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– a review of floral preferences

Konkurrens mellan vilda bin och domesticerade honungsbin
– en sammanställning av blompreferenser

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Swedish University of Agricultural Sciences, SLU
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Ethology and Animal welfare program
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Abstract

The decline of wild pollinators has given ground for a debate on the effects of managed honeybees to wild populations. Even though honeybees are native to some areas, management and domestication has had an indisputable effect on their foraging behaviour and thus the potential effect on surrounding taxa. Whilst a majority of wild species are solitary, honeybees are social and exhibits a complex social behaviour. Previous studies have shown that honeybees displace foraging wild bees rather than deplete foraging resources or direct interference. This could likely affect wild bees' ability to collect sufficient floral resources and thus decrease fitness. In order to bring awareness to Swedish wild bees that risk potential negative effect of managed honeybees I performed a review of scientific literature on honeybee preference and compared the result with floral preference of wild species. I targeted wild bees with a red-list status of Near threatened (NT) and Vulnerable (VU) and found that a majority of these species forage on flowers that are also preferred by honeybees. According to the literature honeybees prefer open flowers that offers a large reward of pollen or nectar. This includes most flowers from the Asteraceae, Fabaceae and Brassicaceae family. The Asteraceae and Fabaceae families are also preferred by a majority of red-listed wild species. Most wild bee species are specialized on one or more specific plant genera within these families, which reduce risk for competition. Honeybees does not present this tactic and instead visit a lot of different flower but in shorter bouts, so they risk intrude on several species of wild bees. To measure effects on fitness, direct measurements like number of brood or offspring is needed and this is not provided by this review. Instead the information provided here clearly acknowledge a substantial resource overlap for wild species already negatively affected by lack of preferred flowering plants. Adding competition from large colonies should be considered a significant threat to wild populations in some areas and thus, placement of manged honeybees should be evaluated before executed.

Keywords: *honeybees, competition, solitary bees, displacement*

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1. Introduction

1.1. Background

Due to a wide range of factors, pollinator communities are declining worldwide (Biesmeijer et al. 2006). At the same time wild plants and a majority of agricultural crops depend on insects for pollination (Klein et al., 2007). Bees, (*Apoidea*) are the main pollinators and in turn receives nutrition in turns of pollen and nectar from the plants. Even though, *Angiosperms* or 'flowering plants' are the most dominant foliage type on land and provides abundant resources (Crane, 1999a), loss of native flora are considered the main threat towards Swedish wild bees (Linkowski et al., 2004). At the same time managed honeybees are added throughout the landscape, in order to compensate for loss of pollinating insects (Ghazoul, 2005) or to increase crop yield (Aizen & Harder, 2009). Wild bees and honeybees have developed different social structures and foraging strategies in order to utilize a common resource and avoid competition. Contemporary conditions with limiting resources and modernized management of honeybees, may present wild bee species with challenges they are not equipped to over-come.

1.2. The Swedish bee composition

1.2.1. Wild bees

Sweden's wild bee fauna consists of about 270 different species and about one third is listed as threatened or red-listed (Artdatabanken, 2020). A majority of species are solitary and only a few are semi-social. Adult bees forage on nectar and only females collect pollen from flowers as food for their brood. Species are differentiated depending on the foraging strategy they express, specialist or generalists. Polylectic species are generalists and forage or collect pollen from a variety of different flowering plants. Oligolectic species are specialists on a specific group of plant or specific plant species. There are also parasitic bees, where the females lay their eggs in a host's nest. Thus, pollen is already provided but parasitic bees are strongly associated with the hosts plant preference and express the same foraging strategy. About 80% of species are polylectic while the rest is oligolectic to some extent (Artdatabanken 2020). Some species also use preferred foraging plants as rendezvous sites and others as nesting material (Linkowski et al., 2004).

There are several reasons behind a bee´s presence on or preference for a specific plant and its flowers, their so called "floral resource" or "floral preference". Floral preference can differ between a species distribution area, but foraging strategy does not (Franzén et al., 2009). Bees only utilize floral resources in close proximity to the individuals nesting site. According to Steffan-Dewenter et al. (2002) solitary bees search for floral resources within a radius of approximately 250 m and bumble bees 500 m. For honeybees this distance is much greater, up to 3 km from the hive. Preferred floral resource is also associated with bee's reproductive strategy (Biesmeijer et al., 2006). In Sweden, wild bees are restricted by winter months, when there's no provision of nectar or pollen. To manage, some species mate late in the summer season and the eggs or brood remain dormant over winter. Other species hibernate as adult or larva and emerge during spring or early summer. Depending on a species wintering strategy, they emerge during different times in the year and thus forage on plants available during that specific period.

1.2.2. Managed honeybees

Unlike wild species, honeybees are social and form large colonies. They forage on a wide range of different plants and are active throughout the season (Montgomery, 2009). In winter, the colony overwinter inside the hive, where they feed on stored nutritional compounds. Individual honeybees have a lifespan of 2-3 weeks, similar to wild species, but the queen can survive for several years (Michener, 1974). Honeybees (Apis) are a small group of eusocial insects with seven known species. They are native to Asia; *Apis andreniformis, Apis florea, Apis cerana, Apis koschevnikovi, Apis nigrocincta, Apis dorsata*, and to Africa and Europe; *Apis mellifera. A. melifera*, or the Western honeybee, with 31 subspecies, are the most widespread of all bee species and has been introduced on all continents except Antarctica (Michener, 1974).

Management of bees developed over 25.000 years ago and is a well-established business branch of great economic importance (Gallai et al., 2009) but modern beekeeping is not only about honey production. Hives with honeybees are added throughout the landscape in order to increase crop yieled (Aizen & Harder, 2009) or to compensate for loss of pollinating insects (Ghazoul, 2005). Colonies and hives are placed in close proximity to crop fields to boost pollination success and in some places the hives are rotated between different crops and fields (vanEngelsdorp et al., 2010). This practice is not restricted to any specific country, but it has become increasingly popular in intensely managed agricultural landscapes (Aizen & Harder, 2009). Even so, experiments have shown that wild bees are more efficient pollinators than honeybees (Gemeda et al., 2017 and Mallinger & Gratton, 2015) and that honeybees can have a negative impact on wild bee populations (Lindström et al., 2016., Herbertsson et al., 2017). To further understand this relationship, fecundity (Stout and Morales, 2009 and Thomson, 2004), overall abundance (Bommarco et al., 2012), species diversity (Paton, 1996) and foraging behaviour (Woodcock et al., 2012) have been used in order to detect and explain competition but with miscellaneous results.

It has also been debated whether or not modern honeybees should be considered introduced or not in areas with native honeybee populations (Paini, 2004). Mainly since modern honeybees are managed, controlled and distributed by humans (Butz-Huryn, 1997, Paini, 2004). Secondly, since the species have gone through extensive breeding that differentiates todays colonies from wild ones (Weber, 2012). Before domestication honeybees would swarm when adequate floral resources were depleted and relocate to more rewarding areas. This advanced social structure is species specific and no other wild Swedish bee species shares this behaviour (Crane, 1999b). The foraging need for honeybees are much higher than for solitary species but seasonal, which evens out potential effects on local communities (Weber, 2012). This is not how modern honeybees are manged today. Instead, colonies are located in the same area, year after year and in far greater numbers than would naturally occur, potentially creating a situation where wild species are unable to cope with competition from the honeybees (Geslin et al., 2017).

1.3. Competition theories

According to Bregon (1990) competition emerge when an interaction between individuals, brought about by a shared requirement for a resource that is in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of the competing individuals concerned’. In order to cope with competition, species can either relocate (e.g. geographically or temporal), change niche or they will go extinct (Mittelbach, 2012a). All bees share a common resource and thus experience some level of interspecific competition, when the presence and behaviour of one or more species restricts other species ability to access a resource, which can have a negative influence on populations and reduce species diversity and overall reproductive success (Case and Taper, 2000). Competition can also be expressed as exploitative competition, when one or more species consume a shared resource, diminishing that resource and making less of it available for itself and other species (Mittlebach, 2012b). Although, a diminishing population could be equally affected by stochastic events like genetic drift as by lack of a resource due to exploitive competition from another species that have risen in numbers (Case and Taper, 2015).

The ability to coexist with other species, whether or not competition is apparent, is a key-aspect for all living creatures. However, human settlements and our ability to move us and animals around the world has upset the balance of this aspect (Paton, 1996). Honeybees may or may not be considered as native to Sweden, but the way manged honeybees are bred, kept, utilized and distributed cannot be seen as a natural occurrence. Therefore, the effecting wild populations differently than what can be expected of a "natural" honeybee population. The level of potential negative effect is likely to depend on several factors, for example landscape composition, extent of management and overall biodiversity. Wild bees show a strong preference for certain types of flowers and this varies for different bee species. Therefore, the type or types of flowers that honeybees choose to utilize, will have different effects on different wild species. I want to single-out floral preferences for honeybees and relate this to wild bee preferences and detect potential competition situations. In order to raise awareness on honeybee's effect on local wild bee populations.

2. Statement and general aim

Actions to reduce loss of wild pollinators could be negatively influenced by the fact that competition from honeybees is not regarded. Therefore, the overall aim of this thesis is to investigate potential competition between managed honeybees and wild bees. In order to do so, I ask the following questions:

- Which floral resources do honeybees prefer?
- Which wild bee species have the same floral preferences as honeybees?
- To what extent do honeybees and wild bees overlap in use of floral resources?

3. Method

I conducted a scientific literature review, using The Swedish Species Information Centre (SSIC). This database is governed by the Swedish University of Agricultural science and provides reliable information on wild species from multiple sources. I searched the database for Apiformes and limited my search to those species classified as VU or EN. I chose to restrict my data to these categories since they can act as a representation of threatened fauna yet are enough well-known, so that sufficient knowledge on floral preference is available. For each species, I extracted data or references to their floral preferences. Since honeybees are not native wild fauna, information on their floral preferences is not provided by SSIC. As such, I searched Scopus and Web of Science, using the search strings: ABS((honeybee* OR (honey bee*)) AND forag* AND prefer*) AND (LIMIT-TO (LANGUAGE,"English")) in Scopus; and (TS=((honeybee* OR (honey bee*)) AND forag* AND preference*)) AND LANGUAGE:(English), Timespan: All years, in Web of Science. I collected all references in EndNote and excluded all doublets, which resulted in 346 hits. I also excluded all papers where the main species were not bees, if the paper did not focus on floral preference and if the focus was to investigate effectiveness of pollination to crops. I included papers from all countries that targeted any species of honeybees. In the end, 25 papers were analysed and included in this review. I analysed all papers referring to potential preference of floral traits, in the same way as the information in SSIC.

I compiled information on bee species and floral preference in Microsoft ® Excel ® and separated data into two sheets, one for wild bees and one for honeybees. Each wild bee species was given a row and floral preferences was divided into columns. For honeybees, each reference was instead given a row and again floral preferences were put into columns. I then asked the program to count how many times each genus or family from the wild bee sheet was mentioned in the honeybee sheet, using the “IF” function. I compared genus and family, since this is most commonly presented in scientific literature.

4. Results

4.1. Wild bee floral preference

I collected information on 44 different wild bee species from SSIC. Of these, 32 species (82%) share at least one preferred floral resource with honeybees (*Table 2*). Information on floral preference were provided as either taxonomic family or species. The flower species were separated by genera and 11 of these were also acquirable by honeybees (*Table 2*). Here, 47% of the wild species forage on plants belonging to the aster-family and 25% on the legume-family. Plants in the aster-family are common in open and dry areas, where other angiosperms might struggle (Linkowski et al., 2004x). In the legume-family, plants are often rich in nectar and common in most environments, making them a reliable source of nutrition (Linkowski et al., 2004x). Plant genera *Centaurea* (n= 6) from the *Asteraceae* family, *Salix* (n= 5) from the *Salicaceae* family and *Rosa* (n=4) from the *Rosacea*e family has the highest occurrence as preference for wild bees (*Table 2*). Whilst, *Trifolium* from the *Fabaceae* family and *Brassica* from the *Brassicaceae* family are most frequently mentioned by the scientific literature (*Table 3*). For honeybees these genera are to a large extent represented by crops, white clover (*Trifolium repens*) and rape seed oil (*Brassica napus).* This is likely due to the fact that most experiments are performed in an agricultural landscape but could also support the theory that honeybees prefer the most abundant floral resource.

4.2. Wild bee competition

Out of the 32 bee species that share floral resourced with honeybees 12 are polylectic, 11 oligolectic and 9 are parasitic. Foraging strategy affects potential competition rank through total number of preferred taxa. When analysing flower preferences amongst bees, Mining bees (*Andrena*), sweat bees (*Lasiglossum*) and parasitic bees or "cuckoo bees" (*Nomada*) are the genera with most wild bee species represented but *Megachile pyrenaea* and *Osmia maritima* are species that share the most plant genera with honeybees. Both of these species are polylectic and tend to prefer multiple flowering genera (Artdatabanken). Bumblebees (*Bombus*) are one of the largest groups of wild bees in Sweden, together with carpenter bees, cuckoo bees and sweat bees (*Table 1*). Bumblebees and carpenter bees probably share the most traits with honeybees. They have a larger body size, share a polylectic foraging strategy and a floral preference in form of nectar and pollen rich flowers, especially aster plants and legumes (Berg et al., 2018). Both carpenter bees and sweat bees are in general ground-nesting species but sweat bees are oligolectic. They occupy similar spaces but differentiates in foraging strategy. Sweat bees are much smaller and forage on flowers where pollen and nectar are out of reach for larger species. Cuckoo-bees are klepto-parasites and bound to specific host species. They most often forage on the same plants as their host but doesn't collect pollen since they don't rear their brood.

A majority of bee species that share floral resources with honeybees have a "medium" (n = 14) or "high" (n = 11) level of risk of potential competition. Seven species were ranked with a "low" risk and all are polylectic species (*Table 2).* These species visit several different flower genera from several families and share only one genus with honeybees, except Anthophora retusa, that also shares preference for the legume family.

Medium and high ranked bees are both parasitic, oligolectic and polylectic (Artdatabanken). For medium ranked species the floral preference varies. *Asteraceae* (n = 5) is the family most frequently mentioned and *Trifolium* and *Salix* the most mentioned genera. Three medium ranked species are oligolectic bee species *Andrena nycthemera, Andrena similis* and *Andrena humilis*. They are specialists on salix spp. or the legume-family. They forage early in the season, before honeybees are most active which may further decrees risk of potential competition. Most bee species with a medium risk of competition are from the Andrena genus, an indication that carpenter bee in general forage on similar plants as honeybees. However, they are not as dependant on highly rewarding flowers as honeybees and more likely to utilize other plants, independently on honeybee presence.

For high ranked bee species preference is strongly for plants from the *Asteraceae* family (n = 7). These species are mainly from the *Andrena, Lasioglossum* and *Nomada* genera. The non-parasitic species are mainly oligolectic and less likely to alter floral resource. Parasitic species like *Nomada obtusifrons, Nomada integra* and *Coelioxys obtusispina* is likely experiencing a secondary effect of competition from honeybees, due to their independence of their hosts. *Coelioxys* is a small group of parasitic species that parasites only on the *Megachile* genus. *Megachile* or "leaf cutter" bees, is also a relatively large group of bees that prefers aster plants and legumes (Berg, A. et al., 2018. Svenska bin). Most of these species are of a lower redlist-category than *Megachile pyrenaea*, a specialist on Centaurea scabiosa. As with bumblebees, leaf cutter bees are also likely to experience competition from honeybees even though their overall population status is more stable than bee genera discussed in this thesis. However, this is instead noticeable through the number of parasitic species with a shared floral resource (*Table 2*).

Only seven out of 32 wild bee species did not share resources with honeybees, they prefer floral resources from the *Berteroa, Scorzoneroides, Jasione, Campanula* and *Pilosella* genera. For one bee species, *Lasioglossum quadrinotatulum*, Artdatabanken (2020) did not provide information on any specific floral preference. *Biastes truncates* and *Nomada facilis* forage on floral genera that belong to the aster-family (*Scorzoneroides* and *Pilosella*), but they are targeting specific plant genera that does not match honeybee preferences. Another bee, *Andrena chrysopyga* also forage on a specific floral resource from a shared plant family, belonging to the *Bereroa* genera. This plant is small and does not offer any greats rewards of pollen nor nectar and thus competition is unlikely (Linkowski et al., 2004b). Remaining species *Nomada fuscicornis, Dufourea halictula* and *Dufourea intermis* all forage on flowers in the *Campanulaceae* family. Neither *Jasione, Campanula* or the *Campanulaceae* family are mentioned in the literature on honeybee preferences.

4.3. Honeybee preference

Out of 25 papers reviewed, 18 provided information on actual floral preference. While seven instead focus on traits like co lour (Annamma et al., 2018, Goulson et al., 2007, Stanton, 1987), hue (Rohde et al., 2017) and symmetry (Wignall et al., 2006, Wolfe & Barrett, 1987, Ginsberg, 1983) of flowers. The different results indicate preference for blue (Annamma et al., 2018), orange (Goulson et al., 2007) but white and yellow flowers over pink (Stanton, 1987).

Table 2. Wild bee species and associated floral resource that were also reported in the scientific literature as preferred by honeybees. Level of taxonomic rank is represented as high (plant family) and low (plant genus). High taxa is specifically mentio

Native bee species	**Resource (high)**	**Resource (low)**	**Rank**	**Foraging strategy**
Andrena gelriae	*Fabaceae*		*high*	narrow-oligolectic
Andrena labialis	*Fabaceae*	*Rubus*	*high*	medium-oligolectic
Andrena niveata	*Brassicaceae*		*high*	medium-oligolectic
Coelioxys obtusispina	*Asteraceae*	*Centaurea*	*high*	parasitic
Dufourea minuta	*Asteraceae*		*high*	narrow-oligolectic
Lasioglossum brevicorne	*Asteraceae*		*high*	medium-oligolectic
Lasioglossum nitidiusculum	*Asteraceae*		*high*	polylectic
Megachile pyrenaea	*Asteraceae*	*Centaurea, Cirsium, Knautia*	*high*	polylectic
Nomada integra	*Asteraceae*		*high*	parasitic
Nomada obtusifrons	*Asteraceae*	*Cirsium spp.*	*high*	parasitic
Andrena nitida	*Rosaceae*	*Rosa*	*high*	family-preference
Aglaoapis tridentate		*Centaurea*	*medium*	parasitic
Andrena batava		*Salix*	*medium*	polylectic
Andrena bimaculata	*Brassicaceae*	*Salix spp.*	*medium*	family-preference
Andrena nanula		*Pimpinella*	*medium*	medium-oligolectic
Andrena nycthemera		*Salix*	*medium*	narrow-oligolectic
Andrena similis	*Fabaceae*	*Trifolium*	*medium*	narrow-oligolectic
Bombus veteranus	*Asteraceae*	*Trifolium*	*medium*	polylectic
Lasioglossum lucidulum		*Centaurea*	*medium*	polylectic
Nomada baccata		*Calluna*	*medium*	parasitic
Nomada stigma	*Asteraceae*		*medium*	parasitic
Osmia maritima		*Rosa, Salix, Trifolium*	*medium*	polylectic
Andrena bluethgeni	*Brassicaceae*		*medium*	polylectic
Andrena humilis	*Asteraceae*		*medium*	medium-oligolectic
Halictus leucaheneus	*Asteraceae*		*medium*	polylectic
Lasioglossum xanthopus		*Brassica*	*medium*	polylectic
Nomada similis	*Asteraceae*		*medium*	parasitic
Andrena morawitzi		*Salix*	*low*	polylectic
Anthophora retusa	*Fabaceae*	*Vicia*	*low*	polylectic
Lasioglossum boreale		*Salix*	*low*	polylectic
Nomada argentata		*Cirsium*	*low*	parasitic
Nomada armata		*Knautia*	*low*	parasitic

Also, plants with symmetrical flowers (Wignall et al., 2006), clustered flowers (Ginsberg, 1983) and flowers with tall anthers (Wolfe & Barrett, 1987) are preferred. Rohde et al. (2017) stated that honeybee workers preferred flowers of "high spectral purity" in an artificial environment. Indication that more noticeable flowers are target by honeybee workers (Rohde et al., 2017).

In order to define preference studies on pollen load (Baum et al., 2011 and Bilisik et al. 2008), visitation on flowers (Bendel et al. 2019; Bänsch et al., 2020; Mailula & Nofemela, 2017; Macukanovic-Jocic et al., 2011; Pearce, et al., 2012; Pierre, 2001; Sajjad et a., 2017; Tropek et al. 2018 and Wood et a., 2015) honey samples (Chauhan et al., 2017; Letsyo & Ameka 2019; Ramírez-Arriaga et al., 2011 and Rollings & Goulson 2019) and bee bread content (Donkersley et al., 2017) have presented different sampling methods. However, the same conclusion can be made; honeybees optimize their foraging based on available resources

Information on floral preference were reported as either flower species, flower genus or family. In the reviewed papers 32 plant families, 71 genera and 63 species were mentioned as attractive, favoured or preferred by honeybees (see attached file). The Asteraceae (Mailula & Nofemela, 2017; Ramírez-Arriaga et al., 2011; Bilisik et al., 2008) and Fabaceae (Mailula & Nofemela, 2017; Baum et al., 2011; Ramírez-Arriaga et al., 2011; Bilisik et al., 2008) are families mentioned as of high interest for honeybees, in multiple papers. The majority of these papers specify preference by plant species (Bänsch et al., 2020; Bendel et al., 2019; Coffey & Breen, 1997; Donkersley et al., 2017; Macukanovic-Jocic et al., 2011; Pearce et al., 2012; Pierre, 2001; Rollings & Goulson, 2019; Sajjad et al., 2017; Sajwani et al., 2014; Wood et al., 2015) or a mix of several taxonomical ranks (Tropek et al., 2018; Ramírez-Arriaga et al., 2011; Letsyo & Ameka, 2019; Mailula & Nofemela, 2017; Chauhan et al., 2017; Bilisk et al., 2008; Baum et al., 2011). Genus Trifolium, Prospis and Brassica, were mentioned by most papers (*Table 3*), indicating that agricultural crops like clover and oilseed rape are strongly preferred, independently of country. In countries where these crops are not commonly cultivated the literature says other common bushes and shrubs belonging to the *Fabaceae* family are most attractive (*Table 3*). In papers that specifically rate floral resources (Pearce et al., 2012; Ramírez-Arriaga et al., 2011; Bilisik et al., 2008; Chauhan et al., 2017 and Baum et al., 2011) *Brassicacea, Lamiacea* and *Fabaecea* are the plant families with highest ratings.

Table 3. List of plant taxa that were either mentioned in more than one paper from the literature search or shared with wild bee species. They are listed and rated by number of occurrences, with rank 1 represented the genus most reported.

Rating	**Support**	**Family**	**Genus**
1	*Wood et al., 2015, Coffey & Breen, 1997, Sajjad et al., 2017, Donkersley et al., 2017 and Bendel et al., 2019*		*Trifolium*
2	*Bilisik et al., 2008, Baum et al., 2011, Ramírez-Arriaga et al., 2011 and Mailula & Nofemela, 2017,*	*Fabaceae*	
2	*Pierre, 2001, Bilisik et al., 2008, Chauhan et al., 2017 and Bänsch et al., 2020,*		*Brassica*
3	*Bilisik et al., 2008, Ramírez-Arriaga et al., 2011 and Mailula & Nofemela, 2017*	*Asteraceae*	
3	*Coffey & Breen, 1997, Wood et al., 2015 and Donkersley et al., 2017*		*Rubus*
4	*Sajwani et al., 2014 and Chauhan et al., 2017,*		*Prosopis*
4	*Sajwani et al., 2014 and Mailula & Nofemela, 2017*		*Acacia*
4	*Coffey & Breen, 1997 and Donkersley et al., 2017*		*Acer*
4	*Chauhan et al., 2017 and Mailula & Nofemela, 2017*		*Ageratum*
4	*Bilisik. et al., 2008 and Wood et al., 2015*		*Centaurea*
4	*Sajwani et al., 2014 and Sajjad et al., 2017*		*Citrus*
4	*Bilisik et al., 2008 and Sajjad et al., 2017*		*Helianthus*
4	*Ramírez-Arriaga et al., 2011 and Sajjad et al., 2017*		*Mangifera*
4	*Chauhan et al., 2017 and Sajjad et al., 2017*		*Ziziphus*
4	*Chauhan et al., 2017 and Sajjad et al., 2017*		*Moringa*
4	*Wood et al., 2015 and Rollings & Goulson, 2019*		*Origanum*
4	*Coffey & Breen, 1997 and Bilisik. et al. 2008*		*Rosa*
5	*Bilisik. et al. 2008*	*Brassicaceae*	
5	*Bilisik. et al. 2008*	*Rosaceae*	
5	*Bilisik. et al. 2008*		*Salix*
5	*Donkersley et al., 2017*		*Cirsium*
5	*Bilisik. et al. 2008*		*Knautia*
5	*Coffey & Breen, 1997*		*Calluna*
5	*Coffey & Breen, 1997*		*Vicia*
5	*Chauhan et al., 2017*		*Pimpinella*

Another plant family with floral resources that attracts both wild bees and honeybees, are the *Brassicaceae* family. In this case there is a strong discrepancy in the literature, whilst wild bees show preference for *salix spp* (Artdatabanken, 2020), honeybees show more interest *brassica spp* and especially oilseed rape (Bänsch et al., 2020).

When researching honeybee behaviour on oilseed rape, Pierre (2001) found that honeybees preferred the crop over the natural occurring wild radish (Raphanus raphanistrum). Pollen is less accessible in wild radish than oilseed rape, which could indicate that honeybees discard the wild plant in favour for the crop, that offers an easier reward (Pierre, 2001). Still rapeseed-oil is an important resource for wild bees, especially bumble bees and other polylectic species (Herbertsson et al., 2016).

5. Discussion

This review predicts that interspecific competition amongst modern honeybees and wild bee species, over floral resources from specific groups of flowering plants is higher than for others, due to resource overlap. The extent of the competition depends on the landscape context and local floral composition (Linkowski et al., 2004). Using resource overlap as a measurement for competition is controversial, especially since recent reviews highlight the importance of direct measurements on fitness (Wojcik et al., 2018). However, I argue that it is indeed an adequate method to detect potential competition. Understanding how interspecific competition is expressed between wild bees and honeybees, is crucial in order to form management recommendations but it has proven to be a challenge for researchers to form long-term and solid experiments (Paini, 2004). Providing information and indications on where, on what and which species might risk competition, can aid future research. Honeybees are extremely opportunistic in their choice of floral preference and unlike wild species they are not tied to specific plant species or other taxa. Instead, competition will most likely be strongest on the most abundant and rewarding flowers (Steffan-Dewenter & Tscharntke, 1991)

Recent studies state that honeybees displace, rather than interfere or deplete resources (Herbertsson et al., 2016, Lindström et al., 2016). Which means that floral diversity is the most influential factor on wild bee species ability to cope with introduced honeybees (Linkowski et al., 2004). Wild bee species have developed foraging strategies and preferences due to local conditions and floral availability (Crane, 1999). Their floral preference is strongly influenced by local nesting and foraging opportunities and thus, wild species are strictly dependant on the area they inhabit (Martins, 2004, Steffan-Deventer & Westphal, 2008). High floral diversity means a broader set of floral resources to utilize, even for oligolectic species. It can be argued that specialized bees are in higher risk of being negatively influenced by honeybees, than polylectic bees, since they occupy a smaller nisch and are less prone to alter floral resource (Wojcik et al., 2018). On the other hand, polylectic species experience a larger resource overlap and thus risk a more direct competition (Dohzono and Yokoyama. 2010). I would instead argue that none of these theories are applicable by itself. Instead it is the type of preferred floral resource that is the confounding factor and in areas where floral diversity is low, honeybees risk potential negative impact on local wild bee populations, if these wild bee species are dependent on highly rewarding or abundant flowering plants (Lindström et al., 2016).

There have been several experiments on competition between wild species and honeybees that emphasizes on bumblebee species (Steffan-Dewenter & Tscharntke; 2000, Herbertsson et al., 2017; Lindström et al., 2016; Butz Hury, 1997; Woodcock et al., 2013; Thomson 2004). Partly because they are easy enough to study but also because their foraging pattern resemble honeybees (Woodcock et al., 2013). In this review bumblebees are underrepresented with only one species presented. This is due to the fact that most bumblebees are of a lower red list-category and thus are better equipped to deal with the current landscape. Steffan-Dewenter and Tscharntke (2000) suggested that bumblebees did not experience competition from honeybees due to their polylectic foraging strategy, but Herbertsson et al. (2016) and Lindström et al. (2016) revealed a significant displacement of bumblebees when honeybees were introduced. They found that honeybees altered bumblebees foraging behaviour and depresses densities of wild insects, in a homogeneous landscape. Indicating that polylectic foraging behaviour does not mean that species are better equipped to handle competition from honeybees but that they are more likely to find alternative resources when and if they are available. They are still disturbed by honeybees that compete for a shared resource.

I have included about 50% of the Swedish red-listed bee species in my analysis and almost all species forage on flowers that are to be considered as shared with honeybees. I would also regard Biastes truncates, Nomada facilis and Andrena chrysopyga as in risk of competition from honeybees even though they are not included in *Table 2*. I did not group wild bee floral preference genera based on family affiliation to compare preference with honeybees. The three species mentioned above forage on several genera, only within the aster family. Even though the names of these genera were not mentioned in the scientific literature reviewed here, honeybee overall preference for Asteraceae plants surely indicates possible competition also for these wild bees. A similar error but due to other factors are wild bee species with high risk of competition in *Table 2*, that forage on the Brassicaceae family. A majority of research related to honeybee floral preference is focused on specific crop types and do not present a generic perspective of honeybee foraging preference. The genera most mentioned in the scientific literature; Trifolium, Prosopis and Brassica are all related to the agricultural landscape (Bendel et al., 2019, Coffey & Breen, 1997, Sajjad et al., 2017, Donkersley et al., 2017, Wood et al., 2015, Chauhan et al., 2017, Bilisik et al., 2008, Bänsch et al., 2020, Pierre, 2001, Sajwani et al., 2014) and this is the reason why the Brassicaceae family is given a higher competition factor in *Table 2*. The wild species mainly forage on *salix spp.* and are active much earlier in the season than most honeybees (Artdatabanken, 2020), and thus the risk of competition is much lower than stated. If the activity period of honeybees is premature, this alters the situation and the risk of competition increases.

Stout and Morales (2009) concluded that alien insects may compete with native species when; 1) they experience a substantial overlap in floral resources, 2) the resource is limiting and 3) a decrease in procurement of the acquired resource leads to a diminishing in fitness expressed by e.g. a reduction of fecundity, survival or populations size. Since both honeybees and solitary bees share not one but two common resources, nectar and pollen, competition is inevitable. Paini (2004) discuss the potential for competition since wild bees experience strong interspecific competition and each species has developed mechanisms to cope and coexist with a multitude of bee species. Others mean that this complex network of specialized species is fragile and already under pressure (Henry & Rodet, 2018) and adding another competitor risk pushing species over the edge to extinction (Hudewenz & Klein, 2015). Understanding competition between honeybees and wild bees has proved difficult (Paini, 2004, Wojcik et al., 2018). However, recent studies in Sweden has found strong evidence for altered behaviour in wild bees due to honeybees (Herbertsson, et al., 2016 and Lindström et al., 2016). Previous research has also shown that wild bees spend less time foraging (Rus & Herrera, 2001) and forage earlier and later during the day rather than mid-day (Gemeda et al., 2017) when honeybees are introduced. These experiments indicate a strong effect on wild bee foraging behaviour even if they lack measurements on direct impact of competition.

5.1. Conclusion

I argue that wild bees in Sweden do risk negative impact due to competition from manged honeybees since a majority of threatened wild bee species, forage on flowers of a type that honeybees also show a strong preference for. Since wild species only forage for a limited time during each season, displacement and avoidance due to honeybee presence presents a serious risk of decreasing wild bee nutritional intake. The amount of negative impact depends on local floral composition, since this provides the amount of foraging opportunities. A diverse flora offers either sufficient resources for multiple species to coexists or provides displaced individuals with alternative resources. Therefore, managed honeybees should be introduced with caution in order to protect wild bee species.

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7. Populärvetenskaplig sammanfattning

Populationer av vilda bin minskar över hela världens och diskussionen kring huruvida dessa arter påverkas negativt av honungsbin eller ej, pågår aktivt. Honungsbin förekommer naturligt på flera platser i världen men genom avel och domesticering har en ”ny” högproducerande sort introducerats. Dagens biodlare har ofta flera kolonier med tiotusentals individer, vilket innebär mycket fler honungsbin än vad en naturlig population skulle bestå av. Det är därför oundvikligt att dessa individer har en effekt på omgivande arter och ekosystem som inte likställs med en naturlig honungbipopulation. Om denna effekt påverkar de vilda arternas förmåga att reproducera och sprida sig beror på det omgivande landskapet. De flesta vilda bin är solitärlevande, medan honungsbin är sociala och behöver konsumera mycket mer pollen och nektar än de vilda arterna. Det har visat sig att honungsbin stör vilda bin i deras födosök, så att de flyttar sig och försöker hitta en alternativ födokälla. Det är alltså inte så att honungsbin gör slut på resurserna eller aktivt jagar bort de vilda arterna, vilket det har funnits vissa teorier om. För att förstå hur de svenska vilda biarterna riskerar att påverkas av honungsbin, sammanställde jag vetenskaplig litteratur om preferenser hos honungsbin. Dessa jämfördes sedan med vilka växter rödlistade svenska arter, som anses tillhöra rödlistekategorierna ”Starkt hotad” (NT) och ”Sårbar” (VU), väljer. Det har visat sig att honungsbin föredrar öppna blommor som kan ge mycket pollen eller nektarrika blommor. Vilket innefattar de flesta arterna inom familjerna asterväxter och ärtväxter. Växtarter inom dessa familjerna föredras även av många vilda bin men då är bina oftast specialiserade på specifika blommor inom en eller flera växtsläkten. Detta betyder att flera vilda arter av bin kan samexistera på en begränsad yta utan att konkurrera om samma resurser. Honungsbin däremot har en annan födosökstrategi och besöker flera olika blommande växter för att samla så mycket föda som möjligt innan de flyger hem till kupan. Detta betyder att de riskerar att störa flera olika arter av vilda bin under sina blombesök. Den här sammanställningen visar att det finns ett stort överlapp av resursutnyttjande mellan honungsbin och vilda bin. Resursöverlapp är en tydlig signal på att konkurrens kan uppstå och risken för negativa effekter av konkurrens är vedertagen, då vilda bin redan lider av brist på födoväxter. Att tillföra stora samhällen med honungsbin i områden där åtgärder för att gynna vilda bin utförs, kan därför istället motverka arbetet. Jag anser att man borde se efter utplaceringen av honungsbin i större utsträckning och att åtgärder för att främja vilda bin borde gå föra utplacering av bikupor i odlingslandskapet.

References

Aizen, M. A. and Harder, L. D. 2009. The Global Stock of Domesticated Honey Bees Is Growing Slower Than Agricultural Demand for Pollination', Current Biology. Elsevier Ltd, 1911, pp. 915–918.

Artdatabanken. 2020. https://artfakta.se/naturvard/taxon/apiformes-200299, utilized 2020-03-22.

Bänsch, S., Tscharntke, T., Ratnieks, F. L. W. F. L. W., Härtel, S. and Westphal, C. 2020. Foraging of honey bees in agricultural landscapes with changing patterns of flower resources, Agriculture, Ecosystems and Environment. Elsevier, 291(July 2019), p. 106792.

Baum, K. A., Rubink, W. L., Coulson, R. N. and Bryant, V. M. 2011. Diurnal patterns of pollen collection by feral honey bee colonies in southern Texas, USA', Palynology, 35(1), pp. 85–93.

Bendel, C. R., Kral-O'Brien, K. C., Hovick, T. J., Limb, R. F. and Harmon, J. P. 2019. Plant–pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition, Ecosphere, 10(1).

Berg, A., Cederberg, B., Holmström, G. and Hall. K. 2018. Svenska bin. www.artdatabanken.se

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. and Kunin, W. E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands', Science, 3135785, pp. 351–354.

Bilisik, A., Cakmak, I., Bicakci, A. and Malyer, H. 2008. Seasonal variation of collected pollen loads of honeybees (Apis mellifera L. anatoliaca), Grana, 47(1), pp. 70–77. doi: 10.1080/00173130801923976.

Bommarco, R., Lundin, O., Smith, H. G. and Rundlöf, M. 2012. Drastic historic shifts in bumble-bee community composition in Sweden', Proceedings of the Royal Society B: Biological Sciences, 2791727, pp. 309–315.

Butz Huryn, V. M. 1997. Ecological Impacts of Introduced Honey Bees', Review Literature And Arts Of The Americas, 723, pp. 275–297.

Coffey, M. F. M. F. and Breen, J. 1997. Seasonal variation in pollen and nectar sources of honey bees in Ireland, Journal of Apicultural Research, 36(2), pp. 63–76.

Case, T. J. and Taper, M. L. 2015. Interspecific Competition, Environmental Gradients, Gene Flow, and the Coevolution of Species' Borders', Am. Nat, 155Nairn 1997, pp. 1–6.

Chauhan, M. S., Farooqui, A. and Trivedi, A. (2017) ‘Plants foraged by bees for honey production in northern India: The diverse flora of India and its implications for apiculture’, Acta Palaeobotanica, 57(1), pp. 119–132.

Crane, E. 1999a. The world history of beekeeping and honey hunting. p. 7-10. New York, New York USA, Routledge.

Crane, E. 1999b. The world history of beekeeping and honey hunting. p. 19-24. New York, New York USA, Routledge.

Dohzono, I., and J. Yokoyama. 2010. Impacts of alien bees on native plant-pol- linator relationships: a review with special emphasis on plant reproduc- tion. Appl. Entomol. Zool. 45: 37–47.

Donkersley, P., Rhodes, G., Pickup, R. W., Jones, K. C., Power, E. F., Wright, G. A. and Wilson, K. 2017. Nutritional composition of honey bee food stores vary with floral composition, Oecologia, 185(4), pp. 749–761

Franzén, M., Larsson, M. and Nilsson, S. G. 2009. Small local population sizes and high habitat patch fidelity in a specialised solitary bee’, Journal of Insect Conservation, 131, pp. 89–95.

Gallai, N., Salles, J.-M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68, 810–821.

Gemeda, T. K. T. K., Shao, Y., Wu, W., Yang, H., Huang, J. and Wu, J. 2017. Native Honey Bees Outperform Adventive Honey Bees in Increasing Pyrus bretschneideri Rosales: Rosaceae Pollination’, Journal of Economic Entomology, 1106, pp. 2290–2294.

Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., ... & Vereecken, N. J. 2017. Massively introduced managed species and their consequences for plant–pollinator interactions. In Advances in Ecological Research Vol. 57, pp. 147-199. Academic Press.

Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis’, Trends in Ecology and Evolution. Elsevier Ltd, 207, pp. 367–373. doi: 10.1016/j.tree.2005.04.026.

Henry, M. and Rodet, G. 2018. Controlling the impact of the managed honeybee on wild bees in protected areas’, Scientific Reports, 81, p. 9308. doi: 10.1038/s41598-018-27591-y.

Herbertsson, L., Lindström, S. A. M., Rundlöf, M., Bommarco, R. and Smith, H. G. 2016. Competition between managed honeybees and wild bumblebees depends on landscape context’, Basic and Applied Ecology, 177, pp. 609–616. doi: 10.1016/j.baae.2016.05.001.

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. and Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world crops’, Proceedings of the Royal Society B: Biological Sciences, pp. 303–313.

Letsyo, E. and Ameka, G. 2019. Major plants foraged by bees for honey production in Ghana: mapping of bee floral sources for the development of the apicultural industry’, Grana, 58(6), pp. 472–482.

Lindström, S. A. M., Herbertsson, L., Rundlöf, M., Bommarco, R. and Smith, H. G. 2016. Experimental evidence that honeybees depress wild insect densities in a flowering crop’, Proceedings of the Royal Society B: Biological Sciences, 2831843.

Linkowski, W. I., Cederberg, B. and Nilsson, L. A. 2004a. Vildbin och fragmentering.

Linkowski, W., Pettersson, M. W., Cederberg, B. and Nilsson, A. L. 2004b. Nyskapande av livsmiljöer och aktiv spridning av vildbin'.

Mačukanović-Jocić, M., Stevanović, Z. D., Mladenović, M. & Jocić, G. 2011. Flower morphophysiology of selected Lamiaceae species in relation to pollinator attraction, Journal of Apicultural Research, 50:2, 89-101.

Mailula, M. T. and Nofemela, R. S. 2017. Botanical Origin of Pollen Collected by Apis mellifera scutellata Lepeletier (Hymenoptera: Apidae) in a Suburb of Pretoria, South Africa, African Entomology, 25(2), pp. 417–427.

Mallinger, R. E. and Gratton, C. 2015. Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop', Journal of Applied Ecology, 522, pp. 323–330.

Martins, D. J. 2004. Foraging patterns of managed honeybees and wild bee species in an arid African environment: Ecology, biodiversity and competition', International Journal of Tropical Insect Science, 241, pp. 105–115.

Michener C D. 1974. The Social Behavior of the Bees: A Comparative Study. Second Edition. Cambridge MA: Harvard University Press Belknap Press.

Mittelbach, G. G. 2012a. Community Ecology. p. 125-147. Sunderland, Massachusetts USA. Oxford University Press.

Mittelbach, G. G. 2012b. Community Ecology. p. 149-171. Sunderland, Massachusetts USA. Oxford University Press.

Paini, D. R. 2004. Impact of the introduced honey bee Apis mellifera Hymenoptera: Apidae on native bees: A review', Austral Ecology, 294, pp. 399–407.

Paton, D. C. 1996. Overview of feral and managed honeybees in Australia: distribution, abundance, extent of interactions with native biota, evidence of impacts and future research', Australian Nature Conservation Agency, Environment …, March, p. 71.

Pearce, A. M. A. M., O'Neill, K. M. M., Miller, R. S. R. S. and Blodgett, S. 2012. Diversity of Flower-visiting Bees and their Pollen Loads on a Wildflower Seed Farm in Montana, Journal of the Kansas Entomological Society, 85(2), pp. 97–108.

Pedro S. R. & Camargo J. M. 1991. Interactions on floral resources between the Africanized honey bee Apis mellifera L and the native bee community Hymenoptera: Apoidea in a natural cerrado' ecosystem in southeast Brazil. Apidologie 22,

Pierre, J. 2001. The role of honeybees (apis mellifera) and other insect pollinators in gene flow between oilseed rape (brassica napus) and wild radish (raphanus raphanistrum), Acta Horticulturae, pp. 47–51.

Ramírez-Arriaga, E., Navarro-Calvo, L. A. and Díaz-Carbajal, E. 2011. Botanical characterisation of Mexican honeys from a subtropical region (Oaxaca) based on pollen analysis, Grana, 50(1), pp. 40–54.

Rollings, R. and Goulson, D. 2019. Quantifying the attractiveness of garden flowers for pollinators, Journal of Insect Conservation, 23(5–6), pp. 803–817.

Ruz L., Herrera R. 2001. Preliminary observations on foraging activities if Bombus dahlbomii and Bombus terrestris Hym: Apidae on native and non-native vegetation in Chile, Acta Hortic. 561, 165–169.

Sajjad, A., Ali, M. and Saeed, S. 2017. Yearlong association of Apis dorsata and Apis florea with flowering plants: Planted forest vs. agricultural landscape, Sociobiology, 64(1), pp. 18–25.

Sajwani, A., Farooq, S. A. and Bryant, V. M. 2014. Studies of bee foraging plants and analysis of pollen pellets from hives in Oman', Palynology, 38(2), pp. 207–223.

Steffan-Dewenter, I. and Tscharntke, T. 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe', Oecologia, 1222, pp. 288–296.

Steffan-Dewenter, I. and Westphal, C. 2008 The interplay of pollinator diversity, pollination services and landscape change', Journal of Applied Ecology, 453, pp. 737–741.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421-1432.

Stout, J. C. and Morales, C. L. 2009 Ecological impacts of invasive alien species on bees', Apidologie, 403, pp. 388–409.

The Swedish museum of Natural history, 2020. https://www.nrm.se/faktaomnaturenoch- rymden/ djur/insekterochspindeldjur/steklargetingar/binvildbingetingar.14451.html. Used 2020-06-29

Thomson, D. 2004. Competitive Interactions Between the Invasive European', Ecology, 852, pp. 458–470.

Tropek, R., Padyšáková, E., and Janeček S. 2018. Floral resources partitioning by two co-occurring eusocial bees in an afromontane landscape, Sociobiology, 65(3), pp. 527–530.

Van Engelsdorp, D. and Meixner, M. D. 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them', Journal of Invertebrate Pathology. Elsevier Inc., 103SUPPL. 1, pp. S80–S95.

Weber, E. 2012. Apis mellifera : The Domestication and Spread of European Honey Bees for Agriculture in North America', University of Michigan Undergraduate Research Journal, 16229, pp. 20–23.

Wojcik, V. A., Morandin, L. A., Davies Adams, L. and Rourke, K. E. 2018. Floral Resource Competition between Honey Bees and Wild Bees: Is There Clear Evidence and Can We Guide Management and Conservation?', Environmental Entomology, 474, pp. 822–833.

Wood, T. J., Holland, J. M. and Goulson, D. 2015. Pollinator-friendly management does not increase the diversity of farmland bees and wasps, Biological Conservation, 187, pp. 120–126.

Woodcock, B. A., Edwards, M., Redhead, J., Meek, W. R., Nuttall, P., Falk, S., Nowakowski, M. and Pywell, R. F. 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape', Agriculture, Ecosystems and Environment. Elsevier B.V., 171, pp. 1–8.