandry (water, supplementary feeding, disease management)
Aggression	'Feralised' – more aggressive	Selectively bred for docility
Genetic selection	Genetically less prone to adverse environmental conditions due to natural selection	Selectively bred for high nectar production and therefore higher potential for being highly competitive at resource exploitation
Genetic variation	Relatively higher – potential to adapt to new environmental challenges (climate, disease etc.)	Relatively lower – higher susceptibility to inbreeding depression

References: (Manning 1994; DEC 2012; Seeley *et al.* 2015; Pirk *et al.* 2017).

Feral and managed honeybees appear to compete more strongly against each other than against other species (Mallick and Driessen 2009) and introductions of commercial honeybees in Europe exert the strongest effects on feral honeybees, reducing feral honeybee densities and causing significant shifts temporally, spatially, and with respect to flora visited, yet did not affect native bumblebee foraging, or densities, which increased under addition of managed honeybees (Walther-Hellwig et al. 2006).

The number of feral colonies in Australia is unknown, yet feral honeybees appear to be most dense along waterways owing to high water requirements for cooling hives in hot Australian summers (DEC 2012). In a riparian woodland of north-west Victoria, feral honeybees occurred at densities of 50–150/km², fluctuating over the 3 years study (Oldroyd et al. 1997). Based on these estimates, it appears that feral honeybee colonies represent a greater population than do managed bees in Australia (Pirk et al. 2017). However, feral colony estimates may have been overestimated by an order of magnitude, and are also reduced in disturbed habitats (Arundel 2015). As techniques exist to remove feral hives (DEC 2012), feral honeybee removal experiments in Australia are warranted.

Finally, potential threatening processes on native bees can act in a combinatory or compensatory fashion, leading to potentially complex and often counterintuitive responses regarding the relationship of native bees to one or more potential explanatory variables (González-Varo et al. 2013; Goulson et al. 2015). It is therefore important to evaluate honeybee competition within the context of other threatening processes, and how environmental conditions may exacerbate or ameliorate competition.

Disease transmission

Honeybees suffer from parasites, viruses and other pathogens (Goulson et al. 2015). Despite being free of the major diseases that affect honeybee populations across the globe, Australian honeybees still are subject to many parasites and diseases (Frost 2019). There is therefore potential for honeybees to adversely affect native bees by transmitting diseases (Fürst et al. 2014; Goulson and Hughes 2015; Graystock et al. 2016). Indeed, of all potential negative impacts by honeybees on native bees, disease spill-over has received empirical support with no contradicting conclusions (Fürst et al. 2014; Russo 2016). However, clear declines due to disease transmission from honeybees appears to be restricted to closely-related bees (other *Apis* species, and some *Bombus* species) (Goulson et al. 2015; McMahon et al. 2015), whereas the phylogenetically-divergent native bee fauna of Australia may be relatively immune to this potential threat. Nevertheless, research has revealed pathogen sharing between honeybees and native Australian bees (Brettell et al. 2020).

The influence of predators in mediating competition

An Australian study on predation by spiders found honeybees were more vulnerable to predation than native bees (Heiling and Herberstein 2004). A potential explanation of increased numbers of native bees in the presence of higher honeybee abundances may therefore be due to predator saturation effects (Schwarz et al. 1991; Schwarz et al. 1992; Schwarz and Hurst 1997). However, greater abundances of honeybees can increase predator numbers, and consequently consumption of native bees could also increase (Wilson and Holway 2010). Solitary bees would be more negatively impacted by predation than would the colonial honeybee (Moller 1996). Future studies should consider identifying predators, and conducting manipulative studies measuring predator population responses and predation rates on honeybees and native bees under different honeybee abundances.

Considerations for future honeybee competition studies in Australia

Given that almost one quarter of publications on the effect of honeybees on native bees in Australia are reviews/opinion pieces, there is an over-representation of opinion on the topic with a comparatively small set of data from which to draw conclusions. We provide recommendations to advance research on this topic below.

Ecological theory predicts that under competition, either the superior competitor will eventually cause the extinction of the inferior competitor, or natural selection will cause species to evolve mechanisms such as niche shifts (e.g. character displacement, partitioning of resources among multiple dimensions) to reduce competition (Sommer and Worm 2002). Alternatively, non-equilibrium conditions, trade-offs, environmental heterogeneity, patch dynamics, recruitment and aggregation, as well as tritrophic interactions (such as disease or predators, discussed above), may enable co-existence (Sommer and Worm 2002). At what time scale these eco-evolutionary dynamics take place is unknown but would be important, because plant–pollinator dynamics following the invasion of honeybees can result in evolutionary changes to accommodate such new interactions within mere decades (Briggs 2014; Herrera and Pellmyr 2009). Conducting studies on whether native bees are affected by honeybees may be critical if time lags between invasion and competitive elimination occurs and may be vital to reverse the situation for species on the brink of extinction (Kuussaari et al. 2009).

Identifying under what conditions honeybees do or do not have an impact on native bees, and identifying vulnerable native bee species, can allow more targeted, evidence-based management. Studies reviewed above that found positive correlations between honeybee and native bee abundance suggests that opportunities exist to promote both categories

of pollinators. Further studies need to be undertaken to identify what factors determine conditions where both native bees and honeybees can thrive.

Ambiguity about whether honeybees outcompete native bees may stem in part from the difficulties of rigorously testing the competition hypothesis in the field, where there are many interacting and potentially confounding variables. Conducting competition experiments in controlled conditions in enclosures can reduce the effects of environmental vagaries. For example, such an approach provided clear evidence that honeybees could significantly depress fitness of the native European megachilid (*Osmia bicornis*) (Hudewenz and Klein 2015).

Overall, greater recognition, research, investment, and monitoring of Australia's native bee fauna is urgently required. Even though honeybees are not endangered, bee conservation is presented as being synonymous with saving honeybees and their pollination services (Batra 1995; Ollerton *et al.* 2012). Actions to help honeybees are unlikely to preserve native bees because of divergent foraging preferences and nesting habits; moreover, honeybee declines (where present) are largely driven not by loss of natural habitat, but rather due to their unique diseases and poor husbandry (essentially a domestic animal management issue) (Ollerton *et al.* 2012; Packer *et al.* 2016; Geldmann and González-Varo 2018).

Native bees can be key pollinators of both native and managed flora, and their co-evolutionary history with native flora means some oligolectic species perform superior pollination for particular native plants compared with honeybees (Houston 2000, 2014; Phillips *et al.* 2010). Even if honeybees compensate for native bees in terms of pollination services for some flora (e.g. exotic crops), ensuring native pollinators are preserved or restored to landscapes is still a fundamental endeavour, as native pollinators represent a unique evolutionary history that, unlike their pollination services, are irreplaceable (Senapathi *et al.* 2015; Prendergast 2020).

A precautionary approach to impacts of *Apis mellifera* in Australia

Well-resourced, long-term and, in some instances, manipulative experiments, are required to help determine under what circumstances there is a risk for honeybees to exert negative impacts on native bees. The published literature is insufficient to conclude with confidence if, when and where honeybees are competing with native bees. When resource competition is occurring, the published literature also is inconclusive regarding if the severity of competition results in negative consequences to biological fitness, translating to declines at the population level. Investigating all parameters to evaluate competition is challenging (Minckley *et al.* 2003), but a thorough assessment would require measuring honeybee density,

resource levels, and resource overlap, and how this relates to both native bee population density and reproductive output over time, and across scales ranging from the patch, to the habitat, to the landscape. For example, in over 50% of studies, it was assumed that indirect measures of resource competition were associated with fitness costs. Furthermore, indirect measures of competition included overlap in resource use, which is a necessary requirement for competition, but also, conversely, divergences in resource use as can occur under competitive exclusion. Whether indirect measures of resource competition result in reductions in fitness will depend upon resource availability and resource requirements of native bee populations (e.g. Minckley *et al.* 2003; Cane and Tepedino 2017), which have yet to be measured in Australian environments and for Australian bee species. Wild bees face fluctuating resource levels, and especially in urban and natural landscapes, they forage in heterogeneous landscapes. Therefore, when and where competition occurs, and if this translates to negative population outcomes, likely varies over time, as well as space (e.g. Roubik 2001; Prendergast *et al.* 2021a). For example, with adequate resource levels, honeybees and native bees could partition resources between patches, enabling co-existence, with no negative population impacts at larger scales. There has been far greater solid, ongoing experimental research of resource competition between introduced honey bees and native bees in the Neotropics (Roubik 2001; Roubik and Wolda 2001). Such studies may be considered a template to build a research agenda in Australia. However, it would be challenging to extrapolate these results to an Australian context due to a different climate, floristically rich habitats of different species, and a different honey bee subspecies (the Africanised honey bee) (Villanueva-Gutiérrez and Roubik 2004). Moreover, unlike the Neotropics, which has 33 genera (391 species) of Meliponini (Freitas *et al.* 2009), polylectic eusocial species are only a very minor component of Australian bee fauna (Houston 2018), and therefore, much of the Australian endemic fauna have not co-evolved with bees of this niche as a major selection pressure.

It is evident that studies to date are insufficient to draw solid conclusions about the net impact of the introduced European honeybee. However, a lack of evidence should not be interpreted to mean a lack of impacts. Rather, there is a solid theoretical foundation for expecting that under certain conditions this introduced abundant species may exert competitive pressures on native bees with consequences to biological fitness, which can be predicted to be exacerbated due to conditions causing limitations in resources and favouring honeybees over native bees (climate change, land-clearing, increased proportions of exotic flora, increased backyard beekeepers). Therefore, a precautionary principle is warranted (Pyke 1999).

Conclusion

Our review shows that it is premature to conclude that honeybees have either a benign influence or a net detrimental impact on Australian native bee abundance, species richness, or reproductive output. Because the effect of invasive species is likely to be strongly context-dependent and will vary upon the environmental and biotic conditions in space and time (Pyšek et al. 2012), further robust experimental studies on the impact of honeybees on native plant–pollinator networks in Australia are essential. Indeed, significant negative impacts appear to be more likely to be revealed through controlled manipulative studies. A major conclusion from our review was that part of the variation in results stems from variation in species ecology and therefore, more detailed investigations into how particular native bee species or guilds are impacted is needed rather than coarse approaches which may obscure the impacts of this introduced bee on vulnerable species. Future studies should focus on the areas we identified above with the aim of managing honeybees in such a way that does not jeopardise the conservation of native bees.

Supplementary material

Supplementary material is available [online](#).

References

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