CHARLES UNIVERSITY

Faculty of Science

Study programme: Biology

Branch of study: Biology

Alžběta Voldřichová

The Competition Among Pollinators and the Impact of Managed Bees on Wild Pollinator Populations

Kompetice mezi opylovači a vliv chovaných včel na volně žijící populace opylovačů

Bachelor´s thesis

Supervisor: **Mgr. Jakub Straka, Ph.D.**

Prague, 2023

PODĚKOVÁNÍ

V prvé řadě bych moc chtěla poděkovat svému školiteli Mgr. Jakubovi Strakovi Ph.D. za neuvěřitelnou trpělivost, ochotu a jeho inspirativní nadšení. Můj obrovský vděk patří mé rodině včetně více-nohých členů a přátelům. Zbaběle Vás zde nevyjmenuji, abych náhodou někoho nevynechala, přece jen Vás není málo. Také se tak vyhnu případnému vysvětlování vypsaného pořadí. Uvědomuji si, jaké mám neuvěřitelné štěstí, že jsem obklopena tolika báječnými lidmi (i nelidmi). Vím, že to se mnou není jednoduché (obzvlášť po komunikační stránce), o to víc jsem vděčná, že Vás mám a že mi to (do jisté míry) trpíte. Nakonec bych chtěla zmínit ty, co mi nejvíce pomohly s prací samotnou: Kristýnku Suchomelovou za jazykovou korekci většiny textu; Káťu Bezányiovou za rady k první části práce a ochotu pomoci i s další částí, kdybych ji vypracovala včas; Elišku Moťkovou za hlídání při psaní proti mým prokrastinačním tendencím; a Kačenku Papouškovou jež mi pomohla uvědomit si spoustu věcí o sobě.

PROHLÁŠENÍ

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze, 04.05.2023

Alžběta Voldřichová

ABSTRACT

Pollinators play an important role in ecosystems. Their ties to plants are essential for the reproduction of many plant species and thus for the protection of species diversity. Pollinator species therefore need to be protected. But to protect them effectively, it is necessary to understand the relationships between pollinators. However, the interaction between pollinators is a complex topic that needs further research. One of the current threats to pollinator populations is commercial pollinator rearing. Commercially reared species, especially *Apis mellifera* and *Bombus terrestris*, have been introduced almost all over the planet due to their positive effects on crop yields and its by-products. Moreover, in their native ranges they are bred in much higher concentrations than would be possible without human intervention. But high concentrations of commercial pollinators do affect populations of wild ones. This thesis describes forms of pollinator competition and addresses the impact of commercially reared pollinators on wild pollinator populations.

KEY WORDS:

Honeybee – Bumblebee – Hoverfly – Nest usurpation – Pathogen transfer – Species protection – Invasive species

ABSTRAKT

Opylovači jsou důležitou součástí ekosystémů. Jejich vazby na rostliny jsou nezbytné pro rozmnožení nemalého počtu druhů rostlin, a tak i k ochraně diverzity druhů. Proto je potřeba druhy opylovačů chránit. Aby však byla jejich ochrana efektivní, je potřeba rozumět vztahům mezi opylovači. Interakce mezi opylovači je však komplexní téma, které potřebuje další výzkum. Aktuální velká hrozba pro populace opylovačů je jejich komerční chov. Komerčně chované druhy, hlavně *Apis mellifera* a *Bombus terrestris*, byly díky svému pozitivnímu vlivu na úrodu a vedlejším produktům, introdukované téměř po celé planetě. Navíc v areálech jejich původního výskytu jsou chované v mnohem větších koncentracích, než by bylo možné bez zásahu člověka. Avšak vysoká koncentrace komerčních opylovačů má vliv na populace těch volně žijících. Tato práce popisuje formy kompetice mezi opylovači a zabývá se vlivem komerčně chovaných opylovačů na populace opylovačů volně žijících.

KLÍČOVÁ SLOVA:

Včely – Čmeláci – Pestřenky – Usurpace hnízd – Přenos patogenů – Ochrana druhů – Invazivní druhy

TABLE OF CONTENTS

1 INTRODUCTION

Pollinators transfer pollen (male gamete) onto the stigma (female reproductive part) of a plant. Many angiosperms (about 80%) rely on pollination mediated by an animal (Ackerman 2000). There is a huge diversity of pollinators – the number of species that provide pollination is 350.000. The most numerous pollinator groups are Arthropoda: Hymenoptera (bees, wasps), Diptera (hoverflies, bee-flies), Lepidoptera (moths, butterflies), Coleoptera, Thysanoptera; Aves: Hummingbirds, Sunbirds, Honeyeaters; and Mammals: Bats, and other non-flying mammals (Ollerton 2021; 2017).

Competition occurs when a resource is in short supply, this makes it a limiting factor to be fought over. This confrontation can be carried out directly – interference competition (direct aggressive encounter); or indirectly – exploitative competition (carried via the efficiency of resource utilization). Competition among species can take place intraspecifically (occurring within one species) or interspecifically (occurring between different species) (Case and Gilpin 1974; Michael Begon and Colin R. Townsend 2014; Michael Begon, Mortimer, and Thompson 2009). The pollinator species can be divided into generalists and specialists. Specialists are adapted to smaller variety of flowers and have tighter bonds with the flower they pollinate. This usually makes them more efficient in handling this flower, but also more brittle to the population changes of flower they are adapted to (Goulson 2010).

Pollination has a positive effect on crop yield, hence, man started rearing pollinators and introducing them out of their natural range(Goulson 2010, 2; Klein et al. 2007). The most used species are *Apis mellifera* (later in this thesis only called the honeybee, if another honeybee species is mentioned, it is specified) and *Bombus terrestris* (Goulson 2010).

Objectives of this bachelor thesis:

- I. List and describe forms of competition among pollinators
- II. Describe the impact of managed species on wild bee populations

2 THE COMPETITION AMONG POLLINATORS

Competition among pollinators is an important topic for understanding the ecological structures in ecosystems. Understanding of ecological structures is key for the protection of the tight bonds between pollinators and by protecting bonds among pollinators, protecting pollinator species themselves (Thomson and Page, 2020). Furthermore, with higher comprehension we can focus on getting the ideal conditions for pollination and thereby increase crop production.

Unfortunately, studying competition among pollinators is very challenging as it seems to be a very complex problem (Geslin et al., 2017). Additionally, most research is observational – studying negative correlations or species niche overlap. To understand competition better, experimental study would be more beneficial. Regrettably, experiments are logistically very difficult (Thomson and Page, 2020). To understand these interactions, further and more extensive research is needed to be done (Ogilvie and Forrest, 2017; Thomson and Page, 2020; Zimmerman and Pleasants, 1982).

Pollinators can compete: for resources (exploitative competition) – floral resources (nectar and pollen) or nest sites (Thomson and Page, 2020), through pathogen transfer (Durrer and Schmid-Hempel, 1994; Graystock et al., 2015), through social parasitism (Bohart, 1970) or through introgression (transfer of genetic material to the gene pool from other species) (Goulson, 2010) [Fig. 1]. In this chapter forms of interaction are discussed in greater detail.

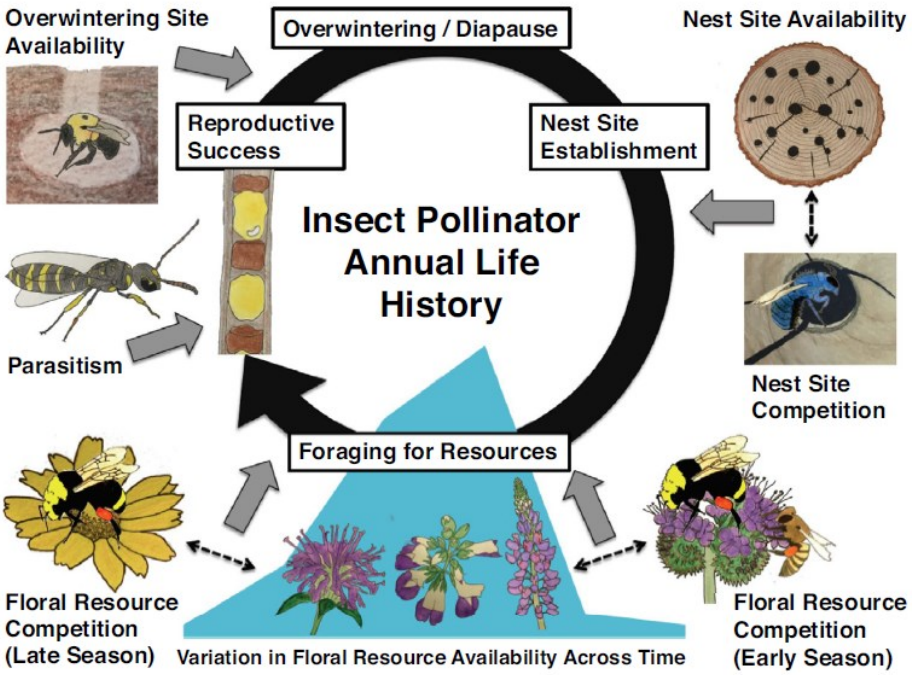

FIGURE 1: Diagram illustrating the impact of different factors (grey arrows) on reproductive success throughout the pollinator life cycle (black arrow). Competition may alter the availability of nest sites and floral resources. The intensity of competition depends on resource abundance (dashed black arrows). The diagram shows parasitism as another factor that might influence fitness. Taken from The Importance of competition between insect pollinators in the Anthropocene (Thomson and Page, 2020)

2.1 Interference competition

Interference competition is conducted through a direct aggressive encounter when competing species interfere in foraging, reproduction or survival (Begon et al., 2006; Case and Gilpin, 1974; Michael Begon and Colin R. Townsend, 2014). Direct interaction among pollinators seems to be rare or not researched enough (Geslin et al., 2017). Nevertheless, some cases of interference competition can be found.

Apis mellifera is known for its robbing behavior when workers rob the stores of different colonies. Honeybees usually rob other honeybee colonies, but it can also stray into other apid colonies. While robbing a nest, a fight usually breaks out at the entrance to the nest. Robbing mostly happens when resources are limited, leaving the weaker colony to starve (Bohart, 1970). Colonies of honeybees that engage in robbing have an increase in foraging and nest defiance. Furthermore, attacks on nestmates returning from foraging have occurred. These attacks were probably due to the change of odor caused by the visit to another colony (Grume et al., 2021). Aside from the honeybee, Bohart in The Evolution of Parasitism Among Bees (1970) mentions some species of bumblebees (*Bombus*) and stingless bees (*Meliponini*) have also adapted this behavior.

In some species of stingless bees (*Meliponini*), aggressive competition for floral resources has been observed (Johnson and Hubbell, 1974; Nagamitsu and Inoue, 1997). Aggressive encounters have been recorded in Mexico between the Africanized honeybee (*Apis mellifera scutellata*) and local stingless bees at flower and water resources (Cairns et al., 2005). On Costa Rica, encounters of *Meliponini* with other bees on occupied flowers goes from a mere threat (threatening posture or hovering) to a wrestling match which often results in the death of one of the opponents. Since aggressive encounters take place over food, it can be assumed that food is the limiting factor in local conditions. The species *Trigona silvestriana* and *T. corvina* have been observed to be especially aggressive (Johnson and Hubbell, 1974). In a later study on Costa Rica, the authors observed that *Trigona fulviventris* is intraspecifically aggressive but not interspecifically and posed a hypothesis that intense intraspecific competition leads to interspecific competition (Hubbell and Johnson, 1977).

In Panama, the nectar robbing *Trigona ferricauda* attacks the hummingbird *Phaethornis supercilious* while visiting a flower, driving the hummingbird away to another part of flower patch. Aggressive behavior from hummingbirds has not been observed. Hummingbirds tend to avoid patches with a high abundance of bees, even though the nectar production of visited flowers exceeded what bees could retrieve (Roubik, 1982). In contrast, in Bamenda Highlands, Cameroon, the nectar robbing songbird (*Cinnyris reichenowi*) aggressively attacks the carpenter bee (*Xylocopa caffra*) on patches of *Hypoestes aristata*, of which *X. caffra* is the main pollinator (Padyšáková et al., 2017). Aggressive encounters have also been observed among hummingbirds in Brazil. Here aggressive behavior was

induced by a lack of resources (Justino et al., 2012). The authors of the study in Brazil, unfortunately, observed only interactions among hummingbirds and not with other pollinators.

2.2 Competition for floral resources

If there are enough resources for everyone, there is little reason to compete. Unfortunately, resources in nature are limited. This leads to exploitative competition for resources among species and individuals (Michael Begon and Colin R. Townsend, 2014).

In competing for floral resources, social insects are assumed to have an advantage in the utilization of floral resources. Social pollinators can forage further than nonsocial pollinators. Honeybees (*Apis mellifera)* can share information about profitable locations with other workers in their hive. Thanks to hives and nests, social pollinators have a stock in case of deficiency of floral resources and can forage earlier in the morning as staying in the hive or nest enables them to easily maintain body temperature (Wignall et al., 2020a). Furthermore, the social way of life enables them to divide tasks among different castes, which gives social insects the ability to do tasks simultaneously (e. g. being able to defend the nest while still foraging and taking care of the brood) (Gullan and Cranston, 2014). This has been shown in cage experiment in which the solitary red mason bee (*Osmia bicornis*) was not able to compete with honeybees which were better at using limited available resources (Hudewenz and Klein, 2015).

In a study conducted in southeast England in 2019 on bramble (*Rubus fruticosus*), in which researchers removed bumblebees, honeybees or both, reciprocal competition between honeybees and bumblebees was proven. In the patches where honeybees were removed, abundance of bumblebees had increased and vice versa. Other pollinator groups have been observed. However, the effect of excluding honeybees and/or bumblebees on other pollinator groups – hoverflies, solitary bees, and wasps, had not been shown. In the case of butterflies, there was so little data that they had to be completely excluded from this study (Wignall et al., 2020a). Reciprocal competition between honeybees and bumblebees has been supported by more studies: a study on lavender (*Levandula* x *intermedia* 'Grosso') in the UK demonstrates that bumblebees are better at using lavender flowers and therefore drive honeybees away (Balfour et al., 2013). On the contrary, the presence of honeybees leads to bumblebee workers having a smaller body size (Goulson and Sparrow, 2009), as worker body size in bumblebees is variable and depends on the conditions such as temperature or floral resources (Dave Goulson et al., 2002). Smaller bumblebee worker size might be caused by scarce floral resources caused by the presence of the honeybee (Goulson and Sparrow, 2009).

Competition also depends on the size of the pollinator (Dave Goulson et al., 2002; Padyšáková et al., 2017; Wignall et al., 2020a). Inside bumblebee colonies, the size of workers varies. Bigger bees are more efficient at foraging (are able to carry more pollen) and therefore they are the ones that collect resources (Dave Goulson et al., 2002). There are two hypotheses regarding the effect of pollinator size on competition: (1) larger pollinator species are better at using resources and are therefore more efficient in their use of resources, or (2) smaller pollinator species have lower energy requirements and therefore do not need as many resources which makes them better competitors (Padyšáková et al., 2017). Excluding honeybees or bumblebees from patches of bramble led to an increased number of large solitary bees. From this result, it can be assumed that size influences the competition. Since larger species have larger demands and therefore react more to the competition – large solitary bees need more resources and therefore avoid more honeybees and bumblebees. Smaller solitary bees do not mind lower availability of nectar and pollen due to their smaller size, hence smaller demands. In conclusion, small solitary bees are not strongly affected by the competition with honeybees and bumblebees (Wignall et al., 2020a). Likewise, a study on the red mason bee *(Osmia bicornis)* on rapeseed (*Brassica napus*) in a cage experiment indicates that the resulting pollination effect correlates with the size of the pollinator as the species of similar size compete together (Jauker et al., 2016).

Even though the competition of hoverflies with other pollinator groups has not been shown, the authors of the study on bramble suggest that hoverflies are competing for the same floral resources by trying to mimic their model (Balfour et al., 2018). Hoverflies use Batesian mimicry, where a mimic (in this case the hoverfly) mimics their model (bees, bumblebees and wasps), resulting in not appearing tasty to its predator (Edmunds and Reader, 2014). Batesian mimicry were first introduced by Henry Bates (1862) in his study on South American butterflies. To avoid predation, hoverflies adapt their behavior to match their model. Therefore, they visit the same flowers at a similar time of the day and compete for the same floral resources. This behavior has been proven on groups of hoverflies mimicking bees and bumblebees. (Howarth et al., 2004).

Intraspecific competition among bumblebees (*Bombus spp.)* is expected, as they occur in a similar niche, use the same food resources, have overlapping active seasons, and are morphologically very similar (D. Goulson 2010). Surprisingly, regardless of their similarities, bumblebees are relatively diverse in the locations they inhabit. This diversity might be caused by the different length of proboscis among bumblebee species, hence an adaptation to a different flower (Inouye, 1980; Pyke, 1982; Ranta, 1984; Ranta and Lundberg, 1980). Bumblebee species can feed on flowers of various depths but are most efficient with the depth of corolla that corresponds in length to their proboscis. Species with longer proboscis can utilize deeper flower corollas and therefore visit a wider variety of flowers but

are less efficient because of longer handling time (Ranta and Lundberg, 1980). Species of bumblebees in the UK do not completely fit into this theory, as species with a similar length of proboscis and high niche overlap are found in high densities (particularly *Bombus lapidarius, B. terrestris* and *B. lucorum*) (Goulson and Darvill, 2004). Ranta (1984) came to the same conclusion with data from Europe and North America: the bumblebee species with the same length of proboscis are present in the same area. The authors therefore concluded that bumblebee species do not compete interspecifically or that the length of proboscis is not the key morphological feature in bumblebee competition (Ranta, 1984). Pyke (1982) came to the same conclusion as Ranta and Lundberg (1980) that the proboscis length correlates with the visited flower corolla depth (bees are most efficient when the corolla they feed on matches their tongue length). Pyke, based on his observations in Colorado, divided bumblebee species by the length of their proboscis into long-, medium- and short-tongued species. In addition to these 3 groups, Pyke has identified one more group: short-tongued species, in which mandibles are very well developed and therefore well equipped for nectar robbing (Pyke, 1982).

Nectar robbing is another adaptation that undermines the theory of competition based on the length of the proboscis in bumblebees. Insects (such as bees and ants) and some species of birds have adapted to this behavior. Nectar robbing occurs when the robber cannot reach the length of corolla with its morphological features and therefore bites a hole near the base of the corolla, hence skips the reproductive organs of the flower (Inouye, 1983, pp. 153–173). Nectar robbing was described by Charles Darwin. In an article titled “Humble-bee”, Darwin (1841) wrote: "What unworthy members of society are these humble-bees, thus to cheat, by boring a hole into the flower instead of brushing over the stamens and pistils, the, so imagined, final cause of their existence!" (Ornduff and Darwin, 1984). Nectar robbers are divided into primary robbers, which make the hole in the flower corolla (usually short-tongued species – *Xylopa sp.* and *Bombus sp.*); and secondary robbers, which use an already existing hole (Inouye, 1983, pp. 153–173). Short-tongued bumblebee species are more likely to turn to nectar robbing while long-tongued species act more as legitimate pollinators (Stout et al., 2000). Nectar robbing can be transmitted socially: when a legitimate pollinator visits a flower that has been robbed, it might become a primary robber itself (Leadbeater and Chittka, 2008). Since robbed plants contain less nectar (Stout et al., 2000), visiting them may lead to lower food intake (Irwin et al., 2010). Richardson (1995) observed that the bumblebee *(Bombus sonorus)* is not able to distinguish a robbed flower from unrobbed one, honeybees (*Apis mellifera*), on the other hand, have avoided robbed *Chilopsis linearis* flowers, which were robbed by the carpenter bee *(Xylocopa californica)* (Richardson, S. C., 1995, pp. 311–315).

As mentioned before, studying competition among pollinators is very complicated, especially competition for floral resources as the quantity of pollen and nectar depends not only on the visit of

pollinator but also on the flower species and its conditions. Therefore, using the amount of pollen accessible on the studied location should have more informative value than using only the number of open flowers on the location (Zimmerman and Pleasants, 1982). More studies examining competition for floral resources among pollinators are needed. Especially ones focused on groups of pollinators other than honeybees and bumblebees (Ogilvie and Forrest, 2017).

2.2.1 Seasonal variation

Competition for floral resources varies seasonally as the utilization of resources changes throughout the year. In a study in Boracéia, tropical rainforest honeybee colonies have shown a peak in harvest of pollen in August and of nectar in December. In the native stingless bee (*Melipona sp.*) a similar peak of nectar collecting has also occurred (Wilms and Wiechers, 1997).

The availability of floral resources fluctuates considerably throughout the flowering season. After the spring bloom (from early April to the end of May), when floral resources are abundant, comes a period beekeepers call the "June Gap" when resources are scarce. Another period with low floral resource availability is at the end of summer (late July to August) (Timberlake et al., 2019) [Fig. 2]. Scarce floral resources in late-summer months were also shown in a study in Sussex (England), where the foraging distances of *Apis mellifera* were measured. The worker bees foraged the greatest distances in July and August, even though the quantity or quality of nectar brought back hadn't changed noticeably, indicating lower availability of floral resources in late-summer months (Couvillon et al., 2014). The shortage of floral resources during July and August leads to stronger competition among honeybees and bumblebees (Wignall et al., 2020b).

Low floral resource availability in late summer months in Great Britain where those studies were located, also correlates with the high seasonal activity of individual pollinator groups within these months. The majority (62%) of pollinator species has its peak in July and August – specifically aculeate wasps (71%), bees (60%) and butterflies (72%). Current agricultural management in Great Britain has few plants blooming in late summer. The high abundances of pollinators and lack of floral resources naturally leads to fiercer competition, which results in a high extinction rate of late-summer foraging pollinator species (Balfour et al., 2018).

By understanding the changes of seasonal needs of pollinators we can adjust land management to protect their biodiversity (Timberlake et al., 2019) and maximize crop production (Grab et al., 2017). Moreover, because, it seems that fiercer competition at the end of summer leads to a higher extinction rate amongst pollinators (Balfour et al., 2018).

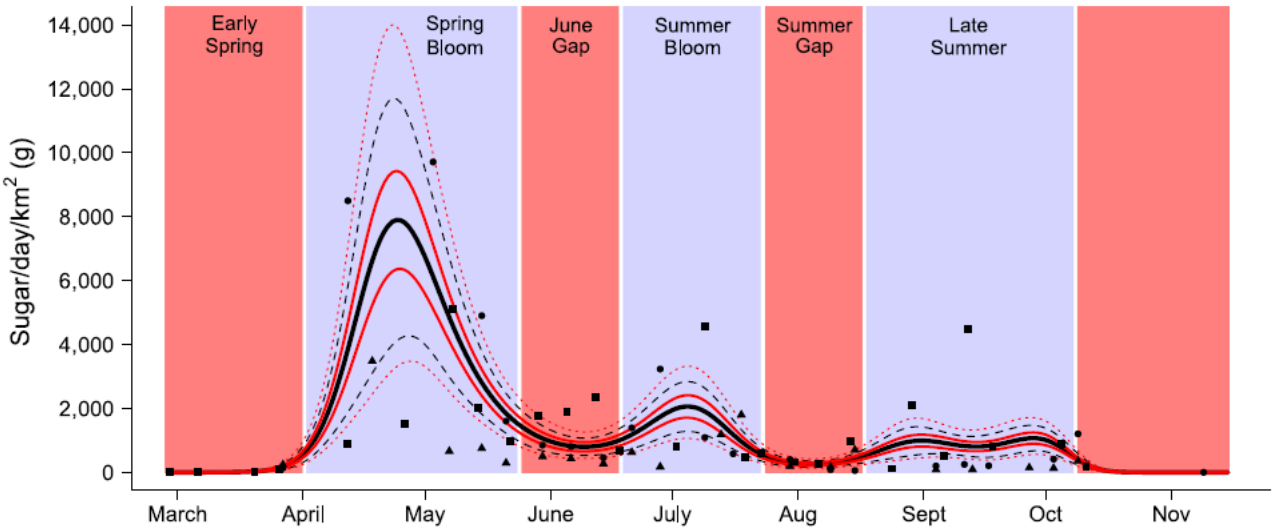

FIGURE 2: Daily sugar production throughout the flowering season on three different farms in England in 2017. Different locations are represented by different symbols. The solid black line represents mean sugar production with standard error (SE) in dashed lines. The red lines represent high and low estimates of sugar production with SE in dotted lines. The flowering season is then divided into periods when floral resources are abundant (in grey) and when scarce – called "gaps" (in pink). (Timberlake et al., 2019)

2.3 Competition for nest sites

Nest sites are one of resources that can become a limiting factor for species and therefore lead to competition if scarce or low quality (Goulson, 2003; Michael Begon and Colin R. Townsend, 2014). Nesting sites among many pollinators overlap which leads to a greater likelihood of shortages (Hubbell and Johnson, 1977; Inoue et al., 2007).

In a study on competition of stingless bees in Costa Rica, interspecific competition for nesting spaces has not been observed. However, the authors suggest exceptions for larger bodied species such as *Trigona fulviventris* or *Trigona silvestriana*. Every observed bee species has a minimal diameter requirement for nesting, but not a maximal limit (smaller species might utilize holes wider than their minimal diameter but not vice versa). This may result in a stronger competition for branches with a wider diameter (Hubbell and Johnson, 1977).

In bumblebees, competition for nest sites depends on the number of queens emerging from hibernation. The larger the number, the fiercer the competition is expected. Competition among emerging queens may result in nest usurpation (Bohart, 1970). Another factor is the time of emergence. Bees that emerge earlier have a better choice of nesting sites. The later emerging ones have to choose nest of worse quality or fight (Higginson, 2017).

2.3.1 Nest usurpation

Nest usurpation is a form of facultative social parasitism (Goulson, 2010; Lhomme and Hines, 2019). A considerable amount of research has been done on social parasitism among bumblebees; therefore, it is described below.

Nest usurpation happens when a hibernated bumblebee queen looks for its future nest. Some queens, especially the ones that start searching later, instead of finding a new empty nest, choose an already established one and fight for dominance over this nest. As evidence of the struggle, the dead queen is left in the nest. The frequency of nest usurpation depends on the number of new queens that season – with high queen abundance nest usurpation tends to become very common. The bigger the established colony is, the less likely it is to be usurped by another queen (Bohart, 1970). Nest usurpation is made possible by the difference in time of emergence from hibernation. This difference is even conspecific (Goulson, 2010). These take-overs happen mostly among the same species, but may occur among species with similar requirements for nests (Bohart, 1970). In his book Bumblebees: Behaviour, Ecology, and Conservation, Goulson (2010) comments that, even though the success rate of nest usurpation is unknown, it must be successful at times, otherwise this strategy would have already disappeared. Previously, in his book The Evolution of Parasitism Among Bees, Bohart (1970), based on his experiments concluded that invaders often win.

In a 2013 study, intraspecific nest owner replacement in solitary bees was commonly observed. In the species *Andrena vaga* and *Anthophora plumipes*, most of the nest replacements was by occupying an abandoned nest. In *Osmia rufa* and *Colletes cuninularis*, around half of the cases of nest replacement were done by true usurpation. In *Colletes,* in over 60% of the usurpations the usurper and the original owner shared the nest for a short period of time, resulting in one or both of them leaving the nest in the end (Černá et al., 2013). Intraspecific nest usurpation has also been observed in the leaf-cutter bee *Megachile apicalis* (Kim, 1997).

Interspecific nest usurpation was recorded in Australia among stingless bee species: *Tetragonula carbonaria* and *Tetragonula hockingsi*. Around 260 nests were monitored each year for 5 years, during which 46 interspecific nest changes happened. Out of these changes 41 were in the direction of *T. carbonaria* to *T. hockingsi*. During the study the population of *T. hockingsi* increased. However, the majority of the hives in the study were *T. carbonaria*, hence proportional studies haven't shown *T. hockingsi* as a better usurper (Cunningham et al., 2014).

2.4 Pathogen transfer

Pollinators, by sharing floral resources, create a pathway for the transmission of pathogens (Proesmans et al., 2021). Pathogen transfer through the plant-pollinator system can be intraspecific or interspecific (Ellner et al., 2020). For example, *Crithidia bombi* infects multiple bee families (Ngor et al., 2020). Moreover, *A. mellifera* viruses have been found in a hoverfly – *Eristalis sp* (Bailes et al., 2018). Studying pathogens can be very challenging as pollinator viruses are difficult to study without damaging the colony. Molecular methods can only determine whether the virus is present, but not whether it affects the species and to which degree (Boncristiani et al., 2021). Furthermore, current research is strongly biased towards honeybee and bumblebee pathogens (Graystock et al., 2020; Proesmans et al., 2021).

Pathogen transfer depends on the character of the landscape. Landscape simplification leads dominant pollinators to alter their foraging patterns and hence changes pathogen prevalence. Pathogen prevalence is diluted in a more diverse landscape (Figueroa et al., 2020). Parasite prevalence varies through the season. Pathogen transmission increases as the number of social bees (honeybees and bumblebees) rises and decreases with the rising number of flowers (Graystock et al., 2020). Specialized pollinators that visit a smaller variety of flowers may have a lower exposure risk. Generalists, on the other hand, can act as a link between multiple forage plant species hence increase the chance pathogen transfer (Figueroa et al., 2020).

2.5 Hybridization

Another risk to pollinator species is hybridization with other species. In the first half of 20th century, a new variety of bumblebee *Bremus affinis 'novae-angliae'*, which was formed by the mating of *Bremus affinis* and *Bremus terricola* (Plath 1922). *Bremus* is synonym to *Bombus* used in older literature. Concerning is the risk of introgression between native and introduced species (Seabra et al. 2019; Kanbe et al. 2008; Kondo et al. 2009; Yoon et al. 2009). This is described in the later chapter – threads to wild populations.

3 THE IMPACT OF MANAGED BEES ON WILD BEE POPULATIONS

With a larger population of people on the planet, a change of agriculture had to come. To satisfy the growing demands for food, measures to maximize crop production were taken (Aizen et al., 2008; Klein et al., 2007; Lautenbach et al., 2012; Pirk et al., 2017). One way of increasing crop production is pollination as it leads to higher numbers and larger crops. Crops that have increased fruit and vegetable production by pollination make up 20 percent of the overall production and 15 percent comes from crops that have increased seed production by pollination (Klein et al., 2007). Thanks to modern agriculture which relies on monocultural systems, farmers must turn to the use of transported pollination. Especially for crops such as almonds, soybeans, alfalfa, clover, canola and more (Gullan and Cranston, 2014). The annual profit from pollination by the honeybee in the United States in 2000 was estimated up to 14.6 billion US dollars (Morse and Calderone, 2000). Given the benefits of pollination, it is not surprising that the most used pollinator, the honeybee, has been introduced world-wide, making it one of the most massively introduced species (Goulson, 2010).

Aside from the honeybee, which is intensively used, species of bumblebee have also been introduced around the world – especially *B. terrestris* (Goulson, 2010). The choice of named species is no surprise as the social way of life makes the management easier (Willmer et al., 2008). Furthermore, there are other advantages: (1) managed pollinator species (MPS) are generalists and therefore can be used for a wide range of crops (Goulson, 2003; Thomson, 2004); (2) MPS are foraging at great distances, f. e. honeybees are able to forage up to 12 km away (Abrol, 2011, p. 690; Frisch, 1993), with the average foraging distance being 5.5 km (Beekman and Ratnieks, 2000); *B. terrestris* can reach up to 2878 m while foraging (Redhead et al., 2016), furthermore in field experiments, misplaced workers have been able to return from up to 9.8 km (Goulson and Stout, 2001); (3) MPS are bigger on average (Goulson, 2003); (4) MPS are calorizators and therefore are very adaptable to new environments (Goulson, 2010); (5) MPS have a long active season, making them usable for a wide variety of crops (Goulson, 2003); (6) thanks to nests, MPS can maintain body temperature which makes them able to forage daily for longer periods as MPS can get warm faster in the morning hours (Willmer et al., 2008); (7) MPS have the ability to communicate within their nest about locations of resources and hence be more efficient in foraging (Dornhaus and Chittka, 1999).

The above-listed advantages of MPS are also what makes them highly competitively capable. Colonies of MPS offer ideal conditions for pathogen facilitation and spillover onto the wild pollinator populations (Goulson, 2003). Competition asymmetry with wild pollinator species is enhanced by the management of MPS which are fed supplementarily when resources are scarce. Making them persist

in high numbers in habitats where it wouldn't be naturally possible (Goulson, 2003). In conclusion high usage of MPS may lead to a decrease of wild pollinator diversity.

Apart from *B. terrestris* and *A. mellifera*, the leaf-cutting bee *Megachile rotundata* has also been massively introduced. This originally European solitary bee was introduced to America, Australia, and New Zealand (Bohart, 1972). This species is not as researched and widespread as the previous two, so there is not as much attention given to it.

In this chapter the history of introduction of managed species and their impact on wild pollinators is described.

3.1 Apis mellifera

Although *A. mellifera* is native to Africa, western Asia, and southeast Europe (Gullan and Cranston, 2014, p. 334; Han et al., 2012), the honeybee has been introduced worldwide. Currently the honeybee is present on every continent except Antarctica and is found in a variety of environments except the desert and areas with permafrost (Moritz et al., 2005)[FIG. 3]. The public throughout Europe recognizes the honeybee as native to this region, even though it is unlikely that honeybees would persist or thrive in such a high abundance in northern parts of Europe without human intervention (Colla and MacIvor, 2017).

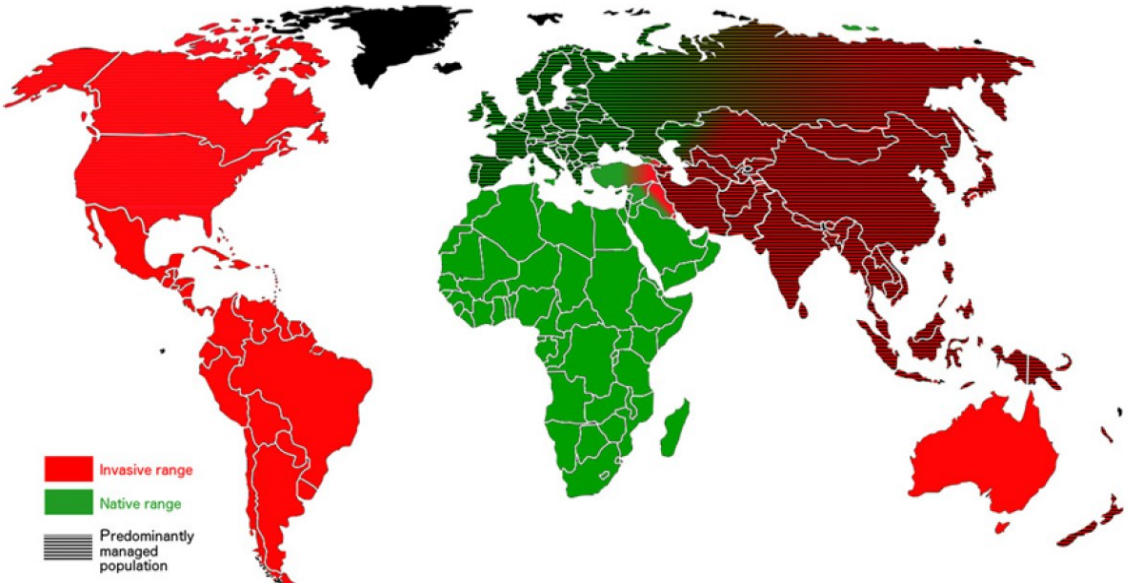

FIGURE 3: Distribution of *Apis mellifera* in its native range (green), invasive/introduced range (orange) and areas where *A. mellifera* is mostly managed (in stripes). Therefore, in Africa, in its native range, most of the species is feral; in Europe, Asia and New Zealand most of the species is managed, and in America and Australia feral populations predominate (Pirk et al., 2017).

3.1.1 Competition with wild-bee species

Wojcik (2018) reviewed previous articles on the competition of the honeybee with wild bee species to quantify the effect on wild-bee communities. When choosing only articles focused on experimental assessments, 19 articles met the criteria: 9 of those studies have shown no interaction or not powerful enough, 10 studies have shown competition with native bee species (Wojcik et al., 2018). The result demonstrates that honeybees compete with wild-bee communities, but describing this competition is far more complicated than whether the honeybee is present or not.

Herrera (2020) accessed the records of field studies of flora, plant-pollinator networks, and crop pollination during 1960-2019 in countries around the Mediterranean Sea, where the honeybee is native, but not in such high densities (Ollerton, 2021). The density of managed honeybees increased steadily over the last 50 years. With the increase of honeybee populations, the proportion of wild bees on flowers significantly decreased. At the beginning of this period, the proportion of wild bees on wildflowers was about four times more than honeybees. Fifty years later the results show an almost 1:1 ratio. On cultivated flowers the shift of the ratio in favor of the honeybee is even more dramatic [Fig 4] (Herrera, 2020). The change of the proportion of the wild-bee and honeybee, however, may be caused or enhanced by the habitat change (Cairns et al., 2005; Goulson, 2003).

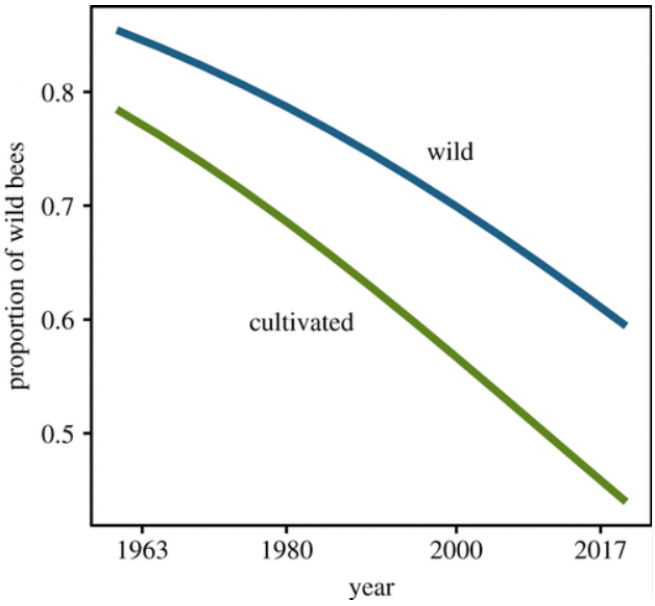

FIGURE 4: Change of proportional number of wild-bee species to all bee species on wildflowers (in blue) and cultivated flowers (in green) through 1963-2017 (Herrera, 2020).

The impact of beekeeping on wild-bee diversity is well demonstrated in a recent study from Greece. This study was conducted through 2005-2015 on 13 islands in Central Greece, on which the intensity of beekeeping substantially varies. Data was collected by pantraps and hand-netting three times over the course of the flowering season per year. The honeybee visitation rate negatively relates

to the wild-bee diversity. The competition for floral resources increased with a larger population of honeybees. The intensity of competition varied significantly for different bee families. In low honeybee densities, the competition was fiercest with *Apidae*. However, in high honeybee densities the competition was fiercest with *Andrenidae* and *Colletidae* (Lázaro et al., 2021) [Fig 5]. Conversely, in another study carried out in another nature reserve in Greece, no effect of honeybee abundance on wild-bee densities was observed. Here wild-bee densities corelated strongly with floral resource availability (Reverté et al., 2019).

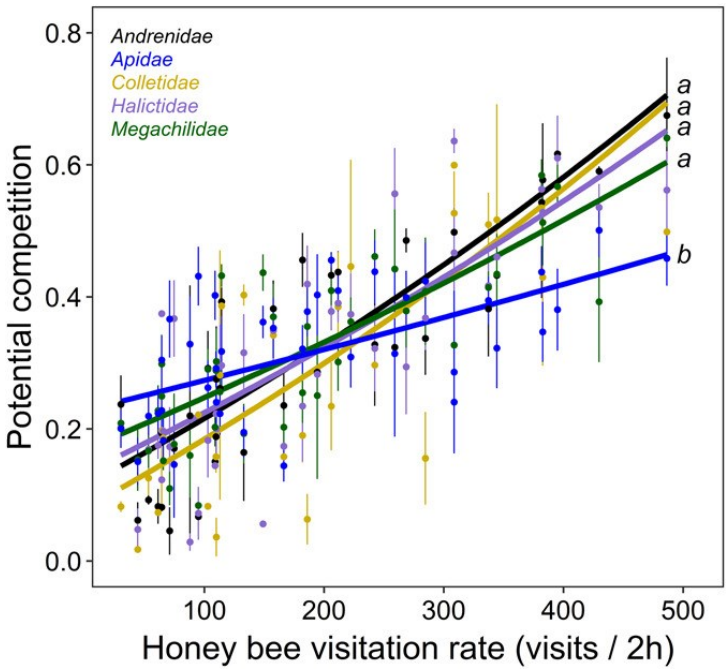

FIGURE 5: Increase of potential competition of honeybees with different bee families (Lázaro et al., 2021).

Herbetsson (2016) observed competition between honeybee and wild bumblebee populations when adding beehives on studied locations. But the competition also depended on other factors: hive density, landscape context and the ratio of natural to disturbed habitat (Herbertsson et al., 2016). The competition of honeybee and wild-bee species correlates with the level of disruption of the landscape (Lázaro et al., 2021). In Mexico, habitats that are disturbed are dominated by the honeybee. Intact habitats, on the contrary, are dominated by the native stingless bee (Cairns et al., 2005). Goulson (2003) similarly observed locations with a high honeybee density being strongly disturbed. Therefore he suggests that besides competition, the reason for low native bee densities may be the unsuitability of the environment for native species (Goulson, 2003). The strength of the competition with wild-bee species does not depend on the honeybee being natural to the habitat or introduced (Wojcik et al., 2018).

Asia has a different native honeybee species – *Apis cerana* (Smith and Hagen 1996). The queens of *A. mellifera* and *A. cerana* use a similar pheromone to attract drones, resulting in interspecific breeding. This mating does not produce offspring (post zygotic barrier), therefore making mated queens sterile (Pirk et al., 2011). Keeping *A. cerana* and *A. mellifera* in proximity led to spillover of the parasitic mite *Varroa destructor* onto *A. mellifera*. Because of *V. destructor* and viruses associated with it, there were huge loses of *A. mellifera* populations in Europe and North America (Rúa et al., 2009). *Varroa* mites have a big diversity in Asia. Moreover, future spillback of a more virulent strain on *A. cerana* is possible (Beaurepaire et al., 2015).

3.2 Bombus terrestris

Even though the bumblebee does not produce honey, its pollination service is frequently searched for. Bumblebees are used in greenhouses, in orchards (f. e. apples, pears, or avocado) or for other crops (f. e. peppers) (Dafni et al., 2010; Goulson, 2010). Compared to honeybees, bumblebees can forage even in low temperatures (even below 10°C) and in rain (Allen et al., 1978; Goulson, 2010; Stelzer et al., 2010). Bumblebees seem to be a better pollinator than honeybees for many crops – f. e. *Bombus sp.*in Scotland on raspberries (*Rubus idaeus*) where bumblebees are less abundant in the habitat than honeybees yet are better at transferring pollen. The main reasons are: (1) *Bombus* is more abundant on raspberry patches; (2) *Bombus* selects younger flowers; (3) foraging early in the morning when pollen separation is at its peak; (4) *Bombus* carries more pollen on its body (it is hairier); (5) *Bombus* visits more flowers per minute; (6) *Bombus* it is more prone to travel across plants, perhaps even across cultivars in a single trip (Willmer et al., 2008).

Another advantage setting the bumblebee apart from the honeybee is the capability of buzz-pollination, which is essential for crops such as tomato (*Solanum lycopersicum*) and other Solanaceae, as some flower species only release pollen once vibrated.(Goulson, 2010). The bee lays its thorax close to the anther, and by contraction of the flight muscles it begins to vibrate (King, 1993) [Fig. 6]. Other species have also been documented to be capable of buzz-pollination f. e.: *Xylopida sp.* (De Luca and Vallejo-Marín, 2013; Morgan et al., 2016), *Euglossa sp., Melipona sp., Protandrena sp., Nomia sp., Oxea sp.* (Buchmann, 1985).

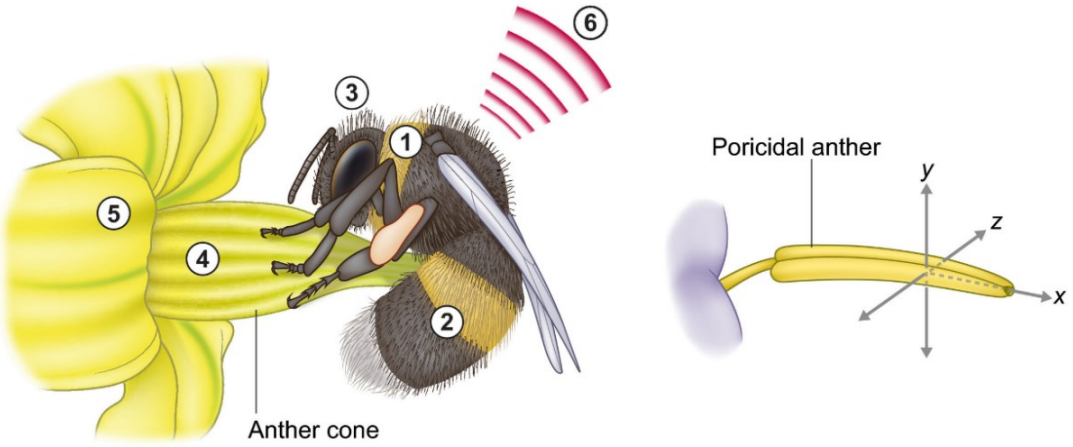

FIGURE 6: Buzz-pollination – a bumblebee on a Solanaceae-type plant. The body of the bumblebee (1-3) is in direct contact with an anther cone (4). Vibration is produced by indirect flight muscles which by contracting deform the shape of the thorax. The vibration spreads to flower petals (5) and produces sound (6) which gives buzz-pollination its name, even though the effect on pollen transfer is minimal. Axis y, z and x represent the directions of the vibration of the anther. The amount of released pollen depends on the vibration velocity of the z and y axis (Vallejo-Marín, 2019).

3.2.1 History of management

The first recorded human-mediated introduction of the bumblebee dates to the 19th century in New Zealand, where colonists had planned to breed cattle and horses, but the local native flora was not nutritious enough for their herds. Hence clover (*Trifolium pratense*) was introduced. However, the local pollinator species were not able to pollinate clover. Accordingly, after a few years of transporting seeds and the unsuccessful introduction of clover, the decision to introduce British pollinators was made. The first ship carrying hibernating queens of multiple bumblebee species sailed in 1885 and this was repeated in several subsequent years. In the end, 4 species of bumblebees were established: *Bombus horturum, B. subterraneus, B. terrestris, B. ruderatus* (Goulson, 2010; Plath, 1925). Unfortunately, *B. terrestris* is not an ideal clover pollinator as it has tendencies for nectar robbing because of the short length of its proboscis (Goulson, 2010; Inouye, 1980). Since then, many more introductions have been made worldwide.

In the 19th century, tomatoes in greenhouses in Europe were pollinated mechanically by vibrating the plant or were treated with hormones. This process was financially extremely demanding. In 1985, a Belgian veterinarian discovered the importance of bumblebees for tomato pollination. Two years later (1987), he founded the company Biobest for the commercial rearing of bumblebees. This initiative was then followed by more companies: Kopert Biological Systems and BBB (Bunting Brinkman

Bees) and has since been followed by many others. Nowadays there are over 30 bumblebee producing companies, but most of the market is covered by the first 3 companies (Velthius and Van Doorn, 2006). The methods of reproduction are kept secret by these companies (Goulson, 2010). Nowadays, if there's no policy preventing the import of commercially reared bumblebees to a country, almost anyone can order a nest (Ollerton, 2021; Prŷs-Jones et al., 2018).

3.2.2 Bombus terrestris invasions

This chapter describes the introduction of *B. terrestris* into different parts of the world and illustrates its invasive potential.

3.2.2.1 Tasmania

A good example of the high invasive potential of *B. terrestris* is how this species spreads on islands. Such an example is Tasmania, where a *B. terrestris* population was established in 1982 (Semmens et al., 1993). Later studies have shown that the population was founded by only two hibernating queens, which were brought by accident with ship cargo probably from New Zealand (Allen et al., 2007; Buttermore, 1997; Schmid-Hempel et al., 2007; Stout and Goulson, 2000). There were unsuccessful attempts at introduction from New Zealand before – in 1909 and 1935 by Tarlton Rayment. Therefore there are speculations about whether the introduction was "unintentional" (Buttermore, 1997). *B. terrestris* can also be found on two surroundings islands – Mewstone and De Witt Island (6 and 22 km south of Tasmania). This draws concern about *B. terrestris* moving across the islands north of Tasmania all the way to Australia (Kardum Hjort et al., 2023).

In a study done in 2002 no negative impact of introduced bumblebees on natural bee populations was noted. This may be explained by the preference of introduced bumblebees for introduced plants and by introduced bumblebees being long-tongued as opposed to the native ones (Goulson et al., 2002). The founding queens brought few parasites (only mite *Kuzinia laevis*) which may have reduced the bottleneck effect on introduced species (Allen et al., 2007) and the negative impact on the native species. In the case of honeybees, which had been introduced to Tasmania in the early 19th century, a greater number of native species was observed in places where honeybees were not present (Goulson et al., 2002).

3.2.2.2 Japan

Japan is another island where a *B. terrestris* population was established and where its spread was recorded. The species was brought in 1991 for pollination in greenhouses (Inoue et al., 2007). Despite warnings from scientists and efforts to secure greenhouses against bee escapes, the population settled in the wild. In 1996 the first naturally occurring nest was discovered in the Hokkaido region which proved the naturalization of the species (Washitani 1998).

Maki N. Inoue (2007) and her team monitored the impact of introduced *B. terrestris* on six native species (*B. hypocrita sapporoensis, B. ardens sakagamii, B. hypnorum koropokkrus, B. schrencki albidopleuralis, B. pseudobaicalensis* and *B. diversus tersatus*) in the south of the Hokkaido region for 3 years (2003-2004). Out of the 6 natural bee species 3 have niche overlap with *B. terrestris*: flower resources and nest sites with *B. hypocrita sapporoensis*, flower resources with *B. pseudobaicalensis* and nest sites with *B. diversus tersatus.* The only native species with a significant population decline during the study is *B. hypocrita sapporoensis*. The results show that nesting sites are a limiting factor, and the introduced species has increased this competition. The effect is enhanced by increased nest usurpation on the locality indicated by a higher number of dead queens per nest (Inoue et al., 2007) [Fig. 7].

Laboratory experiments have shown *B. terrestris* mating with *B. hypocrita sapporoensis*. By their mating, a diploid egg is produced, but none of the eggs have hatched. Results indicates potential competition for mates, but also a low risk of introgression of the gene pool of *B. h. sapporoensis* (Kanbe et al., 2008). Interspecific mating was confirmed in another study, here already observed in the field. *B. hypocrita* queens were mating with *B. terrestris* drones in high frequencies. The frequency was higher in *B. hypocrita sapporoensis* than in *B. hypocrita hypocrita* subspecies. The authors justify high frequencies of interspecific mating by the smaller population densities of native species. No viable offspring have been observed. This makes the queens sterile as they usually mate only once (Kondo et al. 2009).

To protect Japanese native species an “Invasive Alien Species Act” was enforced in 2006. According to this law, farmers must ask the minister to use *B. terrestris*, greenhouses must be secured to prevent escape and all the *B. terrestris* nests must be destroyed after the end of the season (Kanbe et al., 2008). Despite this law, large numbers of drones were recorded escaping from the greenhouses into the wild (Inoue et al., 2007). Nowadays, the greenhouses must be whole covered in a net, that disables the escape of bumblebees. This is also very costly (Mizutani and Goka 2010).

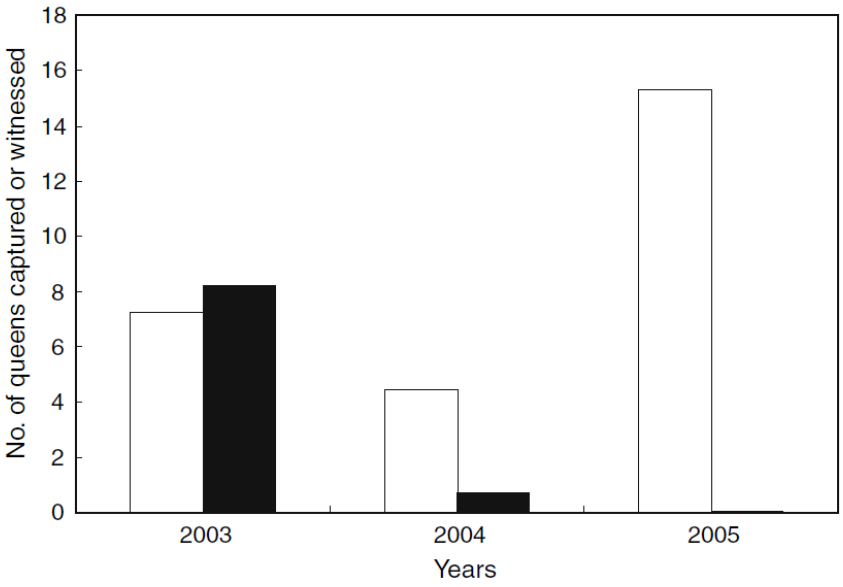

FIGURE 7: The number of overwintered queens of *B. terrestris* (white) and *B. hypocrita sapporoensis* (black) seen by person per hour in the Hokkaido region in the years 2003-2005. Authors explain the decrease of *B. terrestris* in 2004 by high number monitoring volunteers and therefore higher pressure on the bees (Inoue et al., 2007).

3.2.2.3 Patagonia

For the red clover pollination, *B. ruderatus* was chosen as a perfect species and shipped from New Zealand to Chile in the early 1980s (Arretz and Macfarlane, 1986). Subsequently *B. terrestris* from Belgium and Israel was introduced to Chile in 1998 for tomato pollination in greenhouses (Ruz and Herrera, 2001). In 2006 *B. terrestris* was recorded in the wild in Argentina (Torretta et al., 2006). These introductions had a negative impact on the native species *B. dahlbomii* (Morales et al., 2013).

Southern Patagonia only has one native bumblebee species – *B. dahlbomii*. This generalist bumblebee is the largest and the most southern bumblebee worldwide (Franklin, 1912). Morales and her team (2013) recorded bumblebee species visiting amancay (*Alstroemeria aurea*) through the years 1994-2013 in the Challhuaco Valley. In this locality more than 90% of the visits on amancay in 1994 and 1995 was by *B. dahlbomii* (Aizen, 2001). There was a decline in the population of native *B. dahlbomii* after the introduction of *B. ruderatus*. The decline was further enhanced by the introduction of *B. terrestris* to this locality. Furthermore, the introduction of *B. terrestris* led to a sharp decline in the population of *B. ruderatus*. Since 2008 *B. dahlbomii* has not been recorded in the Challhuaco Valley (Morales et al., 2013) [Fig. 8]. Smaller competition of *B. ruderatus* and *B. dahlbomii* can be explained by the contrasting foraging patterns of these species (Aizen et al., 2011). The likely reason for the decline of *Bombus spp.* after the introduction of *B. terrestris* is its pathogen *Apicystis*

bombi which spread to populations of *B. ruderatus* and *B. dahlbomii*. There was no record of *A. bombi* before the introduction of *B. terrestris* and PCR tests have not found its DNA in museum collections of the prior species (Arbetman et al., 2013).

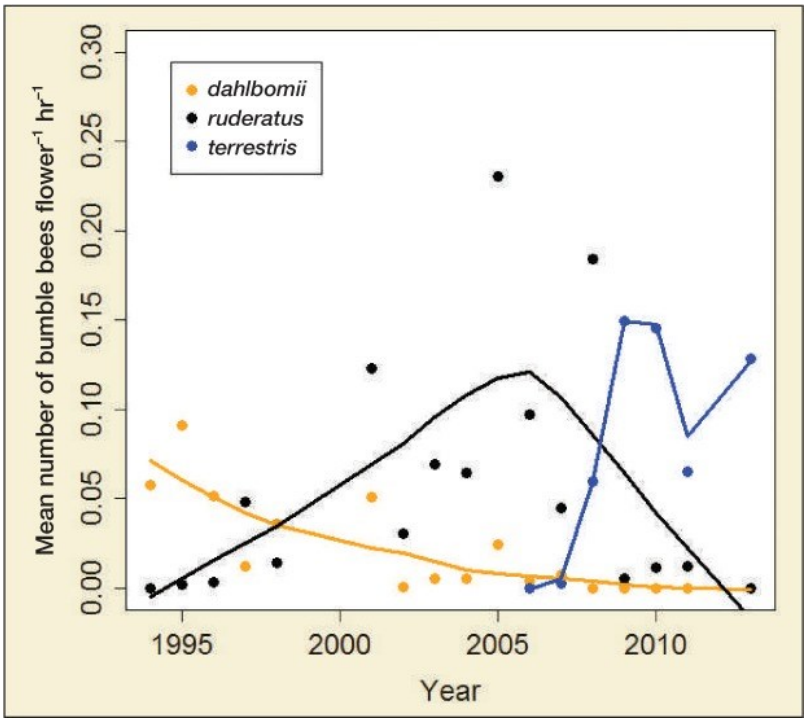

FIGURE 8: Abundance of bumblebee species visiting *Alstroemeria aurea* through 1994-2013 in the Challhuaco Valley (Morales et al., 2013).

In the 2011 survey of bumblebee species abundance through the range of *B. dahlbomii*, 33 sites were sampled in total. *B. dahlbomii* was observed on 48% of the sites but was locally dominant (over 90% of observed individuals) at only 18%, of which 6 were the most southern. *B. ruderatus* was observed on 24% and was not dominant on any site. *B. terrestris* was observed on 88% of the sites and locally dominant on 48% of the sites (Morales et al. 2013) [Fig. 9]

B. terrestris has been introduced so massively that describing all the cases of its introduction and impact on native pollinator communities would far exceed the scope of this thesis. Nevertheless, the possible effects of the introduction of invasive *B. terrestris* and its enormous invasion potential are clearly discernible in the cases described in this chapter. This illustrates the possible ways of competition with native species: unobserved in Tasmania (Goulson et al., 2002), for nesting spaces and through hybridization in Japan (Inoue, Yokoyama, and Washitani 2007; Kanbe et al. 2008; Kondo et al. 2009), or through pathogen spread in Patagonia. Furthermore, this shows that the impact and character of the invasions is very variable.

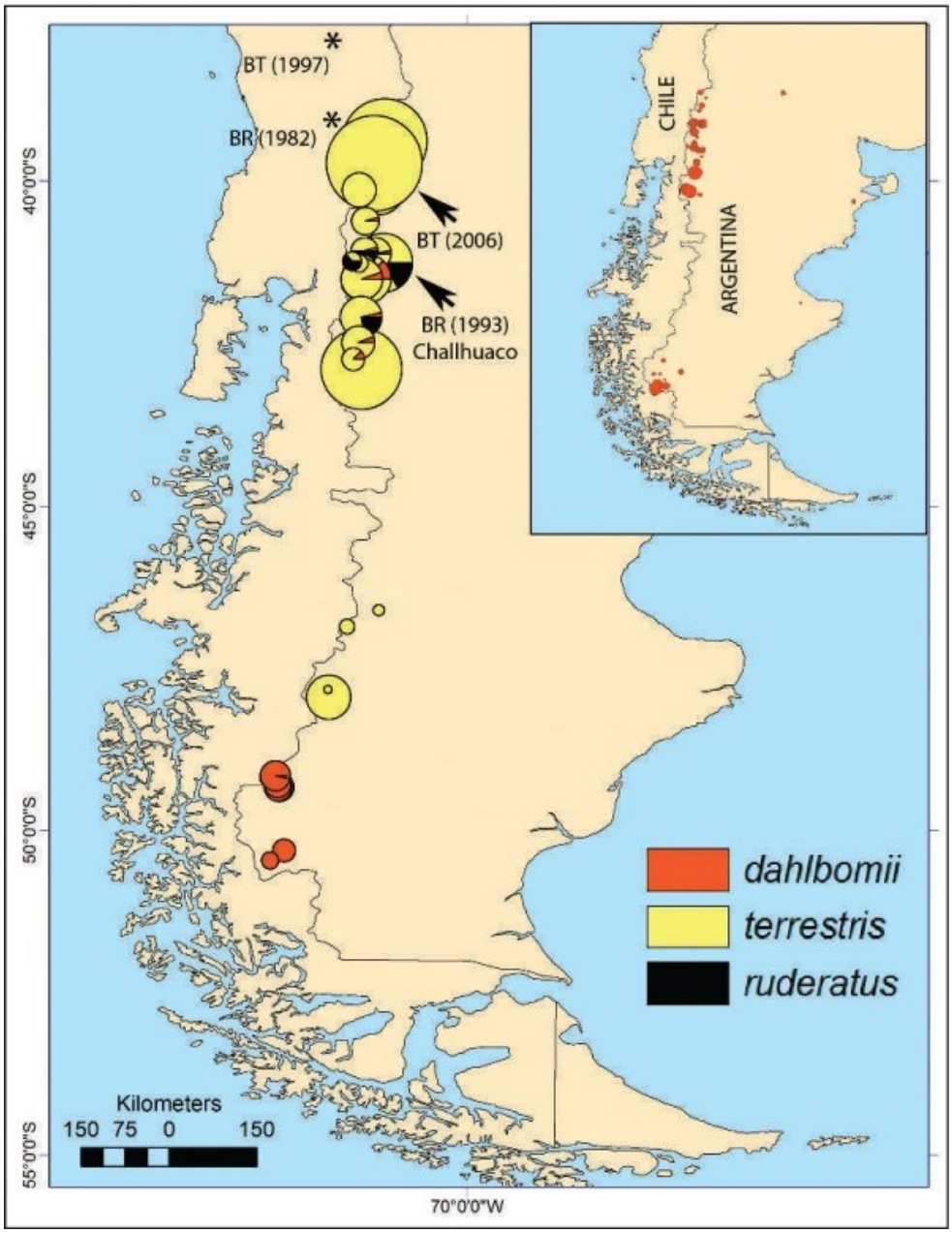

FIGURE 9: Map of sampled sites during a survey in 2011 showing the proportional distribution of *Bombus spp.*. BR1982: location of first introduction of *B. ruderatus*; BR1993: location of first record of naturalization of *B. ruderatus*; BT1997: location of first introduction of *B. terrestris* in Chile; BT2006: location of first record of naturalized *B. terrestris* in Argentina. The map in the right corner shows the distribution of *B. dahlbomii* before the arrival of the invasive *Bombus spp.* (Morales et al., 2013).

3.2.3 Threats to wild pollinators

Various effects of *B. terrestris* on wild-bee populations have been recorded: floral resource competition, competition for nesting sites, transmission of pathogens and parasites, genetic contamination (Dafni et al. 2010).

The long active season is one of the factors of strong competition for floral resources. In some locations in Europe *B.terrestris* has been recorded to have a bivoltine cycle. Observations from the UK show the occurrence of *B.terrestris* even through winter (Stelzer et al. 2010). Dafni (2010) has observed *B. terrestris* queens throughout the year except January in Israel (Dafni et al. 2010).

The commercial use of bumblebees provides an ideal place for pathogen and parasite facilitation. Commercially reared nests often get infected by parasites such as *Crithidia bombi* and *Lucostacarus buchneri*, which then spillover from greenhouses onto the wild population (Otterstatter and Thomson 2008). In North America commercial use of *Bombus occidentalis* had to be stopped as it was tied with outbreaks of *Nosema bombi* (Goulson 2010). And as mentioned before in Patagonia, the spread of *Apicystis bombi* led to local extinctions of *B. dahlbomii* (Morales et al. 2013). On contrary, in a study set in the UK, no evidence of pathogen (*Crithdia spp.* and *Nosema b.*) spreading to wild bumblebees was noticed. Here, the parasitic infection was no higher at commercial farms than at wild farms. Furthermore, in *B. pratorum* was prevalence of *Crithidia* higher in wild farms. The study, however, has shown the increase of prevalence of *Crithidia* in commercial bees at the end of the season, and therefore suggesting a pathogen spillover at the end of the season (Whitehorn et al. 2013).

In Europe different subspecies of *B. terrestris* are naturally distributed. This poses risk of hybridization and introgression between native and commercial subspecies (Goulson 2003). In laboratory conditions the commercial *B. t. dalmatinus* drones mated with queens of native *B. t. audax*, but they preferred queens of the same subspecies (Ings, Raine, and Chittka 2005). Goulson (2010) points out that these laboratory experiments do not mean crossbreeding in nature, where the environment is more complex. Nevertheless, he warns that the hybridization between subspecies would lead to an overall decline in biodiversity (Goulson 2010). In a later study no evidence of hybridization and introgression between *B. t. dalmatinus* and *B. t. audax* has been shown (Hart et al. 2021). As mentioned before, in Japan introduced *B. terrestris* mates with native *B. hypocrita*, which results in non-viable offspring, therefore it makes the queen of the native species sterile (Kondo et al. 2009).

3.2.4 Current management

In factories in Europe, over 1 million *B. terrestris* nest are produced yearly (Goulson, 2010). Many countries see the threat of commercially reared bumblebees and take policies to reduce their impact (Colla and MacIvor, 2017). In Europe, the use of reared bumblebees is permitted, but the nest should be destroyed at the end of the season. However, there is a lot of doubt that farmers go through the proper destruction of the nests at the end of season and concern that even when they do, some bees still escape to nature. Destroying the nests also does not eradicate the threat of pathogen spillover (Goulson, 2010).

One of the policies is to use reared bumblebees but ones native to the country. In America, protests against the non-native bumblebee species have taken place. The previously used *B. impatiens* from Europe was replaced by the native *B. occidentalis*. Later *B. occidentalis* use has been stopped as there was a great pathogen spillover onto the natural population (Rao et al. 2011; Strange 2015). Strange (2015) suggests the use of *B. huntii* and *B. vosnesenskii*, because based on his experiments these native species are equally efficient in pollination of tomatoes (Strange 2015). Japan has turned to the use of the native *B. hypocrita* instead of the *B. terrestris*, but unfortunately, *B. terrestris* had already established a population in the wild (Washitani 1998).

Australia is still *B. terrestris* free and the government is trying to keep it this way. Australian farmers would like to use *B. terrestris* in greenhouses with barriers against leakage (Goulson 2010). When keeping bumblebees inside of the greenhouses, pollen from outside flowers is still found in the nest (Whittington et al., 2004). In Japan, bumblebees escaped even when precautions were taken (Inoue, Yokoyama, and Washitani 2007).

4 CONCLUSIONS

The commercial use of pollinators and enforcement of managed pollinators brings benefits to man but not necessarily to the ecosystem (Kareiva et al., 2007). Yet, the pollination service and honey production is a great industry and its benefits are immense (Goulson, 2010; Klein et al., 2007). The ideal solution would be to find a balance between using commercial pollinators and protecting wild-bee species. For the protection of wild-bee diversity, environmental protection seems to be the crucial step, as wild-bees prosper in natural habitats (Cairns et al., 2005; Goulson, 2003; Herbertsson et al., 2016; Lázaro et al., 2021). Protecting wild-bee species and their diversity would lead to stronger communities that would be better adapted to withstand disturbances (Colla and MacIvor, 2017).

B. terrestris is a massively introduced managed bee species with great invasion speed and a devastating impact on native bee populations. More attention and thought should be taken before introducing it to a new area (Goulson, 2003). Policies for using *B. terrestris* should be adopted and it be monitored whether they are being followed.

One of the solutions for reducing the use of massively managed bee species could be the use of different species of pollinators. The hoverfly *Eristalis tenax* is a great pollinator that has already been reared in laboratory conditions. There are no records of management out of the laboratory yet. This species has a great potential as it is not only an efficient pollinator of many crops, but its larvae also feed on decaying matter providing another service for agriculture (Howlett and Gee, 2019). Other species of hoverflies are interesting for management, because their larvae feed on aphids (Mahr 2016), so they could serve as pest control and reduce the burden of pesticides on the landscape. Another interesting species are 'honey wasps' of the genus *Brachygasta*, which are native to Central and South America. This species collects honey that can be harvested (even though in smaller amounts than honeybees) and predates on various arthropods (f. e. honey wasps preying on amphids have been documented) (da Silva and Noll, 2015; Reyes-Rosas et al., 2013; Torretta et al., 2006), hence it can also be used for pest management.

REFERENCES

Abrol, Dharam P. 2011. *Pollination Biology: Biodiversity Conservation and Agricultural Production*. Springer Science & Business Media.

Ackerman, J. D. 2000. 'Abiotic Pollen and Pollination: Ecological, Functional, and Evolutionary Perspectives'. *Plant Systematics and Evolution* 222 (1): 167–85. https://doi.org/10.1007/BF00984101.

Aizen, Marcelo A. 2001. 'Flower Sex Ratio, Pollinator Abundance, and the Seasonal Pollination Dynamics of a Protandrous Plant'. *Ecology* 82 (1): 127–44. https://doi.org/10.1890/0012-9658(2001)082[0127:FSRPAA]2.0.CO;2.

Aizen, Marcelo A., Lucas A. Garibaldi, Saul A. Cunningham, and Alexandra M. Klein. 2008. 'Long-Term Global Trends in Crop Yield and Production Reveal No Current Pollination Shortage but Increasing Pollinator Dependency'. *Current Biology* 18 (20): 1572–75. https://doi.org/10.1016/j.cub.2008.08.066.

Aizen, Marcelo A., Mariana Lozada, and Carolina L. Morales. 2011. 'Comparative Nectar-Foraging Behaviors and Efficiencies of an Alien and a Native Bumble Bee'. *Biological Invasions* 13 (12): 2901–9. https://doi.org/10.1007/s10530-011-9972-3.

Allen, G. R., O. D. Seeman, P. Schmid-Hempel, and R. E. Buttermore. 2007. 'Low Parasite Loads Accompany the Invading Population of the Bumblebee, Bombus Terrestris in Tasmania'. *Insectes Sociaux* 54 (1): 56–63. https://doi.org/10.1007/s00040-007-0908-y.

Allen, Tracy, Sydney Cameron, Ronald McGinley, and Bernd Heinrich. 1978. 'The Role of Workers and New Queens in the Ergonomics of a Bumblebee Colony (Hymenoptera: Apoidea)'. *Journal of the Kansas Entomological Society* 51 (3): 329–42.

Arbetman, Marina P., Ivan Meeus, Carolina L. Morales, Marcelo A. Aizen, and Guy Smagghe. 2013. 'Alien Parasite Hitchhikes to Patagonia on Invasive Bumblebee'. *Biological Invasions* 15 (3): 489–94. https://doi.org/10.1007/s10530-012-0311-0.

Arretz, P. V., and R. P. Macfarlane. 1986. 'The Introduction of Bombus Ruderatus to Chile for Red Clover Pollination'. *Bee World* 67 (1): 15–22. https://doi.org/10.1080/0005772X.1986.11098855.

Bailes, Emily J., Kaitlin R. Deutsch, Judit Bagi, Lucila Rondissone, Mark J. F. Brown, and Owen T. Lewis. 2018. 'First Detection of Bee Viruses in Hoverfly (Syrphid) Pollinators'. *Biology Letters* 14 (2): 20180001. https://doi.org/10.1098/rsbl.2018.0001.

Balfour, Nicholas J., Mihail Garbuzov, and Francis 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.)?' *Ecological Entomology* 38 (4): 323–29. https://doi.org/10.1111/een.12019.

Balfour, Nicholas J., Jeff Ollerton, Maria Clara Castellanos, and Francis L. W. Ratnieks. 2018. 'British Phenological Records Indicate High Diversity and Extinction Rates among Late-Summer-Flying Pollinators'. *Biological Conservation* 222 (June): 278–83. https://doi.org/10.1016/j.biocon.2018.04.028.

Beaurepaire, Alexis L., Tuan A. Truong, Alejandro C. Fajardo, Tam Q. Dinh, Cleofas Cervancia, and Robin F. A. Moritz. 2015. 'Host Specificity in the Honeybee Parasitic Mite, Varroa Spp. in Apis Mellifera and Apis Cerana'. *PLOS ONE* 10 (8): e0135103. https://doi.org/10.1371/journal.pone.0135103.

Beekman, M., and F. L. W. Ratnieks. 2000. 'Long-Range Foraging by the Honey-Bee, Apis Mellifera L.' *Functional Ecology* 14 (4): 490–96. https://doi.org/10.1046/j.1365-2435.2000.00443.x.

Begon, M., C.R. Townsend, and J.L. Harper. 2006. *Ecology: From Individuals to Ecosystems*. 4th ed. Oxford: Blackwell Publishing. http://books.google.com/books?id=Lsf1lkYKoHEC.

Begon, Michael, Martin Mortimer, and David J. Thompson. 2009. *Population Ecology: A Unified Study of Animals and Plants*. John Wiley & Sons.

Bohart, G. E. 1970. 'The Evolution of Parasitism among Bees'. *41st Fac. Honor Lec., Utah State Univ., Logan*.

Bohart, G. E. 1972. 'Management of Wild Bees for the Pollination of Crops'. *Annual Review of Entomology* 17 (1): 287–312. https://doi.org/10.1146/annurev.en.17.010172.001443.

Boncristiani, Humberto, James D. Ellis, Tomas Bustamante, Jason Graham, Cameron Jack, Chase B. Kimmel, Ashley Mortensen, and Daniel R. Schmehl. 2021. 'World Honey Bee Health: The Global Distribution of Western Honey Bee (Apis Mellifera L.) Pests and Pathogens'. *Bee World* 98 (1): 2–6. https://doi.org/10.1080/0005772X.2020.1800330.

Buchmann, Stephen L. 1985. 'Bees Use Vibration to Aid Pollen Collection from Non-Poricidal Flowers'. *Journal of the Kansas Entomological Society* 58 (3): 517–25.

Buttermore, R. E. 1997. 'Observations of Successful Bombus Terrestris (L.) (Hymenoptera: Apidae) Colonies in Southern Tasmania'. *Australian Journal of Entomology* 36 (3): 251–54. https://doi.org/10.1111/j.1440-6055.1997.tb01463.x.

Cairns, Christine E., Rogel Villanueva-Gutiérrez, Suzanne Koptur, and David B. Bray. 2005. 'Bee Populations, Forest Disturbance, and Africanization in Mexico1'. *Biotropica* 37 (4): 686–92. https://doi.org/10.1111/j.1744-7429.2005.00087.x.

Case, Ted J., and Michael E. Gilpin. 1974. 'Interference Competition and Niche Theory'. *Proceedings of the National Academy of Sciences of the United States of America* 71 (8): 3073–77.

Černá, Kateřina, Monika Zemenová, Lenka Macháčková, Zdislava Kolínová, and Jakub Straka. 2013. 'Neighbourhood Society: Nesting Dynamics, Usurpations and Social Behaviour in Solitary Bees'. *PLOS ONE* 8 (9): e73806. https://doi.org/10.1371/journal.pone.0073806.

Colla, Sheila R., and J. Scott MacIvor. 2017. 'Questioning Public Perception, Conservation Policy, and Recovery Actions for Honeybees in North America: Questioning Public Perception'. *Conservation Biology* 31 (5): 1202–4. https://doi.org/10.1111/cobi.12839.

Couvillon, Margaret J., Roger Schürch, and Francis L. W. Ratnieks. 2014. 'Waggle Dance Distances as Integrative Indicators of Seasonal Foraging Challenges'. *PLOS ONE* 9 (4): e93495. https://doi.org/10.1371/journal.pone.0093495.

Cunningham, John Paul, James P. Hereward, Tim A. Heard, Paul J. De Barro, and Stuart A. West. 2014. 'Bees at War: Interspecific Battles and Nest Usurpation in Stingless Bees.' *The American Naturalist* 184 (6): 777–86. https://doi.org/10.1086/678399.

Dafni, Amots, Peter Kevan, Caroline Gross, and Koichi Goka. 2010. 'Bombus Terrestris, Pollinator, Invasive and Pest: An Assessment of Problems Associated with Its Widespread Introductions for Commercial Purposes'. *Applied Entomology and Zoology - APPL ENTOMOL ZOOL* 45 (February): 101–13. https://doi.org/10.1303/aez.2010.101.

De Luca, Paul A, and Mario Vallejo-Marín. 2013. 'What's the "Buzz" about? The Ecology and Evolutionary Significance of Buzz-Pollination'. *Current Opinion in Plant Biology* 16 (4): 429–35. https://doi.org/10.1016/j.pbi.2013.05.002.

Dornhaus, A., and L. Chittka. 1999. 'Evolutionary Origins of Bee Dances'. *Nature* 401 (6748): 38–38. https://doi.org/10.1038/43372.

Durrer, Stephan, and Paul Schmid-Hempel. 1994. 'Shared Use of Flowers Leads to Horizontal Pathogen Transmission'. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 258 (1353): 299–302. https://doi.org/10.1098/rspb.1994.0176.

Edmunds, Malcolm, and Tom Reader. 2014. 'Evidence for Batesian Mimicry in a Polymorphic Hoverfly'. *Evolution* 68 (3): 827–39. https://doi.org/10.1111/evo.12308.

Ellner, Stephen P., Wee Hao Ng, and Christopher R. Myers. 2020. 'Individual Specialization and Multihost Epidemics: Disease Spread in Plant-Pollinator Networks'. *The American Naturalist* 195 (5): E118–31. https://doi.org/10.1086/708272.

Figueroa, Laura L., Heather Grab, Wee Hao Ng, Christopher R. Myers, Peter Graystock, Quinn S. McFrederick, and Scott H. McArt. 2020. 'Landscape Simplification Shapes Pathogen Prevalence in Plant-Pollinator Networks'. *Ecology Letters* 23 (8): 1212–22. https://doi.org/10.1111/ele.13521.

Franklin, Henry J. 1912. 'The Bombidæ of the New World'. *Transactions of the American Entomological Society (1890-)* 38 (3/4): 177–486.

Frisch, Karl von. 1993. *The Dance Language and Orientation of Bees*. *The Dance Language and Orientation of Bees*. Harvard University Press. https://doi.org/10.4159/harvard.9780674418776.

Geslin, B., B. Gauzens, M. Baude, I. Dajoz, C. Fontaine, M. Henry, L. Ropars, O. Rollin, E. Thébault, and N. J. Vereecken. 2017. 'Chapter Four - Massively Introduced Managed Species and Their Consequences for Plant–Pollinator Interactions'. In *Advances in Ecological Research*, edited by David A. Bohan, Alex J. Dumbrell, and François Massol, 57:147–99. Networks of Invasion: Empirical Evidence and Case Studies. Academic Press. https://doi.org/10.1016/bs.aecr.2016.10.007.

Goulson, D. 2010. *Bumblebees: Behaviour, Ecology, and Conservation.* 2nd ed. Oxford University Press. https://www.cabdirect.org/cabdirect/abstract/20093315935.

Goulson, D., J.C. Stout, and A.R. Kells. 2002. 'Do Exotic Bumblebees and Honeybees Compete with Native Flower-Visiting Insects in Tasmania?' *Journal of Insect Conservation* 6 (3): 179–89. https://doi.org/10.1023/A:1023239221447.

Goulson, Dave. 2003. 'Effects of Introduced Bees on Native Ecosystems'. *Annual Review of Ecology, Evolution, and Systematics* 34 (1): 1–26. https://doi.org/10.1146/annurev.ecolsys.34.011802.132355.

Goulson, Dave, and Ben Darvill. 2004. 'Niche Overlap and Diet Breadth in Bumblebees; Are Rare Species More Specialized in Their Choice of Flowers?' *Apidologie* 35 (1): 55–63. https://doi.org/10.1051/apido:2003062.

Goulson, Dave, James Peat, Jane Stout, James Tucker, Ben Darvill, Lara Derwent, and William Hughes. 2002. 'Can Alloethism in Workers of the Bumblebee, Bombus Terrestris, Be Explained in Terms of Foraging Efficiency?' *Animal Behaviour* 64 (July): 123–30. https://doi.org/10.1006/anbe.2002.3041.

Goulson, David, and Kate R. Sparrow. 2009. 'Evidence for Competition between Honeybees and Bumblebees; Effects on Bumblebee Worker Size'. *Journal of Insect Conservation* 13 (2): 177–81. https://doi.org/10.1007/s10841-008-9140-y.

Goulson, David, and Jane C. Stout. 2001. 'Homing Ability of the Bumblebee Bombus Terrestris (Hymenoptera: Apidae)'. *Apidologie* 32 (1): 105–11. https://doi.org/10.1051/apido:2001115.

Grab, Heather, Eleanor J. Blitzer, Bryan Danforth, Greg Loeb, and Katja Poveda. 2017. 'Temporally Dependent Pollinator Competition and Facilitation with Mass Flowering Crops Affects Yield in Co-Blooming Crops'. *Scientific Reports* 7 (1): 45296. https://doi.org/10.1038/srep45296.

Graystock, Peter, Dave Goulson, and William O. H. Hughes. 2015. 'Parasites in Bloom: Flowers Aid Dispersal and Transmission of Pollinator Parasites within and between Bee Species'. *Proceedings of the Royal Society B: Biological Sciences* 282 (1813): 20151371. https://doi.org/10.1098/rspb.2015.1371.

Graystock, Peter, Wee Hao Ng, Kyle Parks, Amber D. Tripodi, Paige A. Muñiz, Ashley A. Fersch, Christopher R. Myers, Quinn S. McFrederick, and Scott H. McArt. 2020. 'Dominant Bee Species and Floral Abundance Drive Parasite Temporal Dynamics in Plant-Pollinator Communities'. *Nature Ecology & Evolution* 4 (10): 1358–67. https://doi.org/10.1038/s41559-020-1247-x.

Grume, Grayson J., Seth P. Biedenbender, and Clare C. Rittschof. 2021. 'Honey Robbing Causes Coordinated Changes in Foraging and Nest Defence in the Honey Bee, Apis Mellifera'. *Animal Behaviour* 173 (March): 53–65. https://doi.org/10.1016/j.anbehav.2020.12.019.

Gullan, P. J., and P. S. Cranston. 2014. *The Insects: An Outline of Entomology*. 5th ed. John Wiley & Sons.

Han, Fan, Andreas Wallberg, and Matthew T Webster. 2012. 'From Where Did the Western Honeybee (Apis Mellifera) Originate?' *Ecology and Evolution* 2 (8): 1949–57. https://doi.org/10.1002/ece3.312.

Hart, Alex F., Kevin Maebe, Gordon Brown, Guy Smagghe, and Thomas Ings. 2021. 'Winter Activity Unrelated to Introgression in British Bumblebee Bombus Terrestris Audax'. *Apidologie* 52 (2): 315–27.

Herbertsson, Lina, Sandra A. M. Lindström, Maj Rundlöf, Riccardo Bommarco, and Henrik G. Smith. 2016. 'Competition between Managed Honeybees and Wild Bumblebees Depends on Landscape Context'. *Basic and Applied Ecology* 17 (7): 609–16. https://doi.org/10.1016/j.baae.2016.05.001.

Herrera, Carlos M. 2020. 'Gradual Replacement of Wild Bees by Honeybees in Flowers of the Mediterranean Basin over the Last 50 Years'. *Proceedings of the Royal Society B: Biological Sciences* 287 (1921): 20192657. https://doi.org/10.1098/rspb.2019.2657.

Higginson, Andrew D. 2017. 'Conflict over Non-Partitioned Resources May Explain between-Species Differences in Declines: The Anthropogenic Competition Hypothesis'. *Behavioral Ecology and Sociobiology* 71 (7): 99. https://doi.org/10.1007/s00265-017-2327-z.

Howarth, Brigitte, Malcolm Edmunds, and Francis Gilbert. 2004. 'Does the Abundance of Hoverfly (Syrphidae) Mimics Depend on the Numbers of Their Hymenopteran Models?' *Evolution* 58 (2): 367–75.

Howlett, Brad G., and Megan Gee. 2019. 'The Potential Management of the Drone Fly (*Eristalis Tenax*) as a Crop Pollinator in New Zealand'. *New Zealand Plant Protection* 72 (July): 221–30. https://doi.org/10.30843/nzpp.2019.72.304.

Hubbell, Stephen P., and Leslie K. Johnson. 1977. 'Competition and Nest Spacing in a Tropical Stingless Bee Community'. *Ecology* 58 (5): 950–63. https://doi.org/10.2307/1936917.

Hudewenz, Anika, and Alexandra-Maria Klein. 2015. 'Red Mason Bees Cannot Compete with Honey Bees for Floral Resources in a Cage Experiment'. *Ecology and Evolution* 5 (21): 5049–56. https://doi.org/10.1002/ece3.1762.

Ings, Thomas C., Nigel E. Raine, and Lars Chittka. 2005. 'Mating Preference in the Commercially Imported Bumblebee Species Bombus Terrestris in Britain (Hymenoptera: Apidae)'. *Entomologia Generalis*, December, 233–38. https://doi.org/10.1127/entom.gen/28/2005/233.

Inoue, Maki N., Jun Yokoyama, and Izumi Washitani. 2007. 'Displacement of Japanese Native Bumblebees by the Recently Introduced Bombus Terrestris (L.) (Hymenoptera: Apidae)'. *Journal of Insect Conservation* 12 (2): 135–46. https://doi.org/10.1007/s10841-007-9071-z.

Inouye, David. 1983. *The Ecology of Nectar Robbing*. New York: Columbia University Press.

Inouye, David W. 1980. 'The Effect of Proboscis and Corolla Tube Lengths on Patterns and Rates of Flower Visitation by Bumblebees'. *Oecologia* 45 (2): 197–201.

Irwin, Rebecca E., Judith L. Bronstein, Jessamyn S. Manson, and Leif Richardson. 2010. 'Nectar Robbing: Ecological and Evolutionary Perspectives'. *Annual Review of Ecology, Evolution, and Systematics* 41: 271–92.

Jauker, Frank, Martin Speckmann, and Volkmar Wolters. 2016. 'Intra-Specific Body Size Determines Pollination Effectiveness'. *Basic and Applied Ecology* 17 (8): 714–19. https://doi.org/10.1016/j.baae.2016.07.004.

Johnson, Leslie K., and Stephen P. Hubbell. 1974. 'Aggression and Competition among Stingless Bees: Field Studies'. *Ecology* 55 (1): 120–27. https://doi.org/10.2307/1934624.

Justino, Danielle G., Pietro K. Maruyama, and Paulo E. Oliveira. 2012. 'Floral Resource Availability and Hummingbird Territorial Behaviour on a Neotropical Savanna Shrub'. *Journal of Ornithology* 153 (1): 189–97. https://doi.org/10.1007/s10336-011-0726-x.

Kanbe, Yuya, Ikuko Okada, Masahiro Yoneda, Koichi Goka, and Koji Tsuchida. 2008. 'Interspecific Mating of the Introduced Bumblebee Bombus Terrestris and the Native Japanese Bumblebee Bombus Hypocrita Sapporoensis Results in Inviable Hybrids'. *Naturwissenschaften* 95 (10): 1003–8. https://doi.org/10.1007/s00114-008-0415-7.

Kardum Hjort, Cecilia, Henrik G Smith, Andrew P Allen, and Rachael Y Dudaniec. 2023. 'Morphological Variation in Bumblebees (Bombus Terrestris) (Hymenoptera: Apidae) After Three Decades of

an Island Invasion'. *Journal of Insect Science* 23 (1): 10. https://doi.org/10.1093/jisesa/iead006.

Kareiva, Peter, Sean Watts, Robert McDonald, and Tim Boucher. 2007. 'Domesticated Nature: Shaping Landscapes and Ecosystems for Human Welfare'. *Science* 316 (5833): 1866–69. https://doi.org/10.1126/science.1140170.

Kim, Jong-Yoon. 1997. 'Female Size and Fitness in the Leaf-Cutter Bee Megachile Apicalis'. *Ecological Entomology* 22 (3): 275–82. https://doi.org/10.1046/j.1365-2311.1997.00062.x.

King, Marcus J. 1993. 'Buzz Foraging Mechanism of Bumble Bees'. *Journal of Apicultural Research* 32 (1): 41–49. https://doi.org/10.1080/00218839.1993.11101286.

Klein, Alexandra-Maria, Bernard E. Vaissière, James H. Cane, Ingolf Steffan-Dewenter, Saul A. Cunningham, Claire Kremen, and Teja Tscharntke. 2007. 'Importance of Pollinators in Changing Landscapes for World Crops'. *Proceedings of the Royal Society of London B: Biological Sciences* 274 (1608): 303–13. https://doi.org/10.1098/rspb.2006.3721.

Kondo, Natsuko Ito, Daisei Yamanaka, Yuya Kanbe, Yoko Kawate Kunitake, Masahiro Yoneda, Koji Tsuchida, and Koichi Goka. 2009. 'Reproductive Disturbance of Japanese Bumblebees by the Introduced European Bumblebee Bombus Terrestris'. *Naturwissenschaften* 96 (4): 467–75. https://doi.org/10.1007/s00114-008-0495-4.

Lautenbach, Sven, Ralf Seppelt, Juliane Liebscher, and Carsten F. Dormann. 2012. 'Spatial and Temporal Trends of Global Pollination Benefit'. *PLOS ONE* 7 (4): e35954. https://doi.org/10.1371/journal.pone.0035954.

Lázaro, Amparo, Andreas Müller, Andreas W. Ebmer, Holger H. Dathe, Erwin Scheuchl, Maximilian Schwarz, Stephan Risch, et al. 2021. 'Impacts of Beekeeping on Wild Bee Diversity and Pollination Networks in the Aegean Archipelago'. *Ecography* 44 (9): 1353–65. https://doi.org/10.1111/ecog.05553.

Leadbeater, Ellouise, and Lars Chittka. 2008. 'Social Transmission of Nectar-Robbing Behaviour in Bumble-Bees'. *Proceedings of the Royal Society B: Biological Sciences* 275 (1643): 1669–74. https://doi.org/10.1098/rspb.2008.0270.

Lhomme, Patrick, and Heather M Hines. 2019. 'Ecology and Evolution of Cuckoo Bumble Bees'. *Annals of the Entomological Society of America* 112 (3): 122–40. https://doi.org/10.1093/aesa/say031.

Mahr, Susan. 2016. 'Know Your Friends. Hover Flies'. 4 June 2016. https://web.archive.org/web/20160604163106/http://www.entomology.wisc.edu/mbcn/kyf211.html.

Michael Begon, Robert W. Howarth, and Colin R. Townsend. 2014. *Essentials of Ecology, 4th Edition | Wiley*. 4th ed. Blackwell Pub. https://www.wiley.com/en-us/Essentials+of+Ecology%2C+4th+Edition-p-9780470909133.

Mizutani, Tomoo, and Koichi Goka. 2010. 'Japan's *Invasive Alien Species Act*'. *Applied Entomology and Zoology* 45 (1): 65–69. https://doi.org/10.1303/aez.2010.65.

Morales, Carolina L, Marina P Arbetman, Sydney A Cameron, and Marcelo A Aizen. 2013. 'Rapid Ecological Replacement of a Native Bumble Bee by Invasive Species'. *Frontiers in Ecology and the Environment* 11 (10): 529–34. https://doi.org/10.1890/120321.

Morgan, Tan, Penelope Whitehorn, Gillian C. Lye, and Mario Vallejo-Marín. 2016. 'Floral Sonication Is an Innate Behaviour in Bumblebees That Can Be Fine-Tuned with Experience in Manipulating Flowers'. *Journal of Insect Behavior* 29: 233–41. https://doi.org/10.1007/s10905-016-9553-5.

Moritz, Robin F. A., Stephan Härtel, and Peter Neumann. 2005. 'Global Invasions of the Western Honeybee (Apis Mellifera) and the Consequences for Biodiversity'. *Écoscience* 12 (3): 289–301. https://doi.org/10.2980/i1195-6860-12-3-289.1.

Morse, Roger A., and Nicholas W. Calderone. 2000. 'The Value of Honey Bees As Pollinators of U.S. Crops'. In *NSF Proposal*. https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.472.4894&rep=rep1&type=pdf.

Nagamitsu, Teruyoshi, and Tamiji Inoue. 1997. 'Aggressive Foraging of Social Bees as a Mechanism of Floral Resource Partitioning in an Asian Tropical Rainforest'. *Oecologia* 110 (3): 432–39.

Ngor, Lyna, Evan C. Palmer-Young, Rodrigo Burciaga Nevarez, Kaleigh A. Russell, Laura Leger, Sara June Giacomini, Mario S. Pinilla-Gallego, Rebecca E. Irwin, and Quinn S. McFrederick. 2020. 'Cross-Infectivity of Honey and Bumble Bee-Associated Parasites across Three Bee Families'. *Parasitology* 147 (12): 1290–1304. https://doi.org/10.1017/S0031182020001018.

Ogilvie, Jane E, and Jessica RK Forrest. 2017. 'Interactions between Bee Foraging and Floral Resource Phenology Shape Bee Populations and Communities'. *Current Opinion in Insect Science*, Pests and resistance * Behavioural ecology, 21 (June): 75–82. https://doi.org/10.1016/j.cois.2017.05.015.

Ollerton, Jeff. 2017. 'Pollinator Diversity: Distribution, Ecological Function, and Conservation'. *Annual Review of Ecology, Evolution and Systematics* 48 (November). https://doi.org/10.1146/annurev-ecolsys-110316-022919.

Ollerton, Jeff. 2021. *Pollinators & Pollination: Nature and Society*.

Ornduff, Robert and Darwin. 1984. 'Darwin's Botany'. *Taxon* 33 (1): 39–47. https://doi.org/10.2307/1222027.

Otterstatter, Michael C., and James D. Thomson. 2008. 'Does Pathogen Spillover from Commercially Reared Bumble Bees Threaten Wild Pollinators?' *PLOS ONE* 3 (7): e2771. https://doi.org/10.1371/journal.pone.0002771.

Padyšáková, Eliška, Jan Okrouhlík, Mark Brown, Michael Bartoš, and Štěpán Janeček. 2017. 'Asymmetric Competition for Nectar between a Large Nectar Thief and a Small Pollinator: An Energetic Point of View'. *Oecologia* 183 (4): 1111–20. https://doi.org/10.1007/s00442-017-3817-4.

Pirk, Christian W. W., Robin M. Crewe, and Robin F. A. Moritz. 2017. 'Risks and Benefits of the Biological Interface between Managed and Wild Bee Pollinators'. *Functional Ecology* 31 (1): 47–55. https://doi.org/10.1111/1365-2435.12768.

Pirk, Christian W. W., Catherine L. Sole, and R. M. Crewe. 2011. 'Pheromones'. In *Honeybees of Asia*, edited by H. Randall Hepburn and Sarah E. Radloff, 207–14. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-16422-4_9.

Plath, O. E. 1922. 'Notes on the Nesting Habits of Several North American Bumblebees'. *Psyche: A Journal of Entomology* 29 (5–6): 189–202. https://doi.org/10.1155/1922/34572.

Plath, O. E.. 1925. 'The Role of Bumblebees in the Pollination of Certain Cultivated Plants'. *The American Naturalist* 59 (664): 441–51. https://doi.org/10.1086/280057.

Proesmans, Willem, Matthias Albrecht, Anna Gajda, Peter Neumann, Robert J. Paxton, Maryline Pioz, Christine Polzin, et al. 2021. 'Pathways for Novel Epidemiology: Plant–Pollinator–Pathogen Networks and Global Change'. *Trends in Ecology & Evolution* 36 (7): 623–36. https://doi.org/10.1016/j.tree.2021.03.006.

Prŷs-Jones, Oliver E., Paul H. Williams, and James C. Carolan. 2018. 'Bumblebees of the Azores (Apidae: Bombus)'. *Journal of Natural History* 52 (5–6): 345–49. https://doi.org/10.1080/00222933.2018.1432776.

Pyke, Graham H. 1982. 'Local Geographic Distributions of Bumblebees Near Crested Butte, Colorado: Competition and Community Structure'. *Ecology* 63 (2): 555–73. https://doi.org/10.2307/1938970.

Ranta, Esa. 1984. 'Proboscis Length and the Coexistence of Bumblebee Species'. *Oikos* 43 (2): 189–96. https://doi.org/10.2307/3544768.

Ranta, Esa, and Hans Lundberg. 1980. 'Resource Partitioning in Bumblebees: The Significance of Differences in Proboscis Length'. *Oikos* 35 (3): 298–302. https://doi.org/10.2307/3544643.

Rao, Sujaya, William P. Stephen, Chiho Kimoto, and Sandra J. DeBano. 2011. 'The Status of the "Red-Listed" Bombus Occidentalis (Hymenoptera: Apiformes) in Northeastern Oregon'. *Northwest Science* 85 (1): 64–67. https://doi.org/10.3955/046.085.0106.

Redhead, John W., Stephanie Dreier, Andrew FG Bourke, Matthew S. Heard, William C. Jordan, Seirian Sumner, Jinliang Wang, and Claire Carvell. 2016. 'Effects of Habitat Composition and Landscape Structure on Worker Foraging Distances of Five Bumble Bee Species'. *Ecological Applications* 26 (3): 726–39.

Reverté, Sara, Jordi Bosch, Xavier Arnan, Tomas Roslin, Constantí Stefanescu, Juan Antonio Calleja, Roberto Molowny-Horas, Carlos Hernández-Castellano, and Anselm Rodrigo. 2019. 'Spatial Variability in a Plant–Pollinator Community across a Continuous Habitat: High Heterogeneity in the Face of Apparent Uniformity'. *Ecography* 42 (9): 1558–68. https://doi.org/10.1111/ecog.04498.

Reyes-Rosas, Marco Antonio, Jesús Loera-Gallardo, José Isabel Lopez-Arroyo, and Matthias Buck. 2013. 'Brachygastra Mellifica (Hymenoptera: Vespidae): Feeding Behavior and Preferential Predation on Diaphorina Citri (Hempitera: Liviidae) Life Stages in México'. *Florida Entomologist* 96 (4): 1588–94. https://doi.org/10.1653/024.096.0443.

Richardson, S. C. 1995. *Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico : September 19-23, 1994, Tucson, Arizona*. The Station.

Roubik, David W. 1982. 'The Ecological Impact of Nectar-Robbing Bees and Pollinating Hummingbirds on a Tropical Shrub'. *Ecology* 63 (2): 354–60. https://doi.org/10.2307/1938953.

Rúa, Pilar De la, Rodolfo Jaffé, Raffaele Dall'Olio, Irene Muñoz, and José Serrano. 2009. 'Biodiversity, Conservation and Current Threats to European Honeybees'. *Apidologie* 40 (3): 263–84. https://doi.org/10.1051/apido/2009027.

Ruz, L., and R. Herrera. 2001. 'Preliminary Observations on Foraging Activities of Bombus Dahlbomii and Bombus Terrestris (Hym: Apidae) on Native and Non-Native Vegetation in Chile'. *Acta Horticulturae*, no. 561 (November): 165–69. https://doi.org/10.17660/ActaHortic.2001.561.24.

Schmid-Hempel, P., R. Schmid-Hempel, P. C. Brunner, O. D. Seeman, and G. R. Allen. 2007. 'Invasion Success of the Bumblebee, *Bombus Terrestris*, despite a Drastic Genetic Bottleneck'. *Heredity* 99 (4): 414–22. https://doi.org/10.1038/sj.hdy.6801017.

Seabra, Sofia G., Sara E. Silva, Vera L. Nunes, Vitor C. Sousa, Joana Martins, Eduardo Marabuto, Ana SB Rodrigues, Francisco Pina-Martins, Telma G. Laurentino, and Maria Teresa Rebelo. 2019. 'Genomic Signatures of Introgression between Commercial and Native Bumblebees, Bombus Terrestris, in Western Iberian Peninsula—Implications for Conservation and Trade Regulation'. *Evolutionary Applications* 12 (4): 679–91.

Semmens, T. D., E. Turner, and R. Buttermore. 1993. 'Bombus Terrestris (L.) (Hymenoptera: Apidae) Now Established in Tasmania.' *Journal of the Australian Entomological Society* 32 (4). https://www.cabdirect.org/cabdirect/abstract/19950501112.

Silva, Marjorie da, and Fernando Barbosa Noll. 2015. 'Biogeography of the Social Wasp Genus Brachygastra (Hymenoptera: Vespidade: Polistinae)'. *Journal of Biogeography* 42 (5): 833–42. https://doi.org/10.1111/jbi.12417.

Smith, Deborah R., and Robert H. Hagen. 1996. 'The Biogeography of Apis Cerana as Revealed by Mitochondrial DNA Sequence Data'. *Journal of the Kansas Entomological Society* 69 (4): 294–310.

Stelzer, Ralph J., Lars Chittka, Marc Carlton, and Thomas C. Ings. 2010. 'Winter Active Bumblebees (Bombus Terrestris) Achieve High Foraging Rates in Urban Britain'. *PLOS ONE* 5 (3): e9559. https://doi.org/10.1371/journal.pone.0009559.

Stout, Jane C, John A Allen, and Dave Goulson. 2000. 'Nectar Robbing, Forager Efficiency and Seed Set: Bumblebees Foraging on the Self Incompatible Plant Linaria Vulgaris (Scrophulariaceae)'. *Acta Oecologica* 21 (4): 277–83. https://doi.org/10.1016/S1146-609X(00)01085-7.

Stout, Jane C, and Dave Goulson. 2000. 'Bumble Bees in Tasmania: Their Distribution and Potential Impact on Australian Flora and Fauna'. *Bee World* 81 (2): 80–86. https://doi.org/10.1080/0005772X.2000.11099475.

Strange, James P. 2015. 'Bombus Huntii , Bombus Impatiens , and Bombus Vosnesenskii (Hymenoptera: Apidae) Pollinate Greenhouse-Grown Tomatoes in Western North America'. *Journal of Economic Entomology* 108 (3): 873–79. https://doi.org/10.1093/jee/tov078.

Thomson, Diane. 2004. 'Competitive Interactions Between the Invasive European Honey Bee and Native Bumble Bees'. *Ecology* 85 (2): 458–70. https://doi.org/10.1890/02-0626.

Thomson, Diane M, and Maureen L Page. 2020. 'The Importance of Competition between Insect Pollinators in the Anthropocene'. *Current Opinion in Insect Science*, Ecology • Parasites/Parasitoids/Biological control, 38 (April): 55–62. https://doi.org/10.1016/j.cois.2019.11.001.

Timberlake, Thomas P., Ian P. Vaughan, and Jane Memmott. 2019. 'Phenology of Farmland Floral Resources Reveals Seasonal Gaps in Nectar Availability for Bumblebees'. *Journal of Applied Ecology* 56 (7): 1585–96. https://doi.org/10.1111/1365-2664.13403.

Torretta, Juan P., Diego Medan, and Alberto H. Abrahamovich. 2006. 'First Record of the Invasive Bumblebee Bombus Terrestris (L.) (Hymenoptera, Apidae) in Argentina'. *Transactions of the American Entomological Society* 132 (3): 285–89. https://doi.org/10.3157/0002-8320(2006)132[285:FROTIB]2.0.CO;2.

Vallejo-Marín, Mario. 2019. 'Buzz Pollination: Studying Bee Vibrations on Flowers'. *New Phytologist* 224 (3): 1068–74. https://doi.org/10.1111/nph.15666.

Velthius, Hayo H. W, and Adriaan Van Doorn. 2006. 'A Century of Advances in Bumblebee Domestication and the Economic and Environmental Aspects of Its Commercialization for Pollination'. *A Century of Advances in Bumblebee Domestication and the Economic and Environmental Aspects of Its Commercialization for Pollination* 37 (4): 421–51.

Washitani. 1998. 'Conservation-Ecological Issues of the Recent Invasion of Bombus Terrestris into Japan'. *Jpn J Ecol* 48: 73–78.

Whitehorn, Penelope R, Matthew C Tinsley, Mark J F Brown, and Dave Goulson. 2013. 'Investigating the Impact of Deploying Commercial Bombus Terrestris for Crop Pollination on Pathogen Dynamics in Wild Bumble Bees'. *Journal of Apicultural Research* 52 (3): 149–57. https://doi.org/10.3896/IBRA.1.52.3.06.

Whittington, R., M. L. Winston, C. Tucker, and A. L. Parachnowitsch. 2004. 'Plant-Species Identity of Pollen Collected by Bumblebees Placed in Greenhouses for Tomato Pollination'. *Canadian Journal of Plant Science* 84 (2): 599–602. https://doi.org/10.4141/P02-192.

Wignall, Veronica R., Matthew Brolly, Cassandra Uthoff, Kala E. Norton, Hannah M. Chipperfield, Nicholas J. Balfour, and Francis L. W. Ratnieks. 2020. 'Exploitative Competition and Displacement Mediated by Eusocial Bees: Experimental Evidence in a Wild Pollinator Community'. *Behavioral Ecology and Sociobiology* 74 (12): 152. https://doi.org/10.1007/s00265-020-02924-y.

Wignall, Veronica R., Isabella Campbell Harry, Natasha L. Davies, Stephen D. Kenny, Jack K. McMinn, and Francis L. W. Ratnieks. 2020. 'Seasonal Variation in Exploitative Competition between Honeybees and Bumblebees'. *Oecologia* 192 (2): 351–61. https://doi.org/10.1007/s00442-019-04576-w.

Willmer, P., Ali Bataw, and J. Hughes. 2008. 'The Superiority of Bumblebees to Honeybees as Pollinators: Insect Visits to Raspberry Flowers'. *Ecological Entomology* 19 (March): 271–84. https://doi.org/10.1111/j.1365-2311.1994.tb00419.x.

Wilms, W., and B. Wiechers. 1997. 'Floral Resource Partitioning between Native Melipona Bees and the Introduced Africanized Honey Bee in the Brazilian Atlantic Rain Forest'. *Apidologie* 28 (6): 339–55. https://doi.org/10.1051/apido:19970602.

Wojcik, Victoria A, Lora A Morandin, Laurie Davies Adams, and Kelly E Rourke. 2018. 'Floral Resource Competition Between Honey Bees and Wild Bees: Is There Clear Evidence and Can We Guide Management and Conservation?' *Environmental Entomology* 47 (4): 822–33. https://doi.org/10.1093/ee/nvy077.

Yoon, Hyung-Joo, Seong-Yeol Kim, Kyeong-Yong Lee, Sang-Beom Lee, In-Gyun Park, and Ik-Soo Kim. 2009. 'Interspecific Hybridization of the Bumblebees Bombus Ignitus and B. Terrestris'. *International Journal of Industrial Entomology* 18 (1): 41–48.

Zimmerman, Michael, and John M. Pleasants. 1982. 'Competition among Pollinators: Quantification of Available Resources'. *Oikos* 38 (3): 381–83. https://doi.org/10.2307/3544681.