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Floral Resource Competition Between Honey Bees and Wild Bees: Is There Clear Evidence and Can We Guide Management and Conservation?

Victoria A. Wojcik,¹ Lora A. Morandin, Laurie Davies Adams, and Kelly E. Rourke

Pollinator Partnership, 423 Washington Street, 5th floor, San Francisco, CA 94111, and ¹Corresponding author, e-mail: vw@pollinator.org

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Abstract

Supporting managed honey bees by pasturing in natural landscapes has come under review due to concerns that honey bees could negatively impact the survival of wild bees through competition for floral resources. Critique and assessment of the existing body of published literature against our criteria focussing on studies that can support best management resulted in 19 experimental papers. Indirect measures of competition examining foraging patterns and behavior yielded equivocal results. Direct measures of reproduction and growth were investigated in only seven studies, with six indicating negative impacts to wild bees from the presence of managed honey bees. Three of these studies examined fitness impacts to *Bombus Latreille* and all three indicated reduced growth or reduced reproductive output. Because there is a severe lack of literature, yet potential that honey bee presence could negatively impact wild bees, exemplified with bumble bee studies, we advocate for further research into the fitness impacts of competition between managed and wild pollinators. Conservative approaches should be taken with respect to pasturing honey bees on natural lands with sensitive bumble bee populations. Correspondingly, forage opportunities for honey bees in managed, agricultural landscapes, should be increased in an effort to reduce potential pressure and infringement on wild bee populations in natural areas.

Key words: *Apis mellifera*, *Bombus* spp., competition, wild bee, floral resource

Managed honey bees (*Apis mellifera* L.) and wild bees both feed on nectar and pollen from flowers, and therefore, there is potential for competition. Although concerns that pasturing managed honey bees in natural areas may limit resources for native bees are not new (Schaffer et al. 1983), recent evidence of declines in native bee populations from a variety of factors (e.g., Allen-Wardel et al. 1998, Kremen et al. 2007, Potts et al. 2010, Colla et al. 2012, Bartomeus et al. 2013) have intensified worries of the potential added impacts of competition to wild bee species and communities.

Nearly 45% of the world's most commonly grown crop species (52 of 115) are dependent on pollinators for reproduction (Klein et al. 2007). Bees are the most important crop pollinators; 22.6% of all agricultural production in the developing world and 14.7% in the developed world are directly connected to the actions of bees (Aizen et al. 2009). Honey bees are the most important managed pollinator for global agriculture (Delaplane and Mayer 2000, vanEngelsdorp and Meixner 2010) and are estimated to contribute nearly \$40 billion (U.S. dollars) annually to crop production across the European Union and North America (Gallai et al. 2009).

Wild bees are key pollinators of flowering plants in natural landscapes, but are also important pollinators of crops (Garibaldi

et al. 2013), and have intrinsic biodiversity value (MEA 2005). In many cases, wild pollinators are more efficient pollinators of crop plants when compared to managed honey bees and can contribute the majority of required pollination service to 86% of pollinator-dependent crops (Garibaldi et al. 2013). In addition, diverse populations of wild bees can ensure stability and resilience of pollination services, even when honey bees are present (Greenleaf and Kremen 2006, Garibaldi et al. 2013). Because many species of wild bees may already be under stress from human activities, there is concern that added competition and other interactions with managed honey bees could increase population declines. Finding a balance between maintaining and improving honey bee health, while not causing detrimental effects to vulnerable wild bee populations is crucial for biodiversity preservation and the future of sustainable food production.

Honey bees are managed by beekeepers to maintain high-quality colonies for crop pollination and to produce honey and other hive products for commercial markets. Although not native to North America, honey bees have become a fixture in agricultural production. With the significant role that managed honey bees play in crop pollination represented by upwards of 350 million dollars annually in pollination services in the United States (USDA 2016a), their health

and well-being are key concerns for food production and food security (Aizen and Harder, 2009). The health of honey bee colonies in North America has been increasingly compromised in the last few decades, manifesting as high winter colony losses in some regions (USDA 2016b) and greater difficulty managing colonies throughout the summer (vanEngelsdorp et al. 2009, Berthoud et al. 2010; Ellis et al. 2010). Poor honey bee health and colony losses can be attributed to a number of factors including: pests and diseases, such as *Varroa destructor* Anderson and Trueman; exposure to pesticides; stress from migratory operations; recent climate extremes represented by exceptionally long and cold winters; and lack of adequate forage and nutrition (vanEngelsdorp et al. 2009, vanEngelsdorp and Meixner 2010, Seitz et al. 2015, see also NRC 2007). Access to abundant, diverse forage sources that provide complete and balanced nutritional requirements (i.e., lipids, proteins, and amino acids) is believed to be a key component of maintaining colony health (Di Pasquale et al. 2013, Donkersley et al. 2017), and may play an important role in the ability of honey bees to better cope with diseases (Alaux et al. 2010), pesticide stresses (Schmehl et al. 2014), and other stressors (Huang 2012).

To support managed colonies when there is a lack of sufficient floral resources in the adjacent environment, beekeepers can supplement with specialized bee diets, sugar syrup, and pollen substitutes. Instinctively, beekeepers prefer to provide bees with a natural source of pollen and nectar, and if possible seek areas of forage where they can pasture their bees. Historically, beekeepers in the United States have used U.S. Forest Service, U.S. Fish and Wildlife Service, Bureau of Land Management, and other public lands as supplementary bee pastures. Agricultural lands that are in the Conservation Reserve Program (CRP), roadsides and utility corridors, and other public and private lands are also popular choices for providing honey bees with forage. These floral-rich lands are also recognized significant habitats and food resources for native, wild pollinators (Russell et al. 2005, Hopwood 2008, Hopwood et al. 2010, Wojcik and Buchmann 2012, Cane and Tepedino 2016). Trends in rural landscape development, as well as shifts in crop production practices and prices, have dramatically changed honey bee forage availability in agricultural landscapes (Otto et al. 2016). Where beekeepers once had ample forage in managed agricultural lands, today many more seek access to alternative lands, such as natural areas, to make up deficits.

Recently, some beekeepers have seen access to public and private natural lands questioned, limited, or rejected because of concern that wild bees are being put under undue stress due to competition with managed honey bees for food. Decisions made in these cases have largely been based on opinion rather than on scientific evidence or have made use of published resources that suggest precautionary approaches to managing honey bees and conserving wild bees that are not based on direct experimental evidence. Management decisions have also focussed strongly on the origins of honey bees, as it is the mandate of some public and private organizations to support native species, and thus not to promote nonnative species.

There are currently no comprehensive and critical reviews of the experimental literature on resource-based competition between managed honey bees and wild bees at a technical level that would help inform land management (see Cane and Tepedino 2016). Such a review is essential to establish what information is available to guide science-based decision making and to understand what information is currently lacking. There have been several reviews reflecting on the relationships between honey bees and other social and solitary bees (see Supplementary Appendix 1, Eickwort and Ginsberg 1980, Pyke and Balzer 1985, Butz Huryn 1997, Pyke 1999, Goulson 2003, Paine 2004, Moritz and Härtl 2005, National Research Council of

the National Academies 2007, Stout and Morales 2009, Dohzono and Yokoyama 2010, Potts et al. 2010, Burkle and Alarcón 2011). Collectively these reviews indicate that competition between managed honey bees and other bees for floral resources is likely, and suggest honey bees to have the competitive advantage based on biological traits, but few cite direct experimental evidence. Most reviews have extrapolated the possible impacts of competition between honey bee and wild bees from observed floral visitation patterns, often documented over limited time periods. Some studies using occurrence data provide indirect evidence of competition between honey and native bees (Thomson 2004, Goulson and Sparrow 2009), usually with negative impacts to wild bees, but not always (Balfour et al. 2013). Other studies examining occurrence data have not detected any negative impact of honey bees on the visitation patterns of native bees (see Steffan-Dewenter and Tscharrntke 2000, Paine 2004, Forup and Memmott 2005, Shavit et al. 2013, Torné-Noguera et al. 2016), but advocate for a precautionary approach to honey bee management and conservation of wild bees. Furthermore, in this review, we address the shortcomings of using observed foraging patterns as indicators of competition.

In this review, we assessed literature on competition between managed honey bees and wild bees, focussing on studies that conducted direct tests of competition using experimental and/or manipulative methodologies that examine behavior, growth, and reproduction as a response to the presence or absence of managed honey bees. The scope of this review is narrowed to questions of resource competition in response to current management challenges. A recently published review by Mallinger et al. (2017) provides a high-level aggregation and comparison of bee interactions, including pathogen spillover and floral community impacts. Here, we present a higher resolution critique of studies aimed at providing sound, evidence-based guidance, where possible, on managing natural landscapes and bee health.

Competition Between Managed and Wild Bees

Competition is defined as a negative interaction among organisms when two or more organisms require the same limited resource. There are two main types of competition; interference, and exploitative. In interference competition, organisms directly interact through fighting or other physical contact. In contrast, exploitative competition involves the use and depletion of a resource, thereby reducing amounts available for other organisms, and is thought to be the most common form of competition among terrestrial animals (Schoener 1983). Direct, interference competition between honey bees and other bees can occur, but most researchers agree that it is not likely to be a significant factor impacting native bees (Balfour et al. 2013, Torné-Noguera 2016 and references therein; however, see Pinkus-Rendon et al. 2005 for a counter point). Rather, exploitative competition for floral resources is thought to be the most probable form of competition that could result in negative effects on native bee populations (Cane and Tepedino 2016). Competitive interactions have structured ecosystems and enhanced patterns of diversity as species partition niche space, but competition can also result in negative impacts to species, including exclusion from the ecosystem or extinction.

Competition is expected to be highest when there is the greatest overlap in niche space. Feeding habits vary greatly across bee families, genera, and species, making predicting competitive interactions complicated. Bees are commonly classified using the breadth of their pollen feeding along a spectrum of specialization to generalism (Cane and Sipes 2009). Specialization for the pollen of one host

plant species, known as “monolectic” feeding, is far less common, known in only a few families of bees. *Oligolectic* and *mesolectic* feeding patterns defined as feeding on the pollen of multiple species within one or more genera, again are less common than generalization. Bees with a broader repertoire that visit multiple species within multiple genera and families are considered “polylectic” to various degrees; approximately 25% of bee families are considered polylectic, with honey bees and bumble bees as primary examples (Cane and Sipes 2009). Seasonality, body size, and tongue length are some of the additional traits that determine feeding ranges for bees.

There are two alternative theories regarding the segment of the wild bee community that would be potentially subjected to the greatest negative impacts in the presence of honey bees. One suggests that more specialized pollen feeders would suffer the most from new competitive interactions within their narrow niche space; these species would also be less able to shift to feed on other plants (Wasser and Ollerton 2006 and references therein). According to this first hypothesis, more specialized feeders or those that occur in very narrow spatiotemporal niches would be most at risk, such species could include Andrenidae which occur briefly in the spring season and preferentially feed on early season blooms. The other hypothesis suggests that generalist feeders would experience the most resource overlap with honey bees and be more likely to directly compete for the same resources (Wasser and Ollerton 2006, Dohzono and Yokoyama 2010 and references therein), although these species have a greater capacity to shift their resource use temporally or spatially escaping some competitive pressure (Walther-Hellwig et al. 2006). According to the second hypothesis, shorter-tongued bumble bees would be most likely to directly compete with honey bees. It has been argued that oligolectic or more specialized bees are adapted to use flowers that are not preferred by generalist feeders, and therefore exist in a separate niche space that would not be used by honey bees (Cane and Sipes 2009). This is the position of many beekeepers who describe the feeding preferences of their bees as general, but targeted toward plants that provide good nectar and that dominate the landscape (Pellett 1948, Somerville 2005). Studies of honey bee foraging support the view that they prefer to forage on the most abundant and most nectar-rewarding floral resource in a landscape (Campana and Moeller 1977, Visscher and Seeley 1982). The nature of interactions between managed honey bees and unmanaged wild bees is likely to be context specific and not uniform across landscapes (e.g., Herbertsson et al. 2016).

Nesting sites are also a crucial resource needed for native wild bees to rear their young. Most bees nest in the ground, requiring loose, bare soil, while some nest in surface litter or above ground plant stems and in wood. In wild conditions, honey bees select cavities suitable for the establishment of a large colony. Nest-site competition is not considered to be a significant factor between honey bees and wild bees.

Review Methodology

We searched multiple databases, including Web of Science and BIOSIS, using key the terms honey bee or *A. mellifera* + native bee or wild bee or bee + competition or foraging or interaction. Searches were conducted periodically from April 2013 to August 2017. Many of the resources retrieved were in themselves secondary-source review papers, and the reference sections of these papers were searched for additional primary publications that were not recovered in the original searches. A list of previously published reviews is provided separately in Supplementary Appendix 1. We also reached out to members of the North American Pollinator Protection Campaign

(NAPPC) and pollinator listserv (pollinator@nappc.org) community to find additional studies, including those published as graduate theses or those found in nonpeer reviewed sources. Our review is restricted to publications that were available in English.

In total, 81 papers were accessed using our search criteria. The search yielded many papers that made statements on competition but were limited to indirect observations of foraging patterns, richness, and abundance of native bees in the presumed presence or absence of honey bees. We found 15 prior reviews of bee competition (see Supplementary Appendix 1). From the total list of resources, we focussed on published papers that conducted direct experimental assessments (either manipulative or paired field observations) of competition between honey bees and wild or native bees. Papers dealing with Africanized honey bees (*A. mellifera scutellata*) (Roubik 1987, 1980, 1983; Roubik et al. 1986; Roubik and Wolda 2001; Roubik and Willanueva-Gutiérrez 2009) and papers examining *A. mellifera* invasions of islands (Kato et al. 1999, Dupont et al. 2004, Kato and Kawakita 2004) were excluded as they represented pre- and post-colonization species inventories and were not experimental in nature. These criteria resulted in 19 experimental papers. To understand the breadth and limitations of current information on bee competition, studies were categorized based on the geographic region, duration, landscape, native bee species or community examined, and floral resource examined. We reviewed the experimental design and results of each primary research paper. We also indicate if fitness impacts were measured in the assessment of competition as this is the most reliable and direct measure of impacts. Conclusions were coded into one of four possible outcomes: “inconclusive”—statistical power was low and definitive conclusions limited or absent; “no competition”—no evidence of reduced reproduction or changes to floral visits to either honey or wild bees; “competition”—honey bee favored; and “competition”—wild bee favored.

Findings and Discussion

Of the 19 papers meeting our criteria, 14 were experiments where either the density of honey bees in a landscape was altered or both the density of honey bees and native bees was manipulated (Schaffer et al. 1983, Sugden and Pyke 1991, Steffan-Dewenter and Tscharrntke 2000, Gross 2001, Thomson 2004, Forup and Memmott 2005, Paini and Roberts 2005, Thomson 2006, Walther-Hellwig et al. 2006, Hudewenz and Klein 2013, Rogers et al. 2013, Shavit et al. 2013, Elbgami et al. 2014, Hudewenz and Klein 2015). The other five were observational experiments carried out in paired landscapes where managed honey bees were considered present or absent (Goulson et al. 2002, Goulson and Sparrow 2009, Herbertsson et al. 2016, Lindstrom et al. 2016, Torné-Noguera et al. 2016, Table 1). Seven studies measured reproductive output in wild bees (Sugden and Pyke 1991, Thomson 2004, Paini and Roberts 2005, Goulson and Sparrow 2009, Hudewenz and Klein 2013, Elbgami et al. 2014, Hudewenz and Klein 2015).

Nativity and the Potential for Competition

Nine of the 19 studies were conducted in regions where honey bees are considered native (Stephen-Dewenter and Tscharrntke 2000, Forup and Memmott 2005, Walther-Hellwig et al. 2006, Goulson and Sparrow 2009, Hudewenz and Klein 2013, Shavit et al. 2013, Elbgami et al. 2014, Hudewenz and Klein 2015, Torné-Noguera et al. 2016). However, these studies focussed on interactions with managed honey bees, not feral or native colonies. Eight studies examined interactions outside of the native range of honey bees; four of these studies were conducted in the United States (Schaffer et al.

Table 1. Categorization of experimental tests of competition between honey bees and wild bees noting the geographic scope of the work, ecosystem type and plant species examined, native bees compared, and the length of the study period

Authors	Duration	Location	Habitat type	Test of growth and/or reproduction (y/n)	Wild bee group examined	Floral resource studied	Inconclusive	No competition	Exploitative—honey bee favored	Exploitative—wild be favored
<i>A. mellifera</i> nonnative to landscape										
Schatfer et al. 1983	1 mo	United States	Southern Arizona, Santa Catalina Mts.	n	<i>Bombs</i> sp. <i>Xylocopa</i> Latreille sp. other small solitary bees <i>Bombus occidentalis</i> <i>Green</i>	<i>Agave schottii</i> Engelm.		x		
Thomson 2004	3 yr	United States	California, Big Sur, coastal scrub	y	<i>Bombus caliginosus</i> Frison <i>Bombus vosesenskii</i> <i>Radoszkowski</i> <i>Bombus edwardsi</i> Cresson <i>Bombus californicus</i> <i>Smith</i> <i>Bombus occidentalis</i> <i>Bombus impatiens</i> <i>Cresson</i>	<i>Eriophyllum stachaeifolium</i> <i>Lagasca</i> <i>Salvia mellifera</i> Greene <i>Eriophyllum stachaeifolium</i> <i>Lagasca</i> <i>Stachys bullata</i> Benth. <i>Phacelia malvifolia</i> Cham. <i>Mimulus aurantiacus</i> <i>Artemisia californica</i> Less. <i>Sabia mellifera</i> Greene <i>Lupinus albifrons</i> Benth. <i>Lotus scoparius</i> (Nutt.) Ortley			x	
Thomson 2006	3 yr	United States	California, Big Sur, coastal scrub	n	<i>Bombus impatiens</i> <i>Cresson</i>	artificial plants with sucrose and peppermint oil			x	
Rogers et al. 2013	2 d	United States	North Carolina, managed hoop house	y	<i>Exoneura asmilima</i> <i>Rayment</i>	<i>Xanthorrhoea</i> Sol. ex Sm. sp.			x	
Sugden and Pyke 1991	6 mo	Australia	Nadgee Nature Reserve, plains and meadows	y	<i>Hylaeus alycyoneus</i> <i>Erichson</i>	native community			x	
Paini and Roberts 2005	2 yr	Australia	Agricultural landscape	y	<i>Leioproctus Smith</i> sp. 1 <i>Lastoglossum Curtis</i> sp.	<i>Dillwynia juniperina</i> Lodd.			x	
Gross 2001	2 yr	Australia	Northern Tablelands of New South Wales, dry forest	n	native bee community	native community				
Goulson et al. 2002	2 mo	Australia	Tasmania, natural areas	n	native bee community	native community		x		
<i>A. mellifera</i> native to landscape										
Steffan-Dewenter and Tscharnke 2000	5 mo	Germany	Habitat remnants within agricultural	n	native bee community	native plan community	x			
Forup and Memmott 2005	6 mo	England	Southern lowland heaths	n	<i>Bombus lucorum</i> L. <i>Bombus terrestris</i> L. <i>Bombus terrestris</i> <i>Bombus lucorum</i> <i>Bombus cryptarum</i> Fabricius <i>Bombus soroeensis</i> Fabricius <i>Bombus pascuorum</i> Scopoli <i>Bombus sylvarum</i> L. <i>Bombus muscorum</i> L.	heather heath: <i>Calluna vulgaris</i> L. (Hull) <i>Phacelia tanacetifolia</i> Benth. other wildflowers: <i>Polygonum persicaria</i> S.F. Gray/ <i>Epiobium angustifolium</i> L. <i>Lotus uliginosus</i> Cav./ <i>Centaurea jacea</i> L.			x	
Walther-Hellwig et al. 2006	2 mo	Germany	Habitat remnants within agricultural	n	native bee community	native plan community		x		

Table 1. Continued

Authors	Duration	Location	Habitat type	Test of growth and/or reproduction (y/n)	Wild bee group examined	Floral resource studied	Inconclusive	No competition	Exploitative—honey bee favored	Exploitative—wild be favored
Goulson and Sparrow 2009	2 mo	Scotland	Lowland pasture	y	<i>Bombus pascuorum</i> L. <i>Bombus lucorum</i> <i>Bombus lapidarius</i> L. <i>Bombus terrestris</i>	<i>Chamaenerion angustifolium</i> L. <i>Centaurea nigra</i> L. other native			x	
Hudewenz and Klein 2013	6 mo	Germany	Lüneburg Heath, man-made conservation area	y	<i>Andrena fuscipes</i> Kirby <i>Colletes succinctus</i> L. <i>Epeolus cruciger</i> Panzer <i>Sphexcodes reticulatus</i> Thomson (<i>clepto parasite</i>) native bee community	heather heath: <i>Calluna vulgaris</i>		x		
Shavit et al. 2013	3 yr	Israel	Northern Israel, national park lands	n	native bee community	<i>Salvia eigi</i> Zohary <i>Salvia pinnata</i> L. <i>Rosmarinus officinalis</i> L. <i>Salvia fruticosa</i> Mill		x		
Elbgami et al. 2014	2 yr	England	Agricultural matrix with remnant forests	y	<i>Bombus terrestris andax</i> (Harris)	borage, red clover, Phacelia, mustard			x	
Hudewenz and Klein 2015	1 mo	Germany	Experiment station cage	y	<i>Osmia bicornis</i> L.	<i>Phacelia tanacetifolia</i> Benth. <i>Fagopyrum esculentum</i> Moench <i>Sinapis alba</i> L. <i>Coriandrum sativum</i> L. <i>Calendula officinalis</i> L. <i>Nigella sativa</i> L. <i>Raphanus sativus</i> L. <i>Centaurea cyanus</i> L. <i>Malva sylvestris</i> L. <i>Anthemum graveolens</i> L. <i>Borago officinalis</i> L.			x	
Herbertsson et al. 2016	1 mo	Sweden	Natural and Agricultural landscapes, homogenous, and heterogeneous landscapes	n	<i>Bombus</i> spp.	mixed floral community			x	
Lindstrom et al. 2016	2 yr	Sweden	Agricultural landscape	n	<i>Bombus</i> spp., native solitary community	<i>Brassica napus</i> L.				x
Torné-Noguera et al. 2016	4 mo	Spain	Garraf national Park: scrubland	n	<i>Bombus terrestris</i> other native bees	<i>Rosmarinus officinalis</i> L. <i>Thymus vulgaris</i> L.		x		

1983, Thomson 2004, Thomson 2006, Rogers et al. 2013) and four were conducted in Australia (Sugden and Pyke 1991, Gross 2001, Goulson et al. 2002, Paine and Roberts 2005). Nativity did not impact the range of interactions reported by authors. In other words, there was no correlation between the outcome of competition and if studies were conducted in the native range of *A. mellifera*. While it has been common to segregate honey bee–wild bee interactions in this manner, it is not informative, nor does it provide any consistent trend that is meaningful for management.

Geographic Scope of Studies

The local and regional geographic scope of bee competition studies is very limited. Although the aim of most studies is to determine the impacts of managed honey bees to wild bees outside of agricultural landscapes, most are carried out in natural or seminatural areas near to production agriculture. This is especially true to studies carried out in Europe (Steffan-Dewenter and Tschamtko 2000, Forup and Memmott 2005, Walther-Hellwig et al. 2006, Goulson and Sparrow 2009, Hudewenz and Klein 2013, Elbgami et al. 2014, Herbertsson et al. 2016, Lindstrom et al. 2016). Experimental tests of bee competition in the United States have been carried out in a single natural landscape type focussing on bumble bees (*Bombus occidentalis* (Green) in locations along the central California Coast Chaparral ecosystem; Thompson 2004, 2006). One significant challenge to providing reliable, relevant advice on mitigating the potential negative competitive interactions between honey bees and wild bees is that the studies we reviewed were not conducted in the landscapes where current conflicts and concerns are occurring (forests in the western region of the United States; south eastern, north eastern conservation lands; and open space in central California near agricultural lands, to name a few, see also Cane and Tepedino 2016 for further commentary).

Evidence for Competition

Nine of the studies did not show a measurable interaction between honey bees and native or wild bees (Schaffer et al. 1983, Goulson et al. 2002, Thomson 2006, Walther-Hellwig et al. 2006, Shavit et al. 2013, Hudewenz and Klein 2015, Torné-Noguera et al. 2016), or had low power (Steffan-Dewenter and Tschamtko 2000, Forup and Memmott 2005). Ten of the studies found evidence for exploitative competition, with behavioral shifts seen in native species (Gross 2001, Thomson 2004, Paine and Roberts 2005, Goulson and Sparrow 2009, Hudewenz and Klein 2013, Rogers et al. 2013, Elbgami et al. 2014, Herbertsson et al. 2016, Lindstrom et al. 2016) or impacts to fitness measures (Sugden and Pyke 1991, Thomson 2004, Paine and Roberts 2005, Goulson and Sparrow 2009, Elbgami et al. 2014, Hudewenz and Klein 2015).

Behavioral Changes

The majority of papers that examined competition focussed on foraging patterns exhibited by native bees in the presence or absence of honey bees (Table 1). These included decreases in the abundance of bumble bee foragers with increases in *A. mellifera* foragers (Forup and Memmott 2005, Herbertsson et al. 2016, Lindstrom et al. 2016) and decreases in the observed richness of native bee foragers with increasing *A. mellifera* activity on flowers (Gross 2001, Goulson et al. 2002). Increasing the number of honey bee colonies in a natural area resulted in bumble bee foragers shifting to floral resources that were less used by *A. mellifera* (Walther-Hellwig et al. 2006). A similar trend was seen by Schaffer et al. (1983), but once additional colonies of *A. mellifera* were removed from the test location,

native bee numbers rebounded quickly, indicating a temporal resource shift. Other studies did not detect any measurable differences in native bee foraging rates or plant species usage as a result of honey bee presence (Sugden and Pyke 1991, Steffan-Dewenter and Tschamtko 2000, Thomson 2006, Shavit et al. 2013, Hudewenz and Klein 2013).

Changes in foraging patterns do not indicate if any resultant fitness impacts are present over the long run. Despite evidence that the presence of honey bees can alter native bee foraging behavior and numbers, behavioral changes do not necessarily signal that there will be a negative impact to local populations. Thomson (2004) and Goulson and Sparrow (2009) note in their studies that the foraging patterns exhibited by *Bombus* in the presence and absence of *A. mellifera* did not correlate with fitness responses measured. Thomson (2004) found increased foraging by *Bombus* in the presence of *Apis* in her early study, which would appear to indicate no response at face value, but this pattern of increased foraging was at the cost of energy inputs into reproduction (see also Thomson 2006). Changes in foraging numbers and patterns may not be reliable indicators of reproductive output and population effects. Furthermore, the limited temporal range of the studies does not allow us to determine if the observed patterns have impacts on populations and community structure over time.

Although the dominant form of competition between bees likely is exploitative competition, there is some evidence that interference competition can occur. Rogers et al. (2013) conducted a hoop-house cage experiment indicating foraging interference between honey bees and *Bombus impatiens*. In this study, bumble bee foragers were significantly less likely to revisit a forage site (synthetic flower with sugar syrup) if they had a physical encounter with a honey bee forager, suggesting interference competition favoring *A. mellifera*. Similar patterns of increased forager departures from the original flower to adjacent flowers when honey bees and non-*Apis* bees encountered each other were noted by Greenleaf and Kremen (2006) in sunflowers. The interpretation of this pattern in their study was positive for potentially enhancing pollination services as honey bees and native bees made more unique floral visit when they encountered native bees on flowers (see Greenleaf and Kremen for more details). Rogers et al. (2013) state that reduced visits by *Bombus* after *Apis* visits are indicative of preemption; however, the results could be interpreted as positive, driving bumble bees to visit more floral resources. It is also difficult to extrapolate the impacts of cage studies with limited resources to natural landscapes and therefore the findings of Rogers et al. are potentially inconclusive.

Impacts to Growth and Reproduction

Experiments examining reproductive consequences of competition were conducted in only seven studies; six found evidence of exploitative competition with negative developmental or reproductive consequences in native bees in the presence of honey bees (Sugden and Pyke 1991, Paine and Roberts 2005, Goulson and Sparrow 2009, Thomson 2004, Elbgami et al. 2014, Hudewenz and Klein 2015). Hudewenz and Klein's (2013) first examination of solitary bee nesting and brood production as a factor of honey bee presence and absence showed no correlation between nest occupancy or brood production and honey bee numbers. It should be noted that gauging reproductive impacts in wild, solitary bees is challenging, with Hudewenz and Klein highlighting that a lack of results in this case may not speak directly to bee interactions, but rather to our ability to assess and measure impacts in field conditions. In a follow-up cage study, Hudewenz and Klein (2015) found that *Osmia bicornis* L. exhibited lower foraging rates and lower reproductive output in the presence of honeybees that foraged on shared, limited resources. The difference between results from their field and cage

studies could be a result of artificial creation of limited resources in the cage experiment, which was not experienced by bees in the field study. It is possible that in the field conditions, honey bees were not reducing floral resources for native bees to an extent that resulted in reduced reproduction (i.e., floral resources were not limiting; reproduction was limited by some other factor). Further, it is also likely that increased precision was achieved in measuring impacts to cavity-nesting species using tube nests in a controlled environment.

Sugden and Pyke accounted for the earliest test of honey bee presence on wild bee reproduction in 1991. In their two-year study, they examined nest parameters including pollen collection, larval and pupae numbers, and larval and pupal size in colonies of *Exoneura asimillima* Rayment, a semisocial bee. In their first year of study, results were equivocal at control sites and at those with artificially augmented presence of honey bees. In the second year, significantly reduced larval number, size, and reduced pollen loads were noted at sites with honey bees. The duration of the study is limited, and these results can be seen as equivocal when both sample years are compared; however, the authors maintain that honey bee presence has the potential to account for reduced fitness.

Paini and Roberts (2005) recorded reduced fecundity in a tunnel-nesting native bee, *Hylaenus alcyoneus* Erichson, in the presence of managed honey bees in a natural field setting. Their study relied on a natural experiment where registered apiary sites were used as treatments and nonapiary sites as controls. Pollen sampling noted *H. alcyones* and *A. mellifera* to share floral resources; *H. alcyones* diet did not change in the presence or absence of honey bees. Tube nest occupancy was found to be on average 23% lower at honey bee sites. They concluded that even when resources are not limited, other factors such as preemption and local exploitation can impact native bees with short foraging ranges (*H. alcyones* is a very small bee with a foraging range of less than 200 m). Once again, a limitation to this study is duration as only two seasons were examined, which does not allow us to determine if reduced nest occupancy results in population impacts over time.

Goulson and Sparrow (2009), Thomson (2004), and Elbgami et al. 2014 focussed their investigations of resource competition with honey bees on bumble bees, which have similar resource usage characteristics and are considered broadly generalist feeders. Goulson and Sparrow's work in lowlands and pastures in Scotland (where honey bees are native but believed to persist in larger numbers due to human management) indicated that while no difference in floral visitation pattern was seen, the workers of some bumble bees (*Bombus pascuorum* L., *Bombus lucorum* L., *Bombus lapidarius* L., and *Bombus terrestris* L.) were smaller in size when sampled from areas where honey bee colonies were present compared to workers sampled from areas without the presence of managed honey bee hives (Goulson and Sparrow 2009). Bumble bee size has been shown to be affected by the amount of pollen consumed during development, with smaller size indicating reduced pollen consumption (Pendrel and Plowright 1981). The smaller worker size in Goulson and Sparrow's study can be interpreted as growth limitation in response to reduced resource provisioning, or reduced worker growth as a response to colony energy reallocation.

Thomson (2004) found that *B. occidentalis* in a Southern California natural landscape shifted energy resource allocation to foraging in the presence of honey bees, and as a consequence produced less brood and fewer males and queens than bumble bees that had colonies further away from honey bee hives. In this study, the impacts to *B. occidentalis* were distance based, with the most dramatic reductions seen when honey bee colonies were within 750 m of bumble bee colonies. Elbgami et al. (2014) examined *B. terrestris* in remnant forests within an agricultural matrix in the presence and

absence of honey bee colonies. Their results showed that *Bombus* colonies near honey bee apiaries gained less weight and produced fewer and smaller queens compared to those located away from honey bees. These three studies are consistent in showing reduced colony growth and reproduction (lower number of queens and/or drones) in the presence of honey bees. Distance-based responses such as these suggest that strategic placement or stocking rate could potentially be used as a viable management strategy to mitigate negative impacts to wild bees. It should also be noted again that the limited temporal range of the studies conducted on competition between honey bees and wild bees does not allow us to determine reduced annual reproductive output (fewer or smaller offspring) have population-level consequences over time.

A Diverse Bee Community Results in a Diverse Set of Responses

Given the diverse set of life histories displayed by native bees, different experimental designs, and the diverse environments of the studies, it is not surprising that a range of responses is reported. Table 2 presents a list of bee species examined sorted by bumble bee species and other wild bees. The body of research is heavily biased toward interactions between honey bees and bumble bees, with a focus on *B. occidentalis* and *B. impatiens* Cresson in the United States and a few other *Bombus* species in Europe. Competition between honey bees and bumble bees was documented in six of nine studies, and in all cases confirming a negative competitive interaction, bumble bees were noted to suffer the consequence (but see Balfour et al. 2013). Shifts in bumble bee foraging to alternative resources (Thomson 2006), not returning to resources after an encounter with honey bees (Rogers et al. 2013), and lower larval and gyne production (Thomson 2004) show that these bumble bee species can potentially suffer some consequence when sharing a resource with honey bees. Although low in number, the consistent negative fitness responses seen in bumble bees in the presence of honey bees can be used to develop a statement of precaution and avoidance for this group of native bees.

Evidence of negative fitness responses to competition from honey bees was noted in only three other native species: *O. bicornis* in Germany (Hudewenz and Klein 2015); *E. asimillima* in Australia (Sugden and Pyke 1991); and *H. alcyoneus*, again in Australia (Paini and Roberts 2005). All three of these species are tube or tunnel nesting, making their homes above ground in hollow grasses, reeds, or wood cavities. These nesting lifestyles are more suited to experimental designs that require counts of brood as they can be assessed more easily, but tunnel nesting bees comprise the minority (about 10%) of the native bee community (Michener 2000). Hudewenz and Klein (2013) attempted a proxy measure of reproductive output in ground nesting species by examining nest occurrence and occupancy, providing an indication of the local nesting female population sizes but not a direct measure of reproduction. There is very little information on the reproductive response of native bees other than bumble bees to the presence of honey bees. Globally, there are thought to be upward of 25,000 species of bees (Michener 2000); in North America alone there are more than 4,000 native bee species. This limited examination does not enable us to provide any meaningful general guidance based on evidence, but does reinforce some evidence for competition in the three non-*Bombus* species where fitness impacts were measured.

Study Duration and Our Ability to Predict Change Over Time

Most of the studies were short term, conducted over one or two seasons, or even narrower observation windows coinciding with the

Table 2. Studies examining honey bee and wild bee interactions, noting documented evidence of competition, grouped as those that examine bumble bee responses and the response of the rest of the native bee community

No response with HB		Negative response to HB	
Authors	Species	Authors	Species
Bumble bees			
Schaffer et al. 1983* Thomson 2006	<i>Bombus</i> sp. <i>Bombus caliginosus</i> <i>Bombus vosesenskii</i> <i>Bombus edwardsi</i> <i>Bombus californicus</i> <i>Bombus occidentalis</i>	Thomson 2004 Rogers et al. 2013	<i>Bombus occidentalis</i> <i>Bombus impatiens</i>
Forup and Memmott 2005	<i>Bombus lucorum</i> <i>Bombus terrestris</i>	Goulson and Sparrow 2009	<i>Bombus pascuorum</i> <i>Bombus lucorum</i> <i>Bombus lapidarius</i> <i>Bombus terrestris</i>
Walther-Hellwig et al. 2006	<i>Bombus terrestris</i> <i>Bombus lucorum</i> <i>Bombus cryptarum</i> <i>Bombus soroeensis</i> <i>Bombus parcuorum</i> <i>Bombus sylvarum</i> <i>Bombus mascorum</i> <i>Bombus terrestris</i>	Elbgami et al. 2014	<i>Bombus terrestris audax</i>
Torné-Noguera et al. 2016*	<i>Bombus terrestris</i>	Herbertsson et al. 2016 Lindstrom et al. 2016*	<i>Bombus</i> spp. <i>Bombus</i> spp.
Other wild bees			
Schaffer et al. 1983* Goulson et al. 2002	<i>Xylocopa</i> sp. Native bee community	Paini and Roberts 2005 Gross 2001	<i>Hylaeus alcyoneus</i> <i>Leioproctus</i> sp. <i>Lasioglossum</i> sp.
Steffan-Dewenter and Tschamtko 2000 Hudewenz and Klein 2013	Native bee community <i>Andrena fuscipes</i> <i>Colletes succinctus</i> <i>Epeolus cruciger</i> <i>Sphecodes reticulatus</i> (clepto parasite)	Hudewenz and Klein 2013 Sugden and Pyke 1991	<i>Osmia bicornis</i> <i>Exoneura asimillima</i>
Shavit et al. 2013 Torné-Noguera et al. 2016*	Native bee community Native bee community	Lindstrom et al. 2016*	Native solitary community

*Studies examined both Bumble bees and other wild bees.

bloom of certain shared floral resources or the active foraging periods of native bees (see Table 1 for details). Short-term and localized studies offer a benefit in that they provide detailed information that has the potential to be more meaningful in determining local management actions specific to ecosystems. The limited duration, however, impacts the ability to make any predictions on changes in native bee community composition or population dynamics over time that may result from interactions with managed honey bees, as noted previously in our assessment of behavioral and reproductive studies.

Win, Lose, or Draw: Are There Trends That Can Inform Management?

Assessing the total body of evidence on competition presents an equivocal view of outcomes, especially when behavioral studies are considered with equal weight to those measuring reproduction and growth. The most clear and consistent evidence is seen in studies that examine growth and reproduction. Narrowing the focus to studies that can assess fitness increases our ability to predict impacts more reliably, but greatly reduces the body of research that can be used to support management actions. Only six studies attempted to measure fitness impacts directly, yet the majority of these studies (five of six) validate negative impacts to the fitness (growth or reproduction) of wild bees in the presence of honey bees.

In these studies, the incidence of documented competition is greatest between honey bees and bumble bees. This suggests that

the incidence of competition is more likely between other generalist feeders, rather than those with more narrow feeding patterns. Bumble bees have the greatest potential niche overlap with managed honey bees. Both the presence of honey bees within the landscape and the proximity of colonies to bumble bee colonies can have measurable impacts on growth and reproduction, as indicated in these studies.

Noncompetitive Interactions

In this review, we focus on competitive interactions between managed honey bees and wild bees that could alter the amount of food (pollen and nectar) that is being collected, ultimately impacting growth and reproduction. There are other interactions that can occur between honey bees and wild bees, and with the floral community, that could have impacts on native community structure and composition. The foraging activities of honey bees in a landscape could alter the floral community, and possibly initiate a shift in plant species dominance (Ogilvie and Forrest 2017). This could result in a net benefit for wild bees by increasing preferred food resources, or there could be an augmentation of plant species not preferred by the native bee community. A change to local pollination networks could be expected, but the direction and impact of this change is difficult to predict, and will be context specific. For a comprehensive review of floral community engineering in the context of competition, see Mallinger et al. (2017) for a review.

Pathogen spillover from one bee species to another is also a concern. Common foraging resources are potential transmission vectors for pathogens, viruses, and parasites (Otterstatter and Thomson 2008). Pathogens can move both to wild populations from managed ones, and to managed populations from wild ones (Morkeski and Averill 2010; Blitzer et al. 2012). Pathogen spillover from managed bee species, is however, more commonly documented into wild populations (Graystock et al. 2016). The movement of Israeli Acute Paralysis virus from managed colonies of honey bees to non-*Apis* wild bees via pollen was recorded by Singh et al. (2010), uncovering a new but likely common reproductive pathway for hymenopteran RNA viruses. Furst et al. (2014) found evidence for transfers of Deformed Wing Virus (DWV) from infected managed colonies of *A. mellifera* and *Bombus* spp. into clean wild populations of *Bombus* and other wild species, and point toward more *Apis* pathogens that have the ability to cross hosts into the wild bee community including *Nosema ceranae* Fries et al. which has been noted in bumble bees (Plischuk et al. 2009, Graystock et al. 2013). Parasite transmission and spillover has also been documented, with the movement of *Varroa jacobsoni* Oudemans between various *Apis* hosts in Asia, the speciation of *V. destructor* (Anderson and Trueman 2000; see also Graystock et al. 2016), and the movement of *Locustacarus buchneri* Stammer from imported European bumble bees into wild Japanese stock (Goka et al. 2001, 2006; see also Graystock et al. 2016).

Gaps in Competition Studies

There have been few replicated, controlled experiments testing fitness impacts competition between honey bees and native bees because these studies are inherently difficult to design and carry out. This review indicates the power and necessity of these studies. Equivocal and difficult to interpret results are yielded by competition studies that examine only behavioral changes. As noted previously, floral visitation patterns are unreliable and in some cases can mask the impact of competition when there are shifts in worker and energy reallocation to compensate for resource preemption. The sampling of studies examined yielded equivocal results when behavior was considered, yet much stronger, consistent results when the growth or reproductive output of bees was compared. Given this, we can confidently say there are only seven reliable studies on the impacts of resource-based competition between managed honey bees and wild bees, and this number is far too limited to provide confidence and clarity for management.

Questions about the impacts that honey bees have on native bee communities originate from management practices that place honey bees in natural, restored, or other floral-rich areas that are important for native bees. A further gap is the geographic extent of studies conducted, particularly in areas where management concerns are raised. The majority of studies have not been conducted in the situations where the potential conflict exists. As an example, about half of the studies that we reviewed were carried out in managed, agricultural landscapes, or in controlled environments, and not in natural landscapes where bee pasturing is practiced or considered.

An incomplete diet (one that is limited in calories, or has an imbalance in key proteins or carbohydrates) can have impacts on the growth, development, and reproduction of bees. Unfortunately, our understanding of native bee nutrition is perhaps least well-developed and limits our capacity to make even loose speculation. Gaps in our understanding of bee nutrition impact study designs that aim to minimize floral variables in order to provide more precise, error-free predictions. Unfortunately, there is not enough known about the complete nutritional requirements of the majority of native bee species, meaning that studies of food limitation will likely continue to focus on a selected group of model bee species (*Bombus*, *Osmia*,

etc.), which will again limit our ability to provide broad predictions for the total native bee community.

Is There a Carrying Capacity for Bees?

Land managers and beekeepers are keen to determine and use a carrying capacity for bees (managed or native) in any given landscape. This is a challenge given the number of bee species in any given landscape combined with the dynamics of pollen and nectar availability, which are specific to each plant, but also impacted by climate, soil, and other variables. To be accurate and effective, this information would be required on individual bee species. Cane and Tepedino (2016) have developed a metric to compare the intensity of colony-level honey bee foraging to individual native bee foraging using the Hive Units Monthly (HUM). The HUM allows for an estimate of the potential fitness impact on the native bee community, much in the same way that grazing is managed on public lands (Cane and Tepedino 2016). Using this metric, one honey bee colony can collect pollen the equivalent of 110,000 brood chambers produced by native bees (*Megachile rotundata* Fabricius in this case). In this manner, the predictive impact of each honey bee colony could be gauged and anticipated. It should be noted, however, that aiming to establish a carrying capacity for natural landscapes may be a flawed approach as true resource limitation is unlikely given that floral pollen and nectar recharges daily and is commonly overproduced as an evolutionary strategy.

Conclusions

The issue of maintaining honey bee colony health for pollination services while causing minimal impact to already threatened communities of native bees should be considered when putting honey bees in floral-rich areas. There is evidence that the addition of honey bee colonies can negatively impact some wild bees, particularly bumble bees that overlap with honey bees in resource use, especially during times of colony growth, queen development, and if local populations of bees are known to be under threats or other stresses.

Further research on potential competitive interactions between managed honey bees and wild bees is essential as we seek to make better-informed management decisions. Follow-up research should include investigations of the interactions between honey bees and a wider range of wild, unmanaged species; longer temporal outlooks that will allow for population-level trends to be examined over time; and most importantly, increased focus on reproductive impacts as they are the true indicators of competition.

The leading cause of global pollinator decline is due to a reduction in habitat from development, agricultural intensification, and urbanization. Other factors such as climate change, pathogens, pesticides and other contaminants, and invasive species are added stresses. The primary tool in protecting pollinators, both managed and wild, is preserving or increasing available habitat acres. Reductions in forage opportunities within agricultural landscapes, such as agricultural intensification and reduced enrollment in CRP and other USDA conservation programs, have pushed beekeepers to seek alternative forage. We recommend improving and enhancing forage opportunities within agricultural areas that are already managed and modified in favor of seeking access to natural lands as a precautionary, proactive approach to pollinator resilience.

Supplementary Material

Supplementary data are available at *Environmental Entomology* online.

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References Cited

- Aizen, M. A., and L. D. Harder. 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr. Biol.* 19: 915–918.
- Aizen, M. A., Garibaldi, L. A., S. A. Cunningham, and A. M. Klein. 2009. How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Ann. Bot.* 103: 1579–1588.
- Alaux, C., F. Ducloz, D. Crauser, and Y. Le Conte. 2010. Diet effects on honeybee immunocompetence. *Biol. Lett.* 6: 562–565.
- Allen-Wardell, G., P. Bernhardt, R. Bitner, A. Burquez, S. Buchmann, J. Cane, P. A. Cox, V. Dalton, P. Feinsinger, P. Ingram, et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.* 12: 8–17.
- Anderson, D. L., and J. W. Trueman. 2000. *Varroa jacobsoni* (Acari: Varroidae) is more than one species. *Exp. Appl. Acarol.* 24: 165–189.
- Balfour, N. J., M. Garbuzov, and F. L. W. Ratnieks. 2013. Longer tongues and swifter handling: why do more bumble bees (*Bombus* spp.) than honey bees (*Apis mellifera*) forage on lavender (*Lavandula* spp.)? *Ecol. Entomol.* 38: 323–329.
- Bartomeus, I., J. S. Ascher, J. Gibbs, B. N. Danforth, D. L. Wagner, S. M. Hedtke, and R. Winfree. 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc. Natl. Acad. Sci. U.S.A.* 110: 4656–4660.
- Berthoud, H., A. Imdorf, M. Haueter, S. Radloff, and P. Neumann. 2010. Virus infections and winter losses of honey bee colonies (*Apis mellifera*). *J. Apic. Res.* 49: 60–65.
- Blitzer, E. J., C. F. Dormann, A. Holzschuh, A. M. Klein, T. A. Rand, and T. Tschardt. 2012. Spillover of functionally important organisms between managed and natural habitats. *Agric. Ecosyst. Environ.* 146: 34–43.
- Burkle, L. A., and R. Alarcón. 2011. The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. *Am. J. Bot.* 98: 528–538.
- Butz Huryn, V. M. 1997. Ecological impacts of introduced honey bees. *Q. Rev. Biol.* 72: 275–297.
- Campana, B. J., and F. E. Moeller. 1977. Honey bees: preference for and nutritive value of pollen from five plant sources. *J. of Econ. Entomology.* 70: 39–41.
- Cane, J. and S. Sipes. 2009. Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty, pp. 99–122. In: N.M. Waser and J. Ollerton. *Plant-pollinator interactions: from specialization to generalization*. University of Chicago Press, Chicago.
- Cane, J. H., and V. J. Tepedino. 2016. Gauging the effect of honey bee pollen collection on native bee communities. *Conserv. Lett.* 10: 205–210. doi: 10.1111/conl.12263.
- Colla, S. R., F. Gadallah, L. Richardson, D. Wagner, and L. Gall. 2012. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. *Biodivers. Conserv.* 21: 3585–3595.
- Delaplane, K. S. and D. F. Mayer. 2000. *Crop Pollination by Bees*. CABI Publishing, New York. Oxford. pp 352.
- Di Pasquale, G., M. Salignon, Y. Le Conte, L. P. Belzunces, A. Decourtye, A. Kretzschmar, et al. 2013. Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? *PLoS One* 8: e72016.
- Dohzono, I., and J. Yokoyama. 2010. Impacts of alien bees on native plant-pollinator relationships: a review with special emphasis on plant reproduction. *Appl. Entomol. Zool.* 45: 37–47.
- Donkersley, P., G. Rhodes, R. W. Pickup, K. C. Jones, E. F. Power, G. A. Wright, and K. Wilson. 2017. Nutritional composition of honey bee food stores vary with floral composition. *Oecologia.* 185: 749.
- Dupont, Y. L., Hasen, D. M., Valido, A., and J. M. Olesen. 2004. Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biol. Conserv.* 118: 301–311.
- Eickwort, G. C., and H. S. Ginsberg. 1980. Foraging and mating behavior in Apoidea. *Ann. Rev. Entomol.* 25: 421–46.
- Elbgami, T., W. E. Kunin, O. H. Hughes, and J. C. Biesmeijer. 2014. The effect of proximity to a honeybee apiary on bumblebee colony fitness, development, and performance. *Apidologie.* 45: 504–513.
- Ellis, J. D., J. D. Evans, and J. Pettis. 2010. Colony losses, managed colony population decline, and colony collapse disorder in the United States. *J. Api. Res.* 49: 134–136.
- Forup, M. L., and J. Memmott. 2005. The relationship between the abundances of bumblebees and honeybees in a native habitat. *Ecol. Entomol.* 30: 47–57.
- Furst, M. A., D. P. McMahon, J. L. Osborne, R. J. Paxton, and M. J. F. Brown. 2014. Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature Lett.* 505: 364–366.
- Gallai, N., Salles, J.-M., Settele, J., and B. E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68: 810–821.
- Garibaldi, L. A., Aizen, M. A., Klein, A. M. Cunningham, S. A., and L. D. Harder. 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences.* 108: 5909–5914. doi: 10.1073/pnas.1012431108.
- Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, O. Afik, et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science.* 339: 1608–1611.
- Goka K., K. Okabe, M. Yoneda, and S. Niwa. 2001. Bumblebee commercialization will cause worldwide migration of parasitic mites. *Mol. Ecol.* 10: 1995–1999.
- Goka, K., K. Okabe, and M. Yoneda. 2006. Worldwide migration of parasitic mites as a result of bumblebee commercialization. *Popul. Ecol.* 48: 285–291.
- Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 34: 1–26.
- Goulson, D., and K. Sparrow. 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *J. Insect Conserv.* 13: 177–181.
- Goulson, D., J. C. Stout, and A. R. Kells. 2002. Do exotic bumblebees and honeybees compete with native flower-visiting insects in Tasmania? *J. Insect Conserv.* 6: 179–189.
- Graystock, P., K. Yates, B. Darvill, D. Goulson, and W. O. Hughes. 2013. Emerging dangers: deadly effects of an emergent parasite in a new pollinator host. *J. Invertebr. Pathol.* 114: 114–119.
- Graystock P., Blane E. J., McFrederick Q. S., Goulson D., and W. O. H. Hughes. 2016. Do managed bees drive parasite spread and emergence in wild bees? *International Journal for Parasitology: Parasites and Wildlife.* 5: 64–75. doi:10.1016/j.ijppaw.2015.10.001.
- Greenleaf, S. S., and C. Kremen. 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci. U. S. A.* 103: 13890–13895.
- Gross, C. L. 2001. The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. *Biol. Conserv.* 102: 89–95.
- Herbertsson, L., S. A. M. Lindström, M. Rundlöf, R. Bommarco, and H. G. Smith. 2016. Competition between managed honeybees and wild bumblebees depends on landscape context. *J. Appl. Ecol.* 17: 609–616.
- Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee conservation. *Biol. Conserv.* 141: 2632–2640.
- Hopwood, J. L., L. Winkler, B. Deal, and M. Chivvis. 2010. The use of roadside prairie plantings by native bees. *Living Roadway Trust Fund* [online]. <http://www.iowalivingroadway.com/ResearchProjects/90-00-LRTF-011.pdf>.
- Huang, Z. 2012. Pollen nutrition affects honey bee stress resistance. *Terr. Arthropod Rev.* 5: 175–189.
- Hudewenz, A., and A. M. Klein. 2013. Competition between honey bees and wild bees and the role of nesting resources in a nature reserve. *J. Insect Conserv.* 17: 1275–1283.

- Hudewenz, A., and A. M. Klein. 2015. Red mason bees cannot compete with honey bees for floral resources in a cage experiment. *J. Insect Conserv.* 17: 1275–1283.
- Kato, M., and A. Kawakita. 2004. Plant-pollinator interactions in New Caledonia influenced by introduced honey bees. *Am. J. Bot.* 91: 1814–1827.
- Kato, M., A. Shibata, T. Yasui, and H. Nagamasu. 1999. Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara). *Res Popul Ecol.* 41: 217–228.
- Klein, A. M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proc. Biol. Sci.* 274: 303–313.
- Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10: 299–314.
- Lindström, S. A. M., L. Herbertsson, M. Rundlo, R. Bommarco and H. G. Smith. 2016. Experimental evidence that honeybees depress wild insect densities in a flowering crop. *Proc R Soc Lond B Biol Sci.* 283: 20161641
- Mallinger, R. E., H. R. Gaines-Day, and C. Gratton. 2017. Do managed bees have negative effects on wild bees? A systematic review of the literature. *PLoS One* 12: e0189268.
- Michener, C. D. 2000. *Bees of the World*. The John Hopkins University Press, Baltimore. pp 913.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being*. <https://www.millenniumassessment.org/documents/document.354.aspx.pdf>.
- Moritz, R. F. A. and S. Härtl. 2005. Global invasions of the western honeybee (*Apis mellifera*) and the consequences for biodiversity. *Ecoscience*. 12: 289–301.
- Morkeski, A. and A. L. Averill. 2010. Wild Bee Status and Evidence for Pathogen Spillover with Honey Bees CAP Updates: 12: <http://www.extension.org/pages/30998/wild-bee-status-and-evidence-for-pathogen-spillover-with-honey-bees>.
- National Research Council. 2007. *Status of Pollinators in North America*. National Academies Press, Washington, DC. Pp. 322.
- Ogilvie, J. and J. Forrest. 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Curr. Opin. Insect Sci.* 21: 75–82.
- Otterstatter, M. C., and J. D. Thomson. 2008. Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? *PLoS One* 3: e2771.
- Otto, C. R. V., Roth, C. L., Carlson, B. L., and M. D. Smart. 2016. Land-use change reduces habitat suitability for supporting managed honey bee colonies in the Northern Great Plains. *Proceedings of the National Academy of Sciences of the United States of America*. 113: 10430–10435. doi: 10.1073/pnas.1603481113.
- Paini, D. R. 2004. Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: a review. *Austral. Ecol.* 29: 399–407.
- Paini, D. R., and J. D. Roberts. 2005. Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (*Hylaenus alcyoneus*). *Biol. Conserv.* 123: 103–112.
- Pellett, F. C. 1948. Plants useful for bee pasture. *Econ. Bot.* 2: 178–197.
- Pendrel, B. A., and R. C. Plowright. 1981. Larval feeding by adult bumble bee workers (Hymenoptera: Apidae). *Behav. Ecol. Sociobiol.* 8: 71–76.
- Pinkus-Rendon, M. A., V. Parra-Tabla, and V. Meléndez-Ramírez. 2005. Floral resource use and interactions between *Apis mellifera* and native bees in cucurbit crops in Yucatán, México. *Can. Entomol.* 137: 441–449.
- Plischuk, S., R. Martín-Hernández, L. Prieto, M. Lucía, C. Botías, A. Meana, A. H. Abrahamovich, C. Lange, and M. Higes. 2009. South American native bumblebees (Hymenoptera: Apidae) infected by *Nosema ceranae* (Microsporidia), an emerging pathogen of honeybees (*Apis mellifera*). *Environ. Microbiol. Rep.* 1: 131–135.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25: 345–353.
- Pyke, G. H. 1999. The introduced Honey bee *Apis mellifera* and the precautionary principle: reducing the conflict. *Aust. J. Zool.* 31: 181–186.
- Pyke, G. H., and L. Balzer. 1985. *The Effects of the Introduced Honey bee (Apis mellifera) on Australian Native Bees*. Occasional Paper nr 7. New South Wales National Prks Wildlife Service, Sydney, Australia.
- Rogers, S. R., P. Cajamarca, D. R. Tarpy, and H. J. Burrack. 2013. Honey bees and bumble bees respond differently to inter- and intra-specific encounters. *Apidologie*. 44: 621–629.
- Roubik, D. W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science*. 201: 1030–1032.
- Roubik, D. W. 1980. Foraging behavior of competing Africanized honeybees and stingless bees. *Ecology* 61: 836–845.
- Roubik, D. W. 1983. Experimental community studies: time-series tests of competition between African and neotropical bees. *Ecology* 64: 971–978.
- Roubik, D. W., and R. Villanueva-Gutiérrez. 2009. Invasive Africanized honey bee impact on native solitary bees: a pollen resource and trap nest analysis. *Biol J Linn Soc Lond.* 98: 152–160.
- Roubik, D. W., and H. Wolda. 2001. Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. *Popul. Ecol.* 43: 53–62.
- Roubik, D. W., E. Moreno, C. Vergara, and D. Wittmann. 1986. Sporadic food competition with the African honey bee: projected impact on neotropical social bees. *J. Trop. Ecol.* 2: 97–111.
- Russell, K. N., H. Ikerd, and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. *Biol. Conserv.* 124: 133–148.
- Schaffer, W. M., D. W. Zeh, S. L. Buchmann, S. Kleinhans, M. V. Schaffer, and J. Antrim. 1983. Competition for nectar between introduced honey bees and native north-American bees and ants. *Ecology*. 64: 564–577.
- Schmehl, D. R., Teal, P. E. A., Frazier, J. L., and C. M. Grozinger. 2014. Genomic analysis of the interaction between pesticide exposure and nutrition in honey bees (*Apis mellifera*). *J. Insect Physiol.* 71: 177–190.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *Am. Naturalist* 122: 240–285.
- Seitz, N., K. S. Traynor, N. Steinhauer, K. Rennich, M. E. Wilson, J. D. Ellis, R. Rose, D. R. Tarpy, R. Sagili, D. M. Caron, et al. 2015. A national survey of managed honey bee 2014–2015 annual colony losses in the USA. *J. Api. Res.* 54: 292–304.
- Shavit, O., Amots, D. and G. Ne'eman. 2013. Competition between honey bees (*Apis mellifera*) and native solitary bees in the Mediterranean region of Israel – implication for conservation. *Isr. J. Plant Sci.* 57: 171–183.
- Singh, R., A. L. Levitt, E. G. Rojotte, E. C. Holmes, N. Ostiguy, D. vanEngelsdorp, W. I. Lipkin, C. W. dePamphilis, A. L. Toth, and D. L. Cox-Foster. 2010. RNA viruses in hymenopteran pollinators: evidence of inter-Taxa virus transmission via pollen and potential impact on non-*Apis* hymenopteran species. *PLoS One* 5: e14357
- Somerville, D. 2005. *Fat Bees Skinny Bees, a Manual on Honey bee Nutrition for Beekeepers*. Rural Industries Research and Development Corporation, Australia. <https://rirdc.inforesources.com.au/items/05-054>.
- Steffan-Dewenter, I., and T. Tscharntke. 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia*. 122: 288–296.
- Stout, J. C. and C. I. Morales. 2009. Ecological impacts of invasive alien species on bees. *Apidologie*. 40: 388–409.
- Sugden, E. A. and G. H. Pyke. 1991. Effects of honey bees on colonies of *Exoneura asmillimia*, an Australian native bee. *Aust. J. Ecol.* 16: 171–181.
- Thomson, D. M. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85: 458–470.
- Thomson, D. M. 2006. Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *OIKOS*. 114: 407–418.
- Torné-Noguera, A., A. Rodrigo, S. Osorio and J. Bosch. 2016. Collateral effects of beekeeping: impacts on pollen–nectar resources and wild bee communities. *Basic Appl. Ecol.* 17: 199–209.
- USDA, National Agricultural Statistics Service. 2016a. *Cost of Pollination* <http://usda.mannlib.cornell.edu/usda/current/CostPoll/CostPoll-12-22-2016.pdf>.
- USDA, National Agricultural Statistics Service. 2016b. *Honey Bee Colonies Service* <http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1943>.
- VanEngelsdorp, D., and M. D. Meixner. 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J. Invertebr. Pathol.* 103(Suppl 1): S80–S95.

- VanEngelsdorp, D., J. D. Evans, C. Saegerman, C. Mullin, E. Haubruge, B. K. Nguyen, M. Frazier, J. Frazier, D. Cox-Foster, Y. Chen, et al. 2009. Colony collapse disorder: a descriptive study. *PLoS One*. 4: e6481.
- Visscher, P. K. and T. D. Seeley. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63: 1790–1801.
- Walther-Hellwig, K., G. Fokul, R. Frankl, R. Buchler, K. Ekschmitt, and V. Wolters. 2006. Increased density of honeybee colonies affects foraging bumblebees. *Apidologie*. 37: 517–532.
- Wojcik, V.A. and S. Buchmann. 2012. A review of pollinator conservation and management on infrastructure supporting rights-of-way. *J. Pollinat. Ecol.* 7: 16–26.