Exotic insect pollinators and native pollination systems

Scott Debnam · Agustin Saez · Marcelo A. Aizen · Ragan M. Callaway

Abstract Insect pollinators have been relocated by humans for millennia and are, thus, among the world's earliest intentional exotic introductions. The introduction of managed bees for crop pollination services remains, to this day, a common and growing practice worldwide and the number of different bee species that are used commercially is increasing. Being generalists and frequently social, these exotic species have the potential to have a wide range of impacts on native bees and plants. Thus, understanding the consequences of introduced species on native pollinator systems is a priority. We generated a global database and evaluated the impacts of the two main groups of invasive bees, *Apis mellifera* and *Bombus* spp., on their pollination services to native flora and impacts on native pollinators. In a meta-analysis, we found that per-visit pollination efficiency of exotic pollinators was, on average, 55% less efficient than native pollinators when visiting flowers of native species. In contrast to per-visit pollination efficiency, our meta-analysis showed that visitation frequency by exotic pollinators was, on average, 80% higher than native pollinators. The higher visitation frequency of exotic pollinators overcame deficiencies in pollen removal and transfer resulting in seed/fruit set levels similar to native pollinators. Also, evidence showed that exotic pollinators can displace native insect and bird pollinators. However, the direct effects of exotic insect pollinators on native pollination systems can be context dependent, ranging from mutualism to antagonism.

Keywords Exotic · Insect pollinator · *Apis mellifera* · Managed bees · Pollination efficiency · Visitation frequency

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Introduction

Bees have been raised and relocated by humans practically since the origin of agriculture. Roughly seven thousand years ago, *Apis mellifera*, honey bees, were shipped up the Nile River to pollinate crops and

produce honey (Crane 1999), making insect pollinators among the world's earliest intentional exotic introductions. *Apis mellifera* was brought to America by European settlers in 1620 and rapidly spread westward, often in advance of European settlements (Crane 1999). In Australia, *A. mellifera* was introduced in the early nineteenth century (Thorp 1987). Africanization of European *Apis mellifera* in Brazil in the 1950s created an exceptionally successful invader that within a few decades had spread across most of the Neotropics (Smith et al. 1989). More recently, several *Bombus* species were found to provide pollination services superior to those of *A. mellifera* for some crops (e.g., tomatoes, eggplants) and have been spread rapidly around the globe by humans. Combinations of *Bombus hortorum*, *B. terrestris*, *B. subterraneus*, and *B. ruderatus* were introduced to New Zealand in 1885, to Israel during the 1960s, Chile during the 1980s, and to Tasmania and Japan in 1990s (Hopkins 1914; Dafni and Shmida 1996; Hingston et al. 2002; Aizen and Feinsinger 1994; Inoue et al. 2008; Morales et al. 2013). Leaf cutter bees, *Megachile apicalis* and *M. rotundata*, were introduced to North America and Europe during the 1930s to pollinate alfalfa (Bohart 1972; Cooper 1984). As commercial crops became more commonly grown in greenhouses, *Bombus* species have been transported to more non-native regions because they are much better pollinators in closed structures than *A. mellifera* (Velthius and van Doorn 2006).

Introduced pollinator species are a biased sample of all insect pollinators. The most important introduced bee pollinators are social and easy to manage, function in large, discrete colonies, have highly generalist pollination behavior and have high reproductive output. Most insect pollinator species do not share these traits. For instance, fewer than 1,000 of the roughly 20,000 bee species are eusocial (Michener 2000). Introduced insect pollinator species can also vary in the degree to which they demonstrate these associated traits, and the characteristics that are attractive to humans may also promote bee colonization, naturalization, and unintentional spread in the places where they are relocated.

Exotic pollinators have the potential to generate profound changes in the ecosystems where they are introduced. Plants can compete with each other for the service of pollinators (Feinsinger and Tiebout 1991; Mitchell et al. 2009; Morales and Traveset 2009;

Lortie and Reid 2012), but competition among pollinators is difficult to demonstrate (see Zimmerman and Pleasants 1982; Thomson 2004, 2006). Because of the very large densities that some exotic insect pollinators can reach, and because of their apparent high pollination efficiency, some exotic pollinators may have strong impacts on native insect pollinators and the plants they service. For example, a recent review by Mallinger et al. (2017) found that managed bees generally had negative effects on wild bees and that roughly the same number of studies reported positive vs. negative effects on plant communities. Furthermore, they found that managed bees commonly increased potential pathogen transmission to wild bees.

The introduction of managed bees for crop pollination remains a common and growing practice worldwide (Aizen et al. 2020) and the number of different bee species that are used commercially is increasing (Potts et al. 2016). Because introduced bees can have a wide range of impacts on native bees and plants, understanding the consequences of introduced species on native systems is a priority. Our broad objectives are to (1) update earlier reviews by Goulson (2003) and Paini (2004) of the effects of exotic pollinators on native plants and pollinators, (2) to conduct the first meta-analysis comparing the pollination efficiency of exotic and native pollinators on native plants, and (3) review comparative studies of the effects of exotic insect pollinators on native insect pollinators. To pursue these goals, we generated a global database that allowed us to evaluate the overall impacts of the two main groups of invasive bees, *Apis mellifera* and *Bombus* spp., on the native flora and pollinators, of which the latter were overwhelmingly insects, with birds as rare exceptions.

Material and methods

Pollination efficiency can be evaluated in a number of ways, including flower visitation frequency, total amount of pollen deposited on stigmas by all pollinators, per pollinator species, or per pollinator visit (sometimes referred as pollinator effectiveness), and/or the origin and genetic diversity of that pollen (Inouye et al. 1994; Ne'eman et al. 2010). Inouye et al. (1994) reported 12 different ways that "pollination efficiency" had been used in the literature, and all of

these aspects can affect the quantity and quality of the seeds produced (Matsuki et al. 2008). Recognizing the broad use of the term, here we define pollination efficiency as any of these components or as different aggregates of these components—the effect of an individual pollinator visit, or of all pollinator visits by a single or all pollinator species, on the production of seeds. In practical terms, we consider the total pollination efficiency of a single pollinator species or group of species as the product of the per-visit effect x visitation rate and also analyzed the two components separately. We surveyed published studies that reported: (a) per-visit pollination efficiency (i.e., number of pollen grains deposited, or seed produced, after a single visit), (b) numeric effect (i.e., visitation rate to flowers), of both native and exotic bees in native plants, and (c) relations between the abundance of native and exotic bees in time or space. We searched for articles on Google Scholar, using different combinations of the following keywords: "pollination efficiency," "per-visit pollen deposition," "per-visit seed production," "visitation rate," "visitation frequency," "fruit set." For the "numeric effect" database [i.e., point (b) above], the exotic pollinators were mostly feral (i.e., when populations are established in the wild, in contrast to managed high concentrations of hives that artificially increase bee density). However, in a few cases, natives were likely affected by nearby managed colonies. Because very few studies recorded distances from apiaries or other nest sites, we did not include this in the analysis of the relation between the abundance of native and exotic bees (point c) above. From published studies, data from tables were downloaded directly to our database, whereas data from figures were retrieved by using the ImageJ software (Schneider et al. 2012). The last search was conducted in November 2020. In total, we retrieved ∼ 300 values from 36 peer-reviewed publications, which comprise the first global database evaluating the effects of introduced bees on native plants and bees (Supplementary Table 1). In all cases, the exotic bees were either *Apis mellifera* or species from the genus *Bombus*.

Data were standardized as *z*-scores prior to analyses to allow comparisons among studies using different methodologies, response variables, and metrics Observations from each variable (Y_i) in each study (j) were standardized by

$$z - score = \frac{(y_{ij} - Y_j)}{SD_j},$$

where y_{ij} represents the observation i from the study j, Y_j the overall mean of the study j, and SD_j the standard deviation of the study j.

We evaluated the influence of bee origin (i.e., native *vs* exotic) on (a) per-visit pollination efficiency and (b) visitation rate to native flowers, using generalized linear mixed-effects models. The origin of bee visitors was incorporated as a fixed effect and each study as a random effect allowing the intercept to vary among studies. We also evaluated the influence of (c) the exotic pollinators on native pollinators (i.e., displacement on time or space) with a linear mixed-effects model. In this analysis, the abundance of exotic pollinators was included as a fixed effect, and each study as a random effect, allowing the intercept to vary among studies. All three analyses were carried out using the *lme* function from the *nlme* package (Pinheiro et al. 2015) of the R software (version 2.15.1), assuming a Gaussian error distribution. Because the model of the effects of origin of pollinators on visitation rate to native flowers did not meet assumptions of homogenous variance, we reran this analysis using a heterogeneous variance model (varIdent function in the *nlme* library), which increased model fit (lower AIC) and improved compliance with model assumptions.

Effects of exotic pollinators on native plants

Per-visit efficiency

In a meta-analysis of 16 publications, and focusing on our first and second objectives, the *z*-scores values for per-visit pollination efficiency on native plants were significantly lower for exotic than for native pollinators ($\beta = -1.23$, $SE = 0.13$, $Z = -9.35$, $P < 0.001$; Fig. 1; Supplementary Table 1). Exotic bees were, on average, ∼ 55% less efficient, per visit, than native pollinators when visiting native plant species. However, this overall meta-analytical result does not reflect the complexity of accurately quantifying per-visit efficiency (see Inouye et al. 1994), and thus, we next explore a number of key studies.

For example, in northeast Brazil, the exotic *A. mellifera* and the native bee *Centris tarsata* remove similar numbers of pollen grains from the flowers of
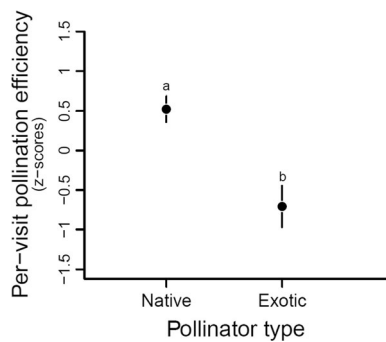
Fig. 1 Estimated mean (± 2SE) from the mixed model of per-visit pollination efficiency (i.e., per-visit effect on pollen deposition, seed set, seed number, or fruit set) of native and exotic pollinators when visiting native flowers. Letters indicate statistical differences between pollinator type (i.e., *P* value < 0.05). Data from different studies were standardized by z-scores prior to running the analysis

cashew, *Anacardium occidentale* (Freitas and Paxton 1998). However, *C. tarsata* deposited, on average, 16 grains per stigma versus eight for *A. mellifera*, suggesting greater effectiveness of the native. *Centris tarsata* is a non-corbiculate species and lacks the pollen basket apparatus of *A. mellifera*, which allows the latter to sequester pollen, and this may decrease deposition rates. *Centris tarsata* is also twice the size of *A. mellifera*, which could increase contact with floral parts. Both species showed very low ratios of pollen deposition to pollen grain removal, around 1%, but this is typical for bee-mediated plant pollinator systems (Harder and Thomson 1989; Young and Stanton 1990). Despite greater pollen deposition by *C. tarsata*, the two species performed similarly in fruit set by their target plants, probably because of a lack of pollen limitation.

In Tasmania, pollination of the native *Eucalyptus globulus* is provided by many native insect and bird species as well as two exotic pollinators: *A. mellifera* and *B. terrestris* (Hingston et al. 2004). When the effectiveness of these pollinators was compared using stigma exclusion experiments, the native swift parrot, *Lathamus discolor*, was the superior pollinator generating 76% seed set after a single visit. Both exotic *A. mellifera* and *B. terrestris* produced 7% seed set after single visits.

In Mexico, the pollination effectiveness of the native *Nannotrigona perilampoides* (a stingless bee) was compared to that of the exotic *Bombus impatiens* (the common eastern bumblebee from northern North America) on habanero peppers, *Capsicum chinense* (Palma et al. 2008). A single visit by the exotic *B. impatiens* removed 40% of pollen grains from anthers, whereas *N. perilampoides* removed only 7%. However, fruit set was lower for flowers pollinated by *B. impatiens* (51%) than for those pollinated by *N. perilampoides* (85%), even though seed number per fruit was similar for both the exotic and native bees. Palma et al. (2008) argued that foraging behavior allowed *N. perilampoides* to overcome the differences in pollen removal. *Bombus impatiens* visited 10 flowers in a 5-min period, whereas *N. perilampoides* visited eight. Individual *B. impatiens* remained on a single flower for only 8 s whereas individual *N. perilampoides* remained on a flower for 36 s, providing a greater opportunity to deliver pollen. Finally, *B. impatiens* visited 20 flowers per foraging trip vs. 42 for *N. perilampoides*. They combined this complex suite of methods for quantifying pollinator efficiency with the "Spear's pollination effectiveness index" resulting in a score for *B. impatiens* of 0.71 vs. 0.78 for *N. perilampoides* (Spears 1983), and these were not statistically different.

In the United States, the invasive plant *Solanum torvum* is pollinated by native *Ceratina* spp. and *Halictidae* spp., and the exotic *Euglossa viridissima*. In areas where only native bee species occurred, *S. torvum* was pollen limited (Liu and Pemberton 2009). In contrast, *S. torvum* showed no pollen limitation where the exotic *E. viridissima* occurred. These native and exotic pollinators also differed in the rate of flowers visited. Native *Halictidae* and *Ceratina* visited *S. torvum* flowers at 1.0 and 5.5 times per minute during timed intervals, respectively, whereas the exotic *E. viridissima* visited 2.0 flowers per minute. *Euglossa viridissima* promoted the same fruit set as native *Ceratina* bees but more than native *Halictidae*.

In New Zealand, exotic pollinators are as efficient or more efficient at pollinating *Brassica rapa*, an exotic plant species, than the native pollinator assemblage (Rader et al. 2009). Two exotics, *A. mellifera* and *B. terrestris*, and six natives, *Leioproctus* sp., *Lasioglossum sordidum, Eristalis tenax, Melangyna novae-zelandiae, Melanostoma fasciatum,* and *Dilophus nigrostigma* were the most common pollinator species to visit *B. rapa* in their experiments. Among these species, *A. mellifera* visited *B. rapa* flowers at a significantly higher rate than all other species combined. Individual *B. terrestris* visited more flowers per

minute than did any other pollinator species. *Apis mellifera* and *B. terrestris* deposited far more pollen grains (123 and 236, respectively) than four of the native species, *D. nigrostigma* (69), *M. fasciatum* (6), *M. novae-zelandiae* (16), and *L. sordidum* (30). Pollen deposition by the two other native species did not differ from those of *A. mellifera* and *B. terrestris*. Combining pollen deposition efficiency with visitation frequency showed that the exotic *A. mellifera* was by far the most effective pollinator overall with a deposition of 7879 pollen grains per hour. Second was the exotic *B. terrestris,* which deposited 2247 pollen grains per hour. Native pollinators were far behind with 1 to 968 pollen grains transferred per hour. *Bombus terrestris* is a much larger pollinator than any other native species in the New Zealand insect pollinator assemblage, which might allow them to remove and deposit pollen at a much higher rate. *Apis mellifera* simply outnumbered all other pollinators in the study and, thus, deposited far more pollen grains than did all other species combined. However, it is important to emphasize that *B. rapa* is also alien to New Zealand, and exotic plants and pollinators can establish invasive complexes that reinforce each other's fitness (Morales and Aizen, 2002).

In a more precise phylogenetic comparison, Madjidian et al. (2008) contrasted the pollination effectiveness of the native *Bombus dahlbomii* to that of the exotic *B. ruderatus* in Argentina. For the native plant species, *Alstroemeria aurea*, they found that *B. dahlbomii* deposited 8.2 grains of pollen per visit versus 3.5 for *B. ruderatus*. However, *B. ruderatus* visited *A. aurea* flowers 10 times more frequently than native *B. dahlbomii*. This resulted in an estimation of the native *B. dahlbomii* delivering 43.3 grains of pollen to a single flower over the lifetime of the flower versus 144.3 grains for the exotic *B. ruderatus*. The key factor was population size, with the exotic *Bombus* dominating pollinator efficiency through a much higher number of visits to flowers (see Numeric Effects). Yet, the reproductive consequences of these estimations must be considered with caution because of the potential negative impact of pollinator overvisitation on post-pollination pollen performance, flower damage, and ultimately on seed production (Harder et al. 2016; Aizen et al. 2014, 2020).

In another phylogenetically controlled comparison, Esterio et al. (2013) evaluated the pollination efficiency of the exotic *B. terrestris* on the Chilean herb

Mimulus luteus. Bombus terrestris was a more inefficient pollinator of *M. luteus* than species in the *Anthophoridae* and *Megachilidae*, which were components of the native pollinator assemblage. However, *B. terrestris* was similar in pollination efficiency to the native *Bombus dahlbomii*. Both *Bombus* species were poor pollinators of *M. luteus* due to low pollen delivery to stigmas and low and intermittent visitation rates.

In China, two exotic *Apis* species, *A. mellifera* and *A. cerana*, which pollinated *Pedicularis densispica*, provided superior services to *Pedicularis densispica* than native *Bombus* species (Sun et al. 2013). *Apis mellifera* and *A. cerana*, likely dispersed from colonies moved into the study areas for crop pollination, displaced *Bombus* foragers from *P. densispica* to other species. Native *Bombus* species provided a higher level of pollen transport than did the two exotic *Apis* sp. and removed 44% of *P. densispica* pollen via a single visit compared to 20% for *A. mellifera*. Also, *Bombus* sp. deposited 12 to 16 grains of pollen in a single visit versus five for the *Apis* sp. However, *Apis* sp. visitation rates were almost tenfold greater than those of the native *Bombus* sp. This higher rate of visitation by *Apis* sp. translated into an estimated doubling of seed set by *P. densispica* (see Numeric Effects).

Per-visit results can be complicated by nectar robbing, and some exotics engage in nectar robbers. For example, *B. terrestris* often robs nectar from flowers by piercing the corolla and consuming nectar without contacting stigmas. Thus, pollination may not occur (but see Maloof and Inouye 2000) and other pollinators often avoid the depleted and damaged flowers, or engange into secondary robbing (Irwin and Brody 1998; Irwin et al. 2010). This behavior can have a substantial impact on plant reproductive success. In Australia, nectar robbing by the exotic *B. terrestris* has been observed by Hingston and McQuillan (1998) and Hingston (2007) on native plant species, including *Epacris impressa*, *Richea scoparia,* and *R. dracophylla* and *Billardiera longiflora*. Matsumura et al. (2004) recorded nectar robbing in Japan by the exotic *B. terrestris* on native and exotic plant species. Stout et al. (2000) found that nectar robbing of *Linaria vulgaris* in the native range of *B. terrestris* appeared to have minimal effects on seed set because robbing seems to be mitigated by legitimate visitation of other native pollinators. In contrast, in the non-native range

of *B. terrestris* in Japan, Dohzono et al. (2008) found that nectar robbing had negative consequences for a native plant species. They compared visitation frequency, insect behavior, flower nectar volume, and seed/fruit set on *Corydalis ambigua* at sites among two native species, *B. ardens* and *B. hypocrita* (also a nectar robber) and the exotic *B. terrestris*. They found that the non-robbing *B. ardens* produced significantly higher seed/fruit set in *C. ambigua* than either of the nectar robbing species. When *B. terrestris* was prevalent, nectar robbing was more common than at other sites and correlated with decreased visitation by *B. ardens*. In turn, this decreased visitation corresponded with pollen limitation in *C. ambigua*.

The studies explored in detail in this section illustrate the many ways that researchers have quantified pollination efficiency, our first objective, and how pollinator species may be highly effective in one component of efficiency but not in another. The complexity inherent to pollination efficiency does not emerge from the meta-analysis. Many studies have compared efficiencies between individual pollinators and, thus, do not account for how whole-population behavior might affect efficiency. For example, *A. mellifera* individuals tend to move frequently among flowers of the same plant species, whereas different individual *A. mellifera* target other plant species in ways that provide the whole hive with diverse pollen resources. Such population-level behavior can substantially increase pollination efficiency in ways that are not detectable when only studying individual insects. On the other hand, the *A. mellifera*, an efficient pollen harvester, can depress pollen availability, reducing the pollination efficiency of other pollinators (Aizen et al. 2020). Finally, the large majority of studies have focused on *Apis melliferia* and *Bombus terrestris*. These species are unusually social pollinators, and this may contribute to pollination effectiveness through high densities, and consequent superior numeric effects, which we focus on in the next section.

Numeric effects

Continuing to focus on our first and second objectives (updating earlier reviews of the effects of exotic pollinators on native plants and pollinators, and a meta-analysis comparing the pollination efficiency of exotic and native pollinators), we analyzed numeric effects of exotic and native pollinators. In contrast to

per-visit efficiency, our meta-analysis of 22 studies of numeric visitation rates (see Supplementary Table 1, many of these are listed under efficiency) showed an approximately 80% increase in the number of visits by exotic pollinators in comparison to native pollinators ($\beta = 0.75$, $SE = 0.19$, $Z = 3.89$, $P < 0.001$; Fig. 2). In addition, the number of visits to native flowers by exotic pollinators was more variable than for native pollinators. Because honey bees and bumble bees were by far the most studied exotic pollinators, their social behavior and large colony sizes, in particular for *A. mellifera*, bias conclusions about the numeric effects of exotic pollinators in general. Aizen et al. (2014) provided theoretical and empirical evidence that the exceptionally high density of many exotic insect pollinators had the potential for important population- and community-level consequences via reducing the reproduction of native plants while increasing the fitness of exotic invasive plants. However, the details of particular studies provide a substantially more complicated picture, as for per-visit efficiency.

In one of the most detailed studies of the impact of exotic pollinators on natives available, Morales et al. (2013) followed pollinators over time and found that over five years the invasive *B. terrestris* and *B. ruderatus* almost completely eliminated the native congener *B. dahlbomii* throughout much of its range in Patagonia. Similar evidence was found in a 20-year survey of pollinators of the endemic herb *Alstroemeria aurea* (Morales et al. (2013). In another study, but without measurements over time, in places where the
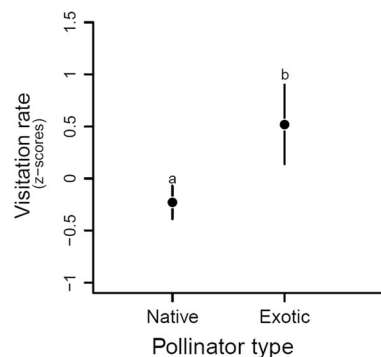

Fig. 2 Estimated mean (± 2SE) from the mixed model of visitation rate of native and exotic pollinators to native flowers. Letters indicate statistical differences between pollinator type (i.e., *P* value < 0.05). Data from different studies were standardized by z-scores prior to running the analysis

native and exotic *Bombus* species co-occurred, the fruiting success of a native orchid was 66–83% higher than where the exotic bees did not occur (Sanguinetti and Singer 2014). This increase was attributed to much higher numbers of exotic pollinators making more frequent visitation to the orchids, but there were no measurements before and after invasion. Similarly, Paton (1997) also found that for *Banskia ornata*, a highly pollen-limited shrub in Australia, the exotic *A. mellifera* increased seed production. In Panama, Roubik (2002) estimated that the exotic *A. mellifera* increased fruit set and seed size by 25% in *Coffea arabica*. However, *A. mellifera* comprised 95% of all flower visits to flowers at all sites making clear comparisons to native pollinators in general difficult.

In French Guiana, Roubik et al. (1996) found that *Mimosa pudica* pollinated by insect communities composed primarily of the exotic *A. mellifera* showed a 6% reduction in fruit set and a 26% reduction in seed set compared to plants pollinated by communities comprised mostly native pollinators. However, at sites where *A. mellifera* displaced other bees at flowers, they appeared to numerically overwhelm natives rather than displace them through foraging behavior. In Australia, exotic *A. mellifera* can displace some bird pollinators, and this displacement corresponded with negative effects on the fecundity of the native plant species, *Callistemon rugulosus* (Paton 1993).

In a greenhouse study, Kenta et al. (2007) measured fruit set for seven plant species native to Japan, and visitation frequency, in response to a number of *Bombus* species. They released mixtures and single-species pollinator assemblages of the native *Bombus hypocrita, Bombus ardens, Bombus diversus,* and the exotic *B. terrestris* into greenhouses planted with a mixture of the plant species. They found that with the exotic *B. terrestris* alone, three of the plant species had lower fruit set. This was caused by a decrease in flower visitation by *B. terrestris* to plants with nectaries that were inaccessible to their short proboscises. The foraging behavior of *B. terrestris* was similar to that of the native *B. hypocrita*, which also possesses a short proboscis, but the native was less prone to robbing than the exotic. The native pollinator assemblage produced superior fruit set for three of the plant species, and for the remaining four native plant species fruit set did not differ from that produced by the exotic. Importantly, in contrast to some of the other studies reviewed here, Kenta et al. (2007) did not study

different aspects of the pollination process, only the ultimate outcome.

In other systems, exotic pollinators appear to have no effect. On the Canary Islands, seed set was compared in two populations of *Echium wildpretii*, one pollinated by an insect community comprised of mostly the exotic *A. mellifera*, and the other pollinated by mostly native insect pollinators. The two *E. wildpretii* populations did not differ in seed set nor seed viability despite higher bee densities at the test site (Dupont et al. 2004). In Australia, the endemic shrub *Dillwynia juniperina* was not more pollen-limited in sites with more exotic *A. mellifera* than native insect pollinators compared to sites with mostly natives (Gross 2001).

In some cases, exotic pollinators preferentially forage on exotic plant species, potentially leaving natives under-pollinated. For example, Goulson et al. (2002) found that the exotic *B. terrestris* and *A. mellifera* bees preferred exotic plant species over native plant species at a site in Tasmania. Only 16.5% of *B. terrestris* and 27.4% of *A. mellifera* foragers visited native species, even though there were far more native inflorescences available. Interestingly, native pollinators also showed this preference for the exotic plants (see also Bartomeus et al. 2008; Brown et al. 2002; Aizen et al. 2008; Tepedino et al. 2008), making it difficult to determine to what degree the exotic pollinators might be contributing to the relative reproductive output and distribution of these species. In New Zealand, *B. terrestris* was recorded visiting 39 different plant species, of which only three were native to New Zealand (Goulson and Hanley 2004). Preference for exotic plants may contribute to invasive plant success, and if exotic pollinators interact much more strongly with exotic plant species this may lead to a form of invasive meltdown in which exotics promote each other (Simberloff and von Holle 1999; Morales and Aizen 2002).

Meta-analysis of the studies reviewed here indicated that exotic insect pollinators are less effective at pollen removal and deposition on a per-visit level than native species (Fig. 1). However, meta-analysis also indicated that exotic pollinators have higher visitation rates than native pollinating insects (Fig. 2). The higher visitation frequency of exotic pollinators may overcome deficiencies in per-visit pollination efficiency resulting in seed/fruit set levels equal to native pollinators (see Madjidian et al. 2008). However, the

higher exotic pollinator densities that lead to this greater visitation frequency suggest the potential for exotic pollinators to have negative impacts on native insect pollinators through competition.

To our knowledge, all studies of the impact of exotic pollinators on native plants have focused on seed and fruit set as indicators of the quality of pollinator interactions. This is reasonable but does not consider whether any difference in seed production affects plant populations. Thus, how seed production translates into population demographics (see Maron et al. 2014) remains a missing link in the comparison of exotic and native pollinators. Factors such as the cost of reproduction (Ehrlen and Eriksson 1995), plant life history traits, compensatory density-dependent seedling recruitment (Kauffman and Maron 2006), seed bank dynamics, and environmental effects (Burkle and Irwin 2009) have the potential to exacerbate or mitigate plant reproductive output and should be considered for a more complete assessment of the impact of exotic pollinators.

Effects of exotic pollinators on native pollinators

Focusing on our third objective, we found that exotic pollinators have the potential to competitively displace native pollinators by dint of large numbers, novel behavior, or by the very social traits that led humans to introduce them. Understanding exotic and native pollinator interactions is crucial, as agricultural land planted with pollinator-dependent crops has been expanding rapidly (Aizen and Harder 2009; Aizen et al. 2019, 2020). Most pollinators are generalists (Waser et al. 1996); thus, native plant species may easily exchange their native pollinators for more abundant exotics. This in turn creates the potential for generalist exotic species, if they are unusually numerous, aggressive, or efficient, to compete strongly with both specialist and generalist native species and replace them (Goulson 2003; Aizen et al. 2014). Aizen et al. (2008) found that exotic generalist pollinators can erode native pollination networks. Because connectivity among native plants and native pollinators declined in networks that were highly invaded by exotics, they suggested that such modifications in the pollination networks might "leave many native species subject to novel ecological and evolutionary dynamics." Such disruption of native pollinator networks may also have profound consequences

for agricultural systems as "wild insect pollinators" can substantially increase fruit set in many crops, even in the presence of exotic pollinators, including *A. mellifera* (Garibaldi et al. 2013). But, despite the potential for exotic pollinators to affect native pollinators, only a few studies have found clear evidence of local displacement of natives by exotics (see Goulson 2003), whereas evidence for significant population decreases of natives in response to exotics is even more limited. Nine of the ten papers that studied native pollinator species abundance in the presence of introduced exotic pollinators show a significant decrease in the densities of native pollinators as densities of exotic pollinators increase ($\beta = -0.31$, $SE = 0.08$, $t = -3.67$, $P < 0.001$, Fig. 3). These results are roughly consistent with those published by Mallinger et al. (2017), who found that slightly more than half of the studies they reviewed found negative effects of managed bees on native bees, but they found that results among studies were highly variable. Clearly, more studies of the impact of exotic pollinators on natives are needed.

In one of the most thorough studies of native pollinator decline in response to exotic pollinators, Morales et al. (2013) explored how the geographic distribution of the native *Bombus dahlbomii* was affected by its exotic congeners *B. ruderatus* and *B. terrestris*. Over 20 years, they conducted 17 annual censuses of the *Bombus* congeners on a shared plant species, *Alstroemeria aurea*, in the Challhuaco Valley, Argentina. They also conducted a survey along a 1270 km latitudinal gradient in the Patagonian region
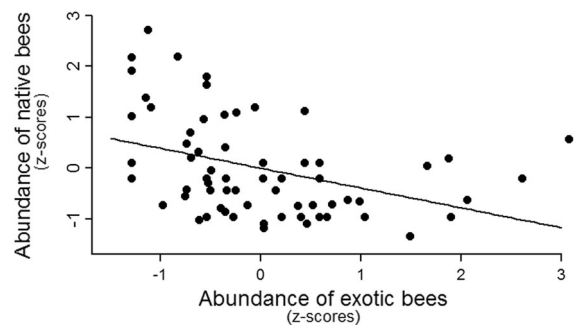

Fig. 3 Relationship between the abundance of native and exotic bees in time or space. Each black point is an observation within a study, whereas the black line is the overall linear model estimation. Data from different studies were standardized by z-scores prior to running the analysis. $\beta = -0.31$, $SE = 0.08$, $t = -3.67$, $P < 0.001$

of Argentina and Chile in 2011 and compared the abundances and distributions of the three *Bombus* species to the estimated distribution and abundance of *B. dahlbomii* (Abrahamovich and Díaz 2001) before the arrival of the exotic *Bombus* species. On the transect, the native *B. dahlbomii* was very rare in the northern parts of its range in places where it was once abundant before the arrival of the exotics. The only locations where *B. dahlbomii* was numerically dominant were in the southern part of its range, where the exotic species had not yet reached (Aizen et al. 2020). The exotic *B. ruderatus* occurred at 24% of sites and was never dominant. *Bombus terrestris* occurred at 88% of sites, was dominant at 48%, and accounted for 86% of all recorded individuals. The occurrence of *B. dahlbomii* was negatively correlated with *B. terrestris* along the transect. In the Challhuaco Valley, the abundance of the native *B. dahlbomii* over the two decades was negatively correlated with the abundance of both exotic species, and the native was not recorded in the last five years of the study, indicating that it was locally extirpated. The collapse of *B. dahlbomii* in this region was thought to be caused by the more generalist foraging behavior of *B. terrestris*, its larger colony size, longer colony life cycle, and possibly by pathogens introduced and spread by the exotic bumble bees (Arbetman et al. 2012). Competition for other resources may be important. Nagamitsu et al. (2010) experimentally trapped and removed exotic *B. terrestris* from sites in Japan and in one of two years found substantial increases in native bees.

Experiments conducted by Thomson (2004, 2006) suggest that competition might be a mechanism for the displacement of native pollinators by exotics and provide good evidence that they can competitively displace natives. She distributed hives of *A. mellifera* at sites in coastal California and then measured how *A. mellifera* affected the foraging behavior and reproductive success of a native eusocial bee, *Bombus occidentalis*. *Bombus occidentalis* colonies near *A. mellifera* hives had lower rates of forager return and shifted their foraging from pollen to nectar. The reproductive success of the native bee was also reduced near *A. mellifera* hives. Thomson (2006) later examined how these experimental results corresponded with niche overlap in resource use and spatial correlations in the abundance *A. mellifera* and *B. occidentalis*. Associational approaches did not correspond well with the effects measured in the experimental study, suggesting that evaluating the impact of exotic pollinators based on spatial or temporal correlations might not detect important negative effects of exotic pollinators. This should be kept in mind for many of the studies discussed next.

Some correlative studies also suggest that exotic pollinators may have important effects on the behavior and local abundance of native pollinators. For example, our analysis of the nine comparisons of the abundance of native and exotic bees in time or space showed a significant decrease in the densities of native pollinators as the densities of exotic pollinators increase (Fig. 3). For example, Roubik et al. (1986) found that the presence of exotic Africanized *A. mellifera* correlated with substantial decreases in the peak foraging rates of native Meliponine bees in Panamanian forests. Paini and Roberts (2005) found a decrease of 23% in nest production of the solitary bee, *Hylaeus alcyoneus*, when nesting occurred in areas where *A. mellifera* was dense. Aizen and Feinsinger (1994) quantified pollinator communities visiting two tree species in fragmented dry tropical forests in northern Argentina. They found that increasing fragmentation corresponded with shifts in pollinator communities towards dominance by the exotic *A. mellifera* and decreases in native pollinators. On individual trees, native pollinators were negatively correlated with the abundance of *A. mellifera*, but whether this was due to the effects of *A. mellifera* on natives or opposite responses to forest fragmentation was not clear.

There are no native *Bombus* species in Australia (Hingston 2005), creating the potential for *Bombus* to invade unfilled niches. In Tasmania, Hingston and McQuillan (1998) investigated resource competition between the exotic *B. terrestris* and two native bee pollinators in the genus *Chalicodoma* on the bladder pea, *Gompholobium huegelii*. In some plots, they excluded *B. terrestris* and allowed only the natives. In other plots, all three species were allowed to forage. In plots where *B. terrestris* occurred, *Chalicodoma* spp. reduced the mean time spent foraging at each flower. However, the presence of *B. terrestris* did not affect the densities of natives and there were no aggressive interactions among the three species. Thus, they suggested that the reduction in foraging time indicated resource depletion by *B. terrestris* which otherwise would have been used by the *Chalicodoma* species.

The effects of *B. terrestris* on native insect pollinators in Israel were investigated on *Arbutus andrachne* in a 14-year population census (Dafni and Shmida 1996), finding a reduction in native visitors and an increase in the exotic *B. terrestris* over time. This census was conducted on a single tree of *Arbutus andrachne*, so it may not represent larger-scale pollinator densities. This research was then expanded to include one-year population censuses of insect pollinators on three other plant species, *Capparis spinose*, *Satureja thymbra*, and *Stachys distans*. The authors found that the presence of *B. terrestris* had mixed impacts on the native pollinator community. On *C. spinosa* plants, the presence of *B. terrestris* correlated with a reduction in native Israeli populations of *A. mellifera*, *Proxylocopa olivieri*, and *Xylocopa pubescens*, whereas small solitary bees were not affected. On *S. thymbra*, *B. terrestris* physically drove native species away from flowers. *Stachys distans* plants showed an increase in *A. mellifera* activity during the time of the day when *B. terrestris* was less active (Dafni and Shmida 1996).

Other studies are less conclusive. For example, Roubik et al. (1996) studied the impact of bee visitation to *Mimosa pudica* by the exotic Africanized *A. mellifera*. From 1977 to 1994, and at 11 study sites in French Guiana, he found that these *A. mellifera* displaced native *Melipona* species during some years of the study, but in other years, the native species returned. Over the entire time period, there was no cumulative change in the densities of native bee species.

Other research has not found effects of exotic pollinators on native pollinators. In a 17-year study on Barro Colorado Island, Panama, which included seven years before honey bee arrival, abundance surveys found no evidence for population-level impacts of exotic *A. mellifera* on native bees (Roubik and Wolda 2001). In a six-year pollen use study conducted in North Khartoum, the impacts of the exotic *Apis florea* on *A. mellifera*, which in this case was the native, were investigated. Pollen analysis from hives, and measurements of visits to the three most utilized plant species, showed that there was little competition between the exotic and native *Apis* species and therefore no likelihood of displacement (Shafie et al. 2002).

There has been a great deal of research into the potential impacts of *A. mellifera* on native pollinators in Australia (Schwarz and Hurst 1997; Paton 1993, 1996, 1997; Wills et al. 1990; Pyke and Balzer 1985). These studies did not find direct evidence for negative impacts of *A. mellifera* on native pollinator abundance, survival, or fecundity. A study of brood rearing, foundress dispersal, and overwintering success found that there was an *increase* in survival of native pollinators in sites where honey bee densities were elevated (Schwarz et al. 1991). However, in a review of the impacts of *A. mellifera* in Australia, Paini (2004) noted that many studies had small sample sizes and included potential confounding factors. These authors argued that a clear understanding of the impact of commercial and feral honey bees required increased replication and longer-term studies.

All meta-analyses are limited by their search terms, and three important papers that were not identified in our search, on how exotic pollinators might affect native pollinators, were Smith-Ramírez et al. (2014), Nagamitsu et al. (2007) and Matsumura et al. (2004). We did not include them in the meta-analysis to avoid bias in the selection process. Smith-Ramírez et al. (2014) sampled insect visits to the temperate rainforest tree, *Eucryphia cordifolia*, in Chile over ten years. They found tremendous variation from year to year, but patterns indicated a long-term decline in native pollinators and increasing exotics. In contrast, in enclosure experiments with different mixtures of native and non-native *Bombus* species, Nagamitsu et al. (2007) found that the body mass of queens and the nest mass of colonies did not differ, thus, showing no effect of the exotic pollinators on the natives. Matsumura et al. (2004) conducted an eight-year population census of *B. terrestris* naturalization at two sites in Monbetsu, Japan. They counted bees, collected pollen samples from bee corbiculae, and located nest sites of the *B. terrestris* and native bumble bees that visited three oak species, *Quercus dentata*, *Q. crispula*, and *Q. serrata*. They found increases in the density of the exotic *B. terrestris* but no decrease in the density of native *Bombus* species.

Most pollinators are generalists, including the exotic pollinators that have been introduced to novel environments for agriculture. These generalist foraging strategies foster weak mutualisms between pollinators and different plant species which are often integrated into native webs in ways that alter their function (Aizen et al. 2008). In this context, exotic pollinators often appear to displace natives, but not

always, and when they do the consequences for pollination systems are mixed. Studies that link changes in pollinator community composition with the effects of that community on native plant fitness would contribute a great deal to this knowledge gap.

Conclusion

In general, comparative studies of the impact of exotic insect pollinators on native pollinator systems show a wide range of outcomes. However, we found that exotic bees are generally less efficient pollinators than natives, and because most pollinators are highly generalist in function, they have substantial potential to disrupt native pollinator-plant networks (Aizen et al. 2008, 2014). Second, despite the fact that studies of impacts of exotic pollinators on natives range widely in their conclusions, findings generally ranged from no impact to negative impact (also see Mallinger et al. 2017). In other words, positive outcomes for native pollinators were rare. But the direct effects of exotic insect pollinators on native plant species can range from highly positive to negative (also see Mallinger et al. 2017), leaving this element of exotic impact much less clear. However, in some cases, the *indirect* effect of exotic pollinator preference for exotic plant species has the potential to be negative for native plants. A better understanding of the effects of exotic pollinators on native plants and insect pollinators will be improved by quantifying the pollination effectiveness of individual species in the native pollinator community, quantifying species-specific responses of native pollinators (see Morales et al. 2013), and by well-replicated experimental manipulations of exotic pollinators in native systems.

Data availability Data are available in the supplementary table.

Code availability Code for the meta-analysis is available on request.

Declarations

Conflict of interest We have no conflicts of interest.

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