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Assessing the impact of alien bees on native ones

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1 Introduction

A species introduced outside of its native range, voluntarily or not, is defined as an alien species (Blackburn et al., 2011). These alien species may become invasive if their establishment and spread negatively affect biodiversity, ecosystem functioning, and/or the economy (Diagne et al., 2021). Biological invasions are among the most important threats to biodiversity worldwide (Kumschick et al., 2015). Frequently pointed out as the second cause of species extinction (Bellard et al., 2016a), the magnitude of negative effects of invasive alien species on biodiversity is nevertheless still regularly debated in the literature (Courchamp et al., 2017). With the exponential rise in global trade, the number of alien species has increased in the past few years (Bellard et al., 2016b), and projections forecast a continuous growth in the number of introductions in the following 30 years (Seebens et al., 2017, 2020).

Among alien species, insects have been less studied (Kenis et al., 2009) despite the importance of their reported negative effects on biodiversity components, especially the ones exerted by social insects such as termites or ants (Bertelsmeier, 2021). Notably, this is the case for bees, be they social or solitary, managed or wild (Russo, 2016; Geslin et al., 2017; Russo et al., 2021). Indeed, bees are generally well-perceived by the public (Sumner et al., 2018), mostly because of their important role in the reproduction of wild (Ollerton et al., 2011) and cultivated plants (Klein et al., 2007; Gill et al., 2016). Therefore, because of this beneficial role, little attention is paid when an alien bee species enters a new ecosystem.

However, to date, Russo (2016) recorded 80 bee species introduced out of their native range (Fig. 1). Among these, *Apis mellifera* (L.) and *Bombus terrestris* (L.) are the

two species that have been the focus of attention (Geslin et al., 2017; Mallinger et al., 2017; Goulson, 2003). These two social and domesticated species have mostly been introduced either to produce honey (for *Apis mellifera*) or to improve pollination services to crops (Aizen et al., 2020), sometimes doing more harm than good (Aizen et al., 2014, 2019; Sáez et al., 2014). Of course, not all 80 alien species described by Russo (2016) have become invasive, but the literature report many examples of deleterious consequences of the introduction of bees outside their native range (Aizen et al., 2019, 2020; Geslin et al., 2017; Mallinger et al., 2017; Traveset and Richardson, 2014; Goulson, 2003).

Hence, alien bees can directly or indirectly affect native ecosystems and therefore become invasive (Dafni et al., 2010; Russo et al., 2021, Fig. 2). They can compete with native bees for the acquisition of food resources (nectar and pollen) or nesting sites potentially affecting local populations (Geslin et al., 2020; Hung et al., 2019; Ollerton, 2017; Schaffer et al., 1983). Alien bees can transport parasites and diseases, which can, in turn, affect native populations

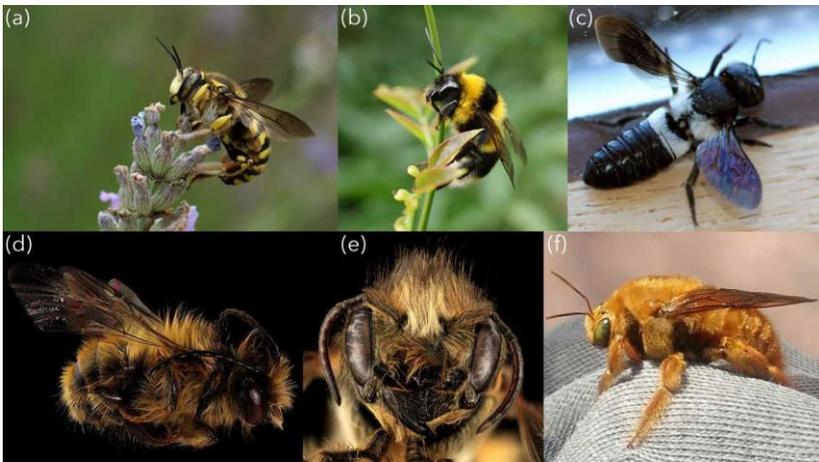


Figure 1 A sample of bee species introduced outside of their native range. (a) *Anthidium manicatum* (Linnaeus, 1758); Frank Vassen/Flickr/CC BY 2.0. (b) *Bombus ruderatus* (Fabricius, 1775); Dave Young/Flickr/CC BY 2.0. (c) *Megachile disjunctiformis* (Cockerell, 1911) (Franziska Maria Luthi). (d) *Osmia taurus* (Smith, 1873) Benjamin Smith/Wikimedia Commons/CC BY 2.0. (e) *Osmia cornifrons* (Radoszkowski, 1887) Flickr/CC 1.0. (f) *Xylocopa augusti* (Lepeletier, 1841) Clinton.sm/Wikimedia Commons/CC BY-SA 4.0.

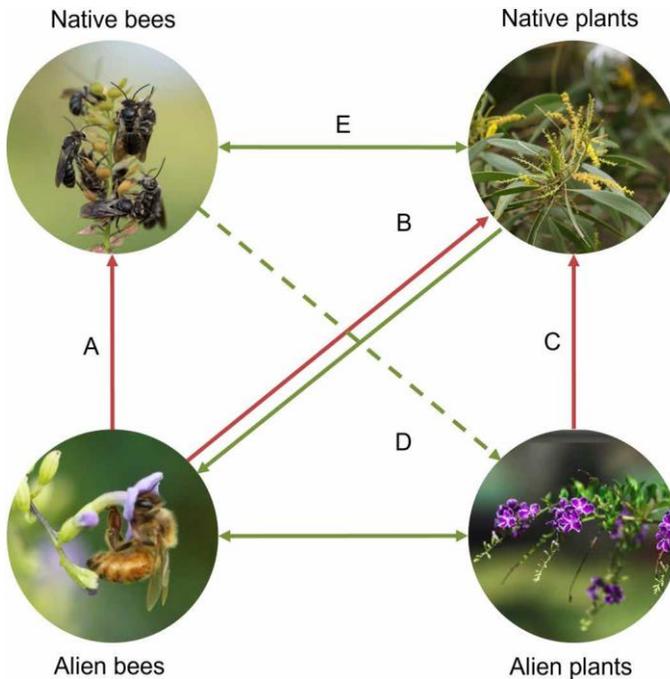


Figure 2 Positive and negative interactions (respectively green and red links) between alien and native species may disrupt native plant–pollinator systems. First, alien bees may compete for floral resources and/or nesting sites, spread parasites and pathogens and hybridize with native bees (A). Then, alien bees may also not be efficient pollinators of some native plants (e.g. due to morphological mismatch) and could thus alter their reproductive success (B). Second, alien plants may compete with native ones for soil resources (C) and corner all or part of their pollinators (D). Finally, it seems that alien plants tend to promote the presence of alien bees and in some cases alien bees visit preferentially those plant species. Thus, alien species may promote the establishment and spread of each other, potentially leading to invasional meltdowns (E). All these interactions may lead to a local decrease of abundance and richness of native species.

(Aizen et al., 2020; Goulson et al., 2015; Graystock et al., 2013). Alien bees can also disrupt plant–pollinator networks by robbing flowers, therefore decreasing their reproductive success (Dafni et al., 2010; Dohzono et al., 2008), modifying the amount or the nature of the pollen deposited (Agüero et al., 2020), or by reinforcing the pollination of particular plant species (Sanguinetti and Singer, 2014). In some cases, alien bees can even interact preferentially with alien or invasive plants, potentially enhancing their spread and negative impacts, a phenomenon called invasional meltdown (Zakardjian et al., 2020; Traveset and Richardson, 2014; Beavon and Kelly, 2012).

Despite these reported effects, the impacts of alien bees on native ecosystems are little considered on a global scale. For example, despite the devastating consequences of multiple introductions of *Bombus terrestris* worldwide (e.g. Acosta et al., 2016), the commercial trade of *Bombus* species outside of their native range

continues (Aizen et al., 2019) to the point that the international trade of bees, mostly bumblebees, is nowadays an important conservation issue for global biodiversity (Sutherland et al., 2016). Therefore, it is important and timely to assess the impact of alien bees on native pollinators.

This chapter focuses on the direct and indirect impacts of alien bees on native pollinators. We will not explore the effect of alien bees on plant communities or plant–pollinator networks to focus solely on their effect on native bees. Also, because we focus on alien bees, we will not provide examples of competitive interactions between wild and domestic bees in the native range of domestic bees. In the second part, we will focus on a case study, the invasion of the alien bee *Megachile sculpturalis* in North America and Europe. We will then delineate some of the main shortcomings and directions for future studies and guide land managers to prevent future introductions.

2 Assessment of key issues related to the introduction of alien bees

2.1 Direct interactions: interference competition

Interference competition is a direct interaction, generally by aggressive contact, through which a resource that an individual should have used is made available by and for another individual (Case and Gilpin, 1974). Among alien bees, interference competition may be used to acquire food resources, nesting sites, or defend mating territories. Although rare, interference competitions between alien and native bees have been reported in other literature.

In Yucatan (Mexico), the Africanised honey bee (*Apis mellifera scutellata*) has aggressively displaced stingless bees from floral and water resources. In this region, some native stingless bees appear to have declined from anthropogenic pressures. Interference competition by honey bees could have compound effects on the most vulnerable native species (Cairns et al., 2005). In Indiana (US), honey bees have also been observed to steal pollen loads directly from the body parts of several native bees such as *Bombus impatiens*, *Megachile montivaga*, and *Melissodes desponsa* (Jean, 2005). As not all pollen loads were removed and those events remain rare, this kind of physical interaction is unlikely to severely impact native bees' fitness.

Anthidium manicatum, the most widespread unmanaged alien bee species worldwide (Strange et al., 2011), uses interference competition to defend floral territories and thus assuring mating opportunities (Starks and Reeve, 1999; Severinghaus et al., 1981). In New Zealand, *Anthidium manicatum* aggressively interferes with native *Lasioglossum* spp. (Soper and Beggs, 2013). However, in this study, native bees were less contacted than conspecific individuals and two other alien species, *Apis mellifera* and *Bombus* spp. Native *Lasioglossum* spp. shared fewer floral resources than *Apis mellifera* and *Bombus* spp. with *Anthidium manicatum*, thus reducing the probability of interference events (Case and Gilpin, 1974).

Although the impact of these interactions was not tested, the authors concluded that *Anthidium manicatum* posed a minor threat to the native bee fauna of New Zealand.

In North America, *Megachile* spp. in an urban area experienced reduced visitation frequencies in the presence of *Anthidium manicatum* (Taggar et al., 2021). Unfortunately, in this study, alien and native *Megachile* spp. were not discriminated, and it was therefore complicated to state whether this decrease was due to interference or exploitative competition. A native bee, *Bombus impatiens*, was shown to avoid floral enclosures where *Anthidium manicatum* was present. Even if the authors did not discriminate between interference and exploitative competition to explain their results, no effect was shown on the colony fitness of the native bumblebee (Graham et al., 2019).

In Europe and North America, several events of aggressive behaviour have been documented for *Megachile sculpturalis*. This species is likely to interfere with native species with similar nesting habits (see the case study below).

Physical interaction events appear to be uncommon between alien and native bees. Thus, interference competition is unlikely to have a deleterious impact on native bee populations. However, such behaviours could increase the potential of a species to become established or spread if coupled with other characteristics such as a high capability of exploitative competition for floral resources and nesting sites.

2.2 Exploitative competition

Alien bees may overlap with native bees in floral resource use (Fig. 3) and/ or nesting sites. Exploitative competition occurs when shared resources are limiting and implies negative impacts on the fitness of native bees.

2.2.1 Exploitative competition for floral resources

Managed eusocial bees, such as *Apis mellifera* and *Bombus terrestris*, have a strong competitive potential over native wild bees. Indeed, the number of workers per managed colony compared to solitary bees and the regular renewal of populations by beekeepers (when needed) make them prone to exploit efficiently floral resources with potential impacts on native bees. Their impacts on native and invaded areas have already been reviewed by several authors (e.g. Aizen et al., 2020; Geslin et al., 2017; Mallinger et al., 2017; Osterman et al., 2021; Russo et al., 2021; Vanbergen et al., 2018), but we present here some examples of exploitative competition.



Figure 3 A honey bee and a bumblebee sharing the same floral resource (CC 1.0).

A 2-year experiment conducted in Western Australia showed that the monolectic resource used by a native bee, *Hylaeus alcyoneus*, was also used by honey bees for pollen and nectar provision. This resource overlap appears to explain the decrease in native bee fecundity (measured as the number of nests constructed) in sites with increasing honey bee density (Paini and Roberts, 2005). In this case, the monolectic behaviour of the native bee likely made it more vulnerable to exploitative competition exerted by honey bees. Another negative impact of honey bees on native bees was demonstrated in Tenerife (Canary Islands), where the number of pollinator species and that of visits by some native bees were lower after the setup of beehives (Valido et al., 2019). In this case, exploitative competition from honey bees had a negative impact on the richness and abundance of generalist native bees, with implications for pollination ecosystem services and plant reproductive success.

Conversely, some studies did not find any evidence of a detrimental effect of the exploitative competition exerted by alien honey bees on native bees. For example, the experimental increase in honey bees in a Patagonian Forest ecosystem did not affect the number of visits made by native pollinators but rather induced exploitative competition with two other invasive alien species (i.e. *Bombus ruderatus* and *Bombus terrestris*; Agüero et al., 2020). However, in this study, native pollinators were studied as a group, and contrasting responses between pollinator species may not have been highlighted. In an urban ecosystem in Montreal (Canada), an increase in honey bee capture rate did not affect the abundance of wild bees (McCune et al., 2019). The authors expected a negative effect and hypothesised that the abundance of floral resources and the very low density of beehives compared with other cities (e.g. see Ropars et al., 2019) mitigated competition. In addition, in the

Ogasawara islands (Japan), *Apis mellifera* appears to have a competitive advantage over native bees (Kato et al., 1999), but the decline of native pollinators is mostly due to an invasive predator (Abe et al., 2008). Finally, in Ontario (Canada), within an agroecosystem (*Cucurbita spp.*), Willis Chan and Raine (2021) found no negative impact of the alien bee *Apis mellifera* on the wild oligolectic hoary squash bees (*Eucera Peponapis pruinosa*) foraging on *Cucurbita spp.*, likely because of an intra-day phenological difference in bees' activities (honey bees were foraging later than hoary squash bees).

Another managed eusocial bee, *Bombus terrestris*, has been massively introduced worldwide and is known to have caused disastrous impacts on native bee populations (see below, e.g. Acosta et al., 2016; Aizen et al., 2008, 2014, 2019; Morales and Aizen, 2006; Morales et al., 2013). In Japan, *Bombus terrestris* may be an efficient competitor for floral resources over some native bumblebees. For example, an experiment demonstrated that *Bombus terrestris* harvested more pollen per unit time and per unit body mass than the native *Bombus ignitus* (Inoue et al., 2010). However, the evidence of exploitative competition effects on native bees is unclear. Indeed, an experiment failed to detect a negative impact of *Bombus terrestris* on two native Japanese bumblebees (*Bombus ardens* and *Bombus hypocrita*; Nagamitsu et al., 2007a). Nevertheless, field removal of *Bombus terrestris* queens from an urban area led to an increased number of these two native bumblebee queens among five native bee species captured in the study area (Nagamitsu et al., 2009). *Bombus ardens* and *B. hypocrita* are likely to overlap for floral resource use with *Bombus terrestris* due to their tongue length (Nagamitsu et al., 2007). Thus, although the effect of competition for nesting sites could not be discriminated, the release of exploitative competition for floral resources was a major hypothesis to explain these results. Corroborating this hypothesis, *Bombus terrestris* may be responsible for the increase in robbed flowers of a native plant (*Corydalis ambigua*) and the subsequent decrease in visitation by *B. ardens* (Dohzono et al., 2008).

However, in an alpine-montane ecosystem in New Zealand, alien bees mostly composed of *Bombus terrestris* did not overlap with native bees for floral resource use (Iwasaki et al., 2018). Indeed, *Bombus terrestris* preferentially visited alien plants when native bees were mostly observed on native ones, suggesting a low potential for exploitative competition for floral resources. In addition, 3-years monitoring conducted in Japan did not show any evidence of an impact of shared plant resources between *Bombus terrestris* and the native species *B. pseudobaicalensis* (Inoue et al., 2008).

Notably, the introduction and invasion of *B. terrestris* and *B. ruderatus* in South America had notorious negative impacts on native ecosystems, including

the decline and local extinction of *B. dahlbomii*, a Patagonian native bumblebee (Aizen et al., 2019; Geslin and Morales, 2015; Morales et al., 2013; Morales, 2007). In particular, *B. ruderatus* overlaps with *B. dahlbomii* for floral resources (Aizen et al., 2008; Morales and Aizen, 2006). However, Aizen et al. (2011) found no evidence of exploitative competition for floral resources between these two species, and the spread of pathogens is a favoured hypothesis to explain the decline of *B. dahlbomii* (see Section 2.3).

When first recorded in a new environment, alien solitary bees generally raise concerns about potential negative impacts on native species. Unfortunately, for most of these species, field studies following their detection rarely test for their effect on the fitness of native bee populations. However, a recent study analysing historical pan trap records in the US showed that the arrival of two alien bees, *Osmia cornifrons*, and especially *Osmia taurus*, was followed by a decline in six native *Osmia* spp. (LeCroy et al., 2020). Several factors have been hypothesised to explain this result, including exploitative competition, either for floral resources or nesting sites. Another study conducted in the US showed that urban sites with a high density of alien bees were associated with a lower abundance of native bees (Fitch et al., 2019). Once again, exploitative competition for floral resources, nesting sites, or spillover of pathogens were all hypothesised to explain these observations.

The effects of wild alien bees on native bees are also context-dependent. A study conducted in an insular system in the Southwest Pacific showed that the presence of alien bees did not affect the number of visits realised by native ones (Zakardjian et al., 2020). However, this result was explained by the generalist foraging behaviour of some insular native bees. In Brazil, a study conducted in an urban area found no impact from two alien bee species (*Apis mellifera* and *Anthidium manicatum*) on the structure of the native bee community (Graf et al., 2020), suggesting that no exploitative competition occurred. The authors proposed two hypotheses to explain this result. First, it is possible that these two alien bees, which were introduced a few decades ago, had an impact at the beginning of their establishment. Second, the urban environment may not be suitable for the species that are the most vulnerable to competition.

Most studies estimate niche overlap and the displacement of visits without measuring the impact of competition on native bee fitness. However, these metrics still reveal an effect of the competitive pressure exerted by alien bees on native ones. Mixed responses of native bees to exploitative competition by alien ones reveal that competitive pressure is context-dependent, varying according to the ecosystem (number of floral resources), the capacity of native bees to adapt their foraging preferences, and the characteristics of alien bees, such as their level of generalism and their reproductive success.

2.2.2 Exploitative competition for nesting sites

Bombus terrestris has the potential to compete with native bumblebees for nesting resources. In Japan, 3 years of monitoring studied the abundance of three native bumblebees, along with the abundance of *Bombus terrestris* queens. The results showed that a native species using the same nesting resources as *Bombus terrestris* declined with an increase in *Bombus terrestris* queens, suggesting exploitative competition for nesting sites between these two species (Inoue et al., 2008).

Concerning wild alien bees, *Megachile sculpturalis* has been reported to be a potential competitor for nesting resources (see above). In Marseille (France), near its first detection point, the presence of *Megachile sculpturalis* in bee hotels reduced the probability of occupation by native *Osmia* spp. (Geslin et al., 2020).

2.3 Apparent competition (pathogens spillover)

Parasites and pathogens may be transferred among bee species when infected individuals are abundant and share floral resources or nesting sites with other species. Thus, bees are ideal candidates for the transmission and dispersion of pathogens.

In New York State (US), the presence of the deformed wing virus (DWV; Fig. 4) in some native *Melandrena* spp. was linked to honey bee abundance (Murray et al., 2019). Even if there was no correlation with two other pathogens (black queen cell virus and sacbrood virus), these results indicate that honey bees may be a source of infection for solitary native bees, potentially increasing viral incidence for at least DWV. Still in North America, wild pollinators found close to beehives with honey bees infected with Israeli acute paralysis virus also presented this virus, contrary to wild pollinators captured close to healthy beehives (Singh et al., 2010). Similarly, Alger et al. (2019) found a strong prevalence of DWV in wild bumblebees foraging close to apiaries, whereas no DWV was found in bumblebees in the absence of honey bees.

In Argentina, *Apicystis bombi*, a parasite that especially infects bumblebees, was possibly co-introduced with *Bombus terrestris* or *B. ruderatus* (Arbetman et al., 2012; Plischuk et al., 2011) and is now also present in Colombia (Gamboa et al., 2015) and Patagonia (Arbetman et al., 2012). In Patagonia, it appears that the alien *B. ruderatus* and the native *B. dahlbomii* were free of this parasite before the invasion of *Bombus terrestris* (Arbetman et al., 2012). Thus, *A. bombi* likely arrived with and spilt over from *Bombus terrestris* to these two bumblebee species. The severe decline of *B. dahlbomii* is potentially linked to this parasite spillover (Arbetman et al., 2012).



Figure 4 Honey bee with deformed wing virus (DWV) and *Varroa destructor* (CC0 1.0).

2.4 Mating interference

In Korea, laboratory experiments demonstrated that interspecific hybridisation may happen between *Bombus terrestris* and two native bumblebees (*B. ignitus* and *B. hypocrita*). Males of the two native species mated with *Bombus terrestris* queens (Yoon et al., 2011, 2009). Thus, *Bombus terrestris* may interfere with native bumblebees for mating males, with potential negative impacts on native bees' fitness. In addition, during this experiment, *Bombus terrestris* males mated with native bumblebee queens, highlighting a risk of genetic contamination.

3 Case study: *Megachiles sculpturalis*

3.1 History of introduction and spread

Megachile (Callomegachile) sculpturalis Smith (Hymenoptera: Megachilidae) – (Msc) is a wild bee species native to Southeast Asia (Korea, China, Taiwan, Hong Kong, and Japan; Fig. 5). We chose this species as a case study because it was the first alien bee to enter the European continent in 2008 (Vereecken and Barbier, 2009), and its spread and impacts have been carefully followed since (Le Féon et al., 2018, 2021). Before arriving in Europe, however, Msc colonised the North American continent. The first mention of Msc outside of its native range dates from 1994 in North Carolina (US; Magnum and Brooks, 1997). Since then, the species has rapidly been detected in other US states, up



Figure 5 *Megachile sculpturalis* female. Le Collet-de-Dèze, France. Picture: Frank Vassen.

to Texas in 2011 (Parys et al., 2015; Hinojosa-Díaz, 2008). Besides the US, *Msc* has also expanded its range to Canada, especially in Ontario (Paiero and Buck, 2003).

In Europe, *Msc* was first detected in Allauch, a small city close to Marseille (France; Vereecken and Barbier, 2009). Between 2008 and 2021, *Msc* has remarkably extended its range in France, with a reported presence in 259 different cities, with the most northern location being approximately 800 km from Marseille, in the northeast of Paris (near Reims, Le Féon et al., 2021). *Msc* now occupies approximately half of France, from the Atlantic coast to the Alps (Le Féon et al., 2018, 2021; Le Féon and Geslin, 2018). Besides France, *Msc* has also spread to many European countries, starting with Italy in 2009 (Quaranta et al., 2014), Switzerland in 2010 (Amiet, 2012), Germany (Westrich et al. 2015), and Hungary in 2015 (Kovács, 2015), Slovenia in 2016 (Gogala and Zadravec, 2018), Austria (Westrich, 2017) and Serbia (Ćetković et al., 2020) in 2017, Spain (Ortiz-Sánchez et al., 2018) and Crimean peninsula (Ivanov and Fateryga, 2019) in 2018, Croatia (inaturalist.org) and Lichtenstein (Lanner et al., 2020a) in 2019, and finally in Bosnia-Herzegovina in 2020 (inaturalist.org; Fig. 6). *Megachile sculpturalis* is therefore now widespread in Europe and occupies several habitats from very urbanised ones such as Marseille, Lyon, or Vienna (Geslin et al., 2020; Lanner et al., 2020b; Fortel et al., 2016), to montane habitats (up to 1846 m above sea level; Le Féon and Geslin, 2018).

The spread of this species is remarkably fast even if similar dispersal rates have been reported for other invasive hymenopterans such as *Bombus terrestris* in South America (Schmid-Hempel et al., 2014) or *Vespa velutina* in Europe (Robinet et al., 2017). One of the hypotheses explaining this fast spread

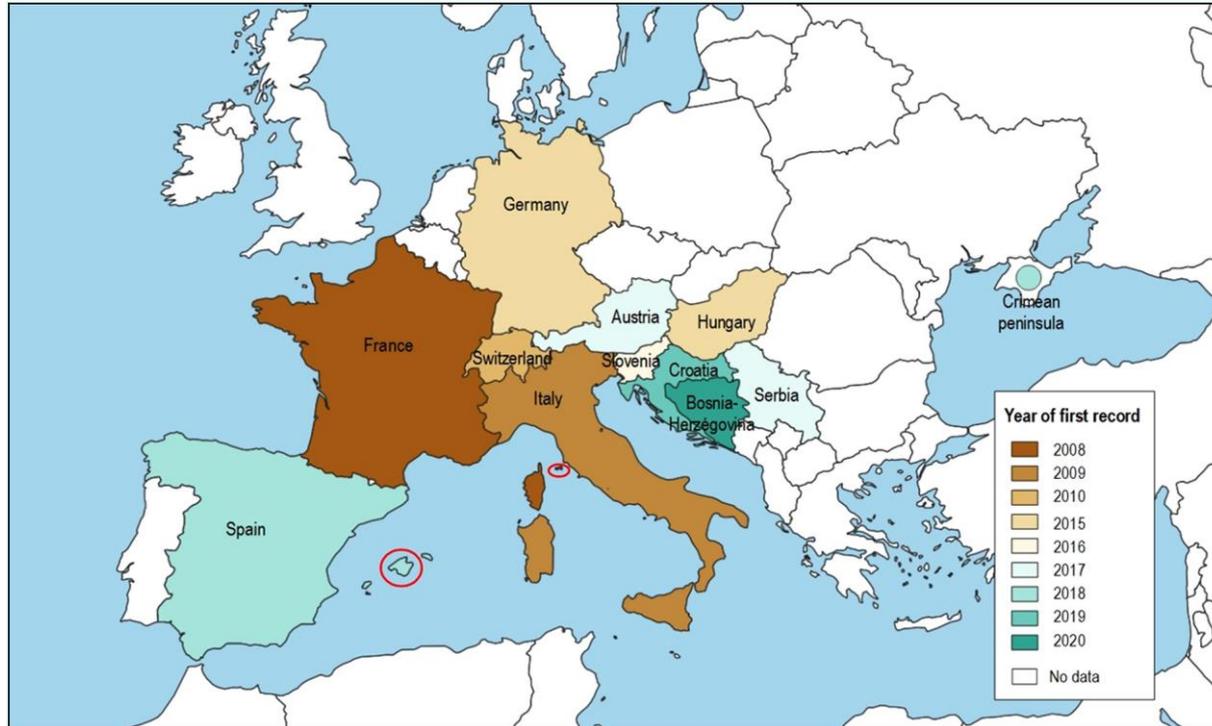


Figure 6: Year of the first record of *Megachile sculpturalis* in European countries (sources: Aguado et al., 2018; Amiet, 2012; Ćetković et al., 2020; Gogala and Zadavec, 2018; Ivanov and Fateryga, 2019; Kovács, 2015; Lanner et al., 2020b; Quaranta et al., 2014; Vereecken and Barbier, 2009; Westrich et al., 2015; Westrich, 2017). The homogeneous colouring of national territories can be misleading. For example, concerning the islands, *Msc* is so far unknown in Corsica, Sicily, and Sardinia. However, it has been recorded on the island of Elba and in Majorca, islands that we have circled in red. Map made with QGIS version 3.14. Base map downloaded from Natural Earth (naturalearthdata.com).

lies in the nesting preferences of *Msc* (in deadwood and cavities, see below), and *Msc* may have benefited from the timber trade through human-mediated transportation (e.g. Le Féon et al., 2018). Using the species distribution model (Lanner et al., 2022) recently showed that the spread of *Msc* is largely explained by anthropogenic factors and particularly facilitated by roads and maritime traffic. Through genetic analysis, Lanner et al. (2021) have also emphasised that several introductions may have occurred in Europe, partly explaining the rapid geographical expansion of *Msc*.

3.2 The morphology and ecology of *Megachile sculpturalis*

One of the vernacular names of *Megachile sculpturalis* is the giant resin bee. This appellation comes from the nesting biology of *Msc*, which closes its nest and brood cells with resin mainly collected from coniferous trees. *Megachile sculpturalis* is a large bee species (male 14–19 mm; female 22–27 mm; Batra, 1998), with orange to brown hairs on the thorax and infuscated wings (Fig. 5). The head is dark, with large mandibles used by females to carry mud and resin to build their nests (Fig. 7). Females carry pollen for their larvae in their ventral scopa.

Bees forage on flowers to gather pollen and nectar. While nectar is useful as a direct energy source for both adults and larvae, pollen is the principal source of protein and is gathered mostly to feed the larvae. Bees can be



Figure 7 *Megachile sculpturalis* female closing its nest with tree resin. In the background two more of her nests can be seen. Oberhofen am Thunersee, Switzerland. Picture: Christa Rohrbach.

a generalist when seeking for nectar but can be more of a specialist when foraging for a particular pollen. *Megachile sculpturalis* is a generalist species when it comes to nectar, meaning that this species can visit many different plant families. For example, in France, *Msc* has been observed foraging on 20 different plant species from 8 families, including Asteraceae (i.e. *Cirsium arvense*), Caprifoliaceae (i.e. *Scabiosa columbaria*), and Lamiaceae (i.e. *Lavendula*) (Le Féon et al., 2018). However, for pollen, *Msc* appears to be more specialist with strong preferences for alien woody species also originating from Asia. In Europe, *Msc* is known for gathering pollen from alien tree species such as *Sophora japonica* (Fabaceae; Andrieu-Ponel et al., 2018) and collecting nectar from *Ligustrum lucidum* (native to Asia) and *Ligustrum vulgare* (native to Europe) (Oleaceae; Aguado et al., 2018).

Megachile sculpturalis nests in pre-existing cavities, mostly in deadwood, bamboo, or reeds. As stated earlier, *Msc* closes its nest entrances with resin, vegetal fibres, mud, and clay. Female *Msc* widely uses insect hotels (or bee hotels) to lay eggs, with much evidence in North America (MacIvor and Packer, 2015) and Europe (Díaz et al., 2021; Geslin et al., 2020; Le Féon et al., 2018; Fortel et al., 2016; Quaranta et al., 2014, Fig. 7). This propensity to nest in human-made structures may also be the reason for the rapid spread of *Msc* in Europe (Lanner et al., 2022).

3.3 Impacts on native bees

The first insight into the potential impacts of *Megachile sculpturalis* on native fauna was published in 2012 (Roulston and Malfi, 2012). The authors reported an aggressive eviction of a native carpenter bee (*Xylocopa virginica*) from its nest by *Msc* in Virginia (US). In the same year, Laport and Minckley (2012) reported the occupation of a nest of an active *X. virginica* by *Msc*. Both observations suggest potential nest competition between *Msc* and local fauna, together with aggressive territorial behaviours. Similar observations were obtained a few years ago in Europe, with (a) aggressive evictions, (b) occupation of nests, and (c) emptying of native bee nests, including *Osmia bicornis*, *O. cornuta*, and recently, *Anthidium septemspinosum* (Le Féon et al., 2018, 2021). In 2020, Geslin et al. conducted a study in urban parks of Marseille (France) to assess the impact of *Msc* on wild bees. They installed 96 bee hotels in 12 parks in the city and explored the relationship between the abundance of *Msc* and native bees emerging from bee hotels. First, they found that the most abundant bee nesting in bee hotels was *Msc*, with more than 40% of individuals. Second, they discovered a negative correlation between the presence of native bees and that of *Msc* within insect hotels, suggesting a negative impact of *Msc* on local native populations of wild bees. Two recent publications have provided new information on the impact of *Msc* on wild fauna. First, Lanner et al. (2020a) reported the killing of several *Heriades* spp. individuals, a French native species, by *Msc*, thereby documenting another direct impact of the alien bee species on native ones. Finally,

Díaz et al. (2021) documented the occupation by *Msc* of *Osmia cornuta* nests without entirely emptying the nests. This means that *Msc* females laid eggs close to the cavity entrance, blocking this entrance with mud and resin. *Osmia cornuta* is active in spring, unlike *Msc*, which is active during summer (from June to September in Europe). Emerging individuals of *O. cornuta* are therefore blocked by this resin, incapable of exiting the nest, and may ultimately die from starvation or exhaustion.

Taken together, these findings show that *Msc* could have a deleterious impact on local wild bee populations (Fig. 8). However, the magnitude of these impacts remains poorly understood. For now, it does not appear easy to determine whether *Msc* could profoundly modify the structure of local bee populations, for example, by causing local extinctions of some species. The extent to which *Msc* disrupts native pollinators remains to be carefully evaluated, and future research will help us explore this question.

3.4 Other impacts

To date, there has been no documentation of other potential impacts of *Msc* on ecosystems or human economy and infrastructures. As stated earlier, *Msc*



Figure 8 *Megachile sculpturalis* female emptying the nest of a female of *Anthidium* sp. Anglet, France. Picture: Pierre-Jean Vandoorne.

appears to preferentially forage for pollen from alien plant species, potentially helping their spread. However, there is currently no evidence for such an effect. In addition, Díaz et al. (2021) showed that *Msc* could be affected by common, widespread generalist macro parasites without a substantial effect on the emerging success of *Msc*. At this stage, it appears difficult to determine whether *Msc* could reinforce parasite populations which could in turn affect native wild bees, and this remains to be explored. Finally, to the best of our knowledge, there is no reported effect of *Msc* on human economy and infrastructures. *Msc* is an opportunistic species that nests in pre-existing cavities and does not dig holes in wood by itself, reducing its potential impact on infrastructure.

Regarding the economy, a single example has been reported in the literature regarding the potential positive impact of *Msc* on agriculture: the pollination of Sunn hemp (*Crotalaria juncea* L.: Fabaceae) in Florida (Hall and Avila, 2016). *Msc* has been associated with a higher seed set for this cover crop, which contributes to soil nitrogen enhancement (Hall and Avila, 2016). Nevertheless, it is worth noting that *C. juncea* is an alien plant in the US. Moreover, this species is classified as invasive in some Pacific islands (see Hall and Avila, 2016); therefore, it is difficult to classify the interaction between *Msc* and *C. juncea* as positive or negative.

4 Conclusion

In this chapter, we have presented an overview of the known impacts of alien bees on native ones. As emphasised in the introduction, we voluntarily excluded the other known impacts of alien bees on native ecosystems, such as the disruption of native plant–pollinator networks, the population enhancement of alien plants (invasional meltdown), or the impact on crop production (except for the case study, for a comprehensive review on this subject see Aizen et al., 2020). As shown here, the potential effects exerted by alien bees on native bees are important and could, in extreme cases, be responsible for dramatic population losses of native bees (the case of *Bombus dahlbomii* in South America; see above). To date, 80 bee species have been recorded outside their native ranges (Russo, 2016). The different cases we exposed in this chapter are among the most iconic, with the strongest recorded negative impacts. Overall, however, the global impact of alien bees on native bees and ecosystems is largely unknown. Very few cases of introductions have been carefully studied, and for some of the recorded alien bees, little is known regarding their impacts on native bees and ecosystems. The case of *Msc* is an exception, being one of the single invasions that is relatively well documented (as is the case of *Bombus terrestris* in South America, Japan, and Tasmania).

Hence, we need to amplify our efforts to document new introductions, the geographic spread of alien bees, and their impacts. The number of new introductions is not expected to drop in the coming years (Seebens et al., 2017), and we need to

anticipate the potentially dramatic consequences of these introductions to avoid them. For example, in 2018, Bortolotti et al. reported the presence of a second alien bee species in continental Europe, *Megachile disjunctiformis*. This species resembles *Msc* morphologically (Fig. 9) and has a similar native geographical repartition. To date, *M. disjunctiformis* has only been detected in Italy and has not yet extended its geographical range to neighbouring countries. However, we believe that this is likely to occur soon. We have little information about the ecology of this new alien species, and the consequences of its introduction should be closely observed in the future.

As stated earlier, the introduction of a new bee species in an ecosystem is often disregarded because of its role in the pollination of plants. However, we should change the way we perceive bee introductions. Like any other introduced species, alien bees can become invasive and affect native pollinators and ecosystem functioning. Introducing a new species into an environment is never a zero-sum game, and such practices must be abolished. Instead, native ecosystems should be preserved, and native bees allowed to thrive. Friendly practices favouring bees, such as the exclusion of pesticides, planting native flowers, and reduced mowing frequency (see Kawahara et al., 2021), should be encouraged. To prevent new invasions, biosecurity between countries must be reinforced and cross-border legal instruments homogenised (Diagne et al., 2021; Aizen et al., 2019; see Section 5).



Figure 9 *Megachile disjunctiformis*. Picture: FranziskaLuthi.

5 Future trends in research

In this section, we have identified five major gaps that should be addressed in future research:

- 1 Even if some new data have been accumulated since, the first simple recommendation we can provide is to amplify research efforts on alien bees. We advocate for a new review of bees introduced worldwide 6 years after the one of Russo (2016). The cases of *M. disjunctiformis* in Italy (Bortolotti et al., 2018) or *Xylocopa pubescens* in the Canary Islands (Ruiz et al., 2020) are examples of introductions that occurred after the review of Russo (2016).
- 2 We should estimate the ecological impacts of alien bees more accurately, be they positive or negative. For example, Russo (2016) determined that 11 out of 80 species could positively affect native ecosystems, but no review on these effects exists to date. Of course, fieldwork and experiments to estimate impacts are costly (Goulson, 2003), but they provide valuable information for estimating impacts (e.g. see Díaz et al., 2021; Geslin et al., 2020).
- 3 We need to estimate the agronomic costs of alien bees. In their recent review, Aizen et al. (2020) provided convincing examples of the deleterious impacts of alien bees on agroecosystems. For example, the invasion of *Bombus terrestris* in Argentina affected the production of raspberries (Sáez et al., 2014, 2017, 2018). One underlying mechanism is the over-visitation of raspberry flowers by *Bombus terrestris*, leading to flower damage, such as style breakage (see Badano and Vergara, 2011 for an example on coffee plantations).
- 4 The economic cost associated with alien bees must be estimated. In addition to the costs related to agricultural production, it has been suggested that some wood-nesting bees can potentially represent a problem for wooden structures as nest excavation may generate structural weakness in lumber (Rust et al., 2004). In their recent review on the global economic costs of invasive species, Diagne et al. (2021) estimated a mean annual cost of invasive invertebrates of US\$ 8.7 billion from 1970 to 2017. However, this review also highlights the critical need for more research on the economic costs of invasive insects.
- 5 If possible, we should provide stakeholders with management techniques to avoid the spread of alien bees. For example, Geslin et al. (2020) showed that *Megachile sculpturalis* rarely nests in bamboo with a hole diameter < 8 mm. This observation could help land managers install and build insect hotels to avoid the nesting of *Msc.*

6 How to improve biosecurity

Among the new pathways of invasions, the increase of commercial offers for the public of both managed and wild bees is of great concern (Geslin et al., 2017). Over the past 30 years, we have seen an exponential development of pollination supplementation practices in order to fight against pollinator declines and to compensate the limitation of pollination service delivered to entomophilous crops and ornamental species which may limit their yields. Since the 1970s, this has led to the first wave of global trade in social bees and bumblebees, initially for greenhouse use. As we have previously seen in this chapter, many reports of escapes of these imported bees into the wild have occurred. More recently, the second wave of the commercial trade of wild bees is emerging. In Europe or in North America, various commercial companies are selling wild solitary bees to promote better pollination service in gardens and field crops, arguing that these bees offer a much greater pollination service than domesticated social bees. Several mason bees and leaf-cutting bees have been selected for commercial purposes according to their nesting habits in cavities, offering an easy way to ship living cocoons in bamboo twigs. However, in the US and Canada, this may also promote the spread of some alien bees (e.g. *Osmia cornifrons*). These new commercial practices bring new pathways for alien pollinators to spread as the business may be done worldwide. For example, by June 2021, a wild bee package shipped from France to Seattle (US) was intercepted in New Caledonia by biosecurity services. Inside the package, we found bamboo twigs containing 23 lived cocoons of *Osmia bicornis* and two recently emerged females (H. Jourdan, *pers. obs.*). This illustrates the tremendous risk of moving large numbers of alien pollinators to a wide range of regions without any biosecurity rules implemented.

Beyond this specific pollinator trade, there are still other pathways for the involuntary spread of alien pollinators associated with global trade. The rule that the more the volume of traded commodities increases between distant countries, the more the biosecurity risk increases for alien arrivals (Hulme, 2009), is also valid for pollinators. Mason bees (including resin bees and leaf-cutting bees) and carpenter bees (including hollow stem nesting species) appear more likely to be propagated by human trade.

To deal with these new threats, enforcement of biosecurity regulations and practices against the transfer or arrival of alien bees is urgently needed. According to the Food and Agriculture Organization of the United Nations standards, biosecurity is defined as 'a strategic and integrated approach that encompasses the policy and regulatory frameworks (including instruments and activities) for analysing and managing relevant risks to human, animal and plant life and health, and associated risks to the environment'. It appears critical

in the context of biological invasions (Hulme, 2010). Islands are particularly at risk and deserve special attention (Cox and Elmqvist, 2000; Moore et al., 2010). But since the late 1980s, most of the biosecurity efforts have focused on preventing the spread of parasites and pathogens of managed bees and not alien bees in general.

In recent decades, Australia has appeared as a good example of biosecurity measures enforced to protect native pollinators. Even if it was established mostly for protecting the bee industry with highly enforced regulation and surveillance against the introduction of *Varroa destructor*, tracheal mites with European (*Apis mellifera*) or Asian (*Apis cerana*) beehives, it is also focusing on some bee diseases to avoid possible spillover between managed bees and wild bees (Heersink et al., 2016; Robert et al., 2017; Dalmon et al., 2021). These biosecurity efforts rely on a national network of sentinel beehives. Such a sentinel coordinated approach is also applied to the larger Pacific region (New Zealand – despite *Varroa* installation – New Caledonia, French Polynesia, and to a lesser extent Fiji).

Another alternative solution to reduce the unfortunate trade of alien pollinators relies on the valuing and promotion of local wild pollinators for pollination effectiveness. This implies the conservation and restoration of “green infrastructures” across landscapes that enhance wild bee populations. In Australia, native stingless bees are promoted in a commercial way to enhance pollination service, and troubles in Tasmania linked to the European Bumblebee (*Bombus terrestris*) have led to research for local alternative pollinators. Thus, native *Amegilla* spp. were identified as highly efficient pollinators in gardens, especially for Solanaceae (McQuillan and Hingston, 1999; Hogendoorn et al., 2000, 2007). But without awareness of the public, a new biosecurity concern may develop, as people may deliberately introduce *Amegilla* spp. into neighbouring oceanian territories, mostly archipelagos, for agricultural purposes. This has been suspected of *Amegilla pulchra* in Fiji, French Polynesia, and New Caledonia (Groom et al., 2017; Zakardjian et al., 2020). However, once introduced, *Amegilla* spp. may not limit their foraging to valuable crop species and are likely to visit alien plants. If those alien plants are usually poorly visited by native pollinators, the arrival of alien bees such as *Amegilla* spp. could result in the spread of those plant species.

Finally, there is an emerging corpus of methodology and theory to better implement efficient biosecurity measures in a changing world (climate change and global trade), especially urgently needed on islands, which could be applied to pollinators (Moore et al., 2010; Aizen et al., 2019; Proesmans et al., 2021). As pointed out by Hulme (2015), pathways for alien species introductions fall into six broad classes: deliberate release; escape from captivity; contamination of a commodity; stowaway on a transport vector; via an infrastructure corridor (without which spread would not be possible) or unaided from already invaded regions. Each of them should be examined carefully in the context of alien pollinators spread, resulting in enforcement of regulation policies and *ad hoc*

surveillance to prevent further biological invasions. More specifically, in the context of safeguarding pollination services, ten general rules have already been promoted as guidelines to improve governmental regulation, including an emphasis on the regulation of movement of managed pollinators and development of long-term monitoring of pollinators and pollination (Dicks et al., 2016). However, movement regulation should be extended to the wild bee trade and closest links should be developed with scientific research for robust long-term monitoring of pollinators and pollination at a global scale across a variety of landscapes. Hulme (2020) also promotes a “one biosecurity approach” relying on multidisciplinary input from ecology, social sciences, and economics. Such a global biosecurity approach should be promoted for pollination service, which is critical to ecosystem’s maintenance and human well-being in our changing world (Hulme, 2020; Proesmans et al., 2021).

7 Where to look for further information

The following articles are the key papers on the impact of alien bee species on native bees:

- Aizen, M. A., Smith-Ramírez, C., Morales, C. L., Vieli, L., Sáez, A., Barahona-Segovia, R. M., Arbetman, M. P., Montalva, J., Garibaldi, L. A., Inouye, D. W. and Harder, L. D. (2018). Coordinated species importation policies are needed to reduce serious invasions globally: The case of alien bumblebees in South America. *J. Appl. Ecol.* 1–7.
- Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E. and Vereecken, N.J. (2017). Massively introduced managed species and their consequences for plant–pollinator interactions. In: *Advances in Ecological Research*, pp. 147–199.
- Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 34, 1–26.
- Mallinger, R. E., Gaines-Day, H. R. and Gratton, C. (2017). Do managed bees have negative effects on wild bees?: A systematic review of the literature. *PLoS ONE* 12, e0189268.
- Paini, D. R. (2004). Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: A review. *Austral Ecol.* 29, 399–407.

- Russo, L. (2016). Positive and negative impacts of non-native bee species around the world. *Insects* 7, 101–103.

For a focus on agricultural production, we recommend:

- Aizen, M. A., Arbetman, M. P., Chacoff, N. P., Chalcoff, V. R., Feinsinger, P., Garibaldi, L. A., Harder, L. D., Morales, C. L., Sáez, A. and Vanbergen, A. J. (2020). Invasive bees and their impact on agriculture, 1st ed., *Advances in Ecological Research*. Elsevier Ltd.

We particularly recommend the work of Dr M. Aizen and his team on this thematic:

- <https://sites.google.com/site/marceloizen/home>.

*The open science projects following the spread of *Megachile sculpturalis* in Europe and in the Balkans can be found here:*

- <https://oabeilles.net/projets/observatoire-a-beilles-exotiques>.
- <https://www.citizen-science.at/blog/blogger/lannerj>.
- <https://srbee.bio.bg.ac.rs/english>.

Key journals to read articles on invasion biology are:

- Biological invasions: <https://www.springer.com/journal/10530>.
- Diversity and Distribution: <https://onlinelibrary.wiley.com/journal/14724642>.
- NeoBiota: <https://neobiota.pensoft.net/>.

Other interesting websites:

- <https://ipbes.net/invasive-alien-species-assessment>.
- <http://www.issg.org/>.
- <https://www.gbif.org/fr/dataset/39f36f10-559b-427f-8c86-2d28aff68ca>.
- <https://easin.jrc.ec.europa.eu/easin>.
- <https://serc.si.edu/research/research-topics/biological-invasions>.

Some interesting outreaches:

- <https://theconversation.com/bee-battles-why-our-native-pollinators-are-losing-the-war-40620>.
- <https://theconversation.com/australian-scientists-need-your-help-keeping-track-of-bees-please-128932>.

- <https://idtools.org/id/bees/exotic/>.

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