CABI Reviews 2022 **17,** No. 006

When bio is not green: the impacts of bumblebee translocation and invasion on native ecosystems

Josefina Lohrmann, Nicolás R. Cecchetto, Nahuel Aizen, Marina P. Arbetman, and Eduardo E. Zattara*

Address: Grupo de Ecología de la Polinización, INIBIOMA, Universidad Nacional del Comahue, CONICET, Quintral 1250, Bariloche 8400, Argentina.

ORCID information: Josefina Lohrmann (orcid: 0000-0002-1283-2491); Nicolás R. Cecchetto (orcid: 0000-0002-7004-424X); Nahuel Aizen (orcid: 0000-0001-6844-196X); Marina P. Arbetman (orcid: 0000-0002-8382-2522); Eduardo E. Zattara (orcid: 0000-0002-9947-9036)

***Correspondence:** Eduardo E. Zattara. Email: ezattara@comahue-conicet.gob.ar

Received: 01 December 2021
Accepted: 16 December 2021

doi: 10.1079/cabireviews202217006

The electronic version of this article is the definitive one. It is located here: http://www.cabi.org/cabireviews

Abstract

Adequate pollination is fundamental to optimize reproduction and yield of most flowering plants, including many staple food crops. Plants depending on insect pollination rely heavily on many wild species of solitary and social bees, and declines or absence of bees often hampers crop productivity, prompting supplementation of pollination services with managed bees. Though honeybees are the most widely deployed managed pollinators, many high-value crops are pollinated more efficiently by bumblebees (*Bombus* spp.), prompting domestication and commercial rearing of several species. This led to a blooming international trade that translocated species outside their native range, where they escaped management and invaded the ecosystems around their deployment sites. Here, we briefly review the history of bumblebee invasions and their main impacts on invaded ecosystems, and close by discussing alternatives to the use of commercially reared bumblebees to enhance crop pollination. As evidence of widespread negative effects on local ecosystems of bumblebee invasions builds up, bumblebee trade adds to the list of examples of "biological" strategies devised to solve agricultural problems that ended up being far from the "green," eco-friendly solutions they were expected to be.

Keywords: biological invasions, pollination services, bee pathogens, bumblebee trade

Review methodology: To write this review, we drafted the main sections based on the different aspects of bumblebee trade and translocation, loosely using [1] as a starting point that needed updating. Then, each author was assigned a section/topic, using Google Scholar as a search engine with keywords related to the topic to complement the list of literature already known to us, and incorporating relevant articles. We also checked the reference lists of all consulted articles to look for relevant works not revealed by our search strategy.

Introduction

> "…(The) history of evolution is that life escapes all barriers.
> Life breaks free.
> Life expands to new territories.
> Painfully, perhaps even dangerously."
> *Michael Crichton, Jurassic Park* [2]

Insufficient or inadequate pollination services translate into lower seed set and poorer fruit yields. Although this fact has been known since humans started translocating crop species beyond their native ranges or growing crops at densities or conditions with which their natural pollinators could not cope, commercial pollinator supplementation is a relatively new agricultural strategy. By far, the most common managed pollinator is the European honeybee *Apis mellifera*, which has been moved all over the world from its native African and Eurasian range, becoming naturalized (and sometimes invasive, see below) in all areas it was introduced to [3, 4]; however, honeybees do not work well in enclosed spaces (like greenhouses) and are less efficient pollinating specialized flowers with deeper corollas or requiring buzz pollination. This prompted attempts to domesticate bumblebees (genus *Bombus*); it took over 60 years to achieve this goal, but in 1987, commercial rearing began, and since then, production and sale of millions of colonies of several species have been the basis for a blooming business [5].

Marketed as a "biological" solution to an agricultural need (i.e., an ecosystem-friendly, "green" alternative to technological solutions), farmers across the world embraced the use of commercial bumblebee colonies and their breeding and trade became a profitable market [6]. Even though the risks of translocating species have always been well known, not all species of *Bombus* are equally easy or profitable to domesticate for commercial breeding; this resulted in both pressures from farmers of regions lacking commercial rearing of native species to import colonies of foreign species and an eagerness from companies producing them to sell them [5]. Despite some early assertions that commercial colonies were unlikely to genetically pollute their wild conspecifics or become invasive (based on commercial colonies being "out of sync" with natural populations, outside their climatic niches or prevented from releasing reproductive individuals through devices like queen excluders), as Jurassic Park's Dr. Ian Malcolm wisely said, "life finds a way": commercial bumblebees quickly escaped, established feral populations, and became invasive (defined as explosively expanding in abundance and geographic range and negatively interfering with ecosystems) almost everywhere they were deployed, leading to disruption of natural habitats and driving some native bee species near extinction [1, 3, 7]. In this article, we review evidence for the impacts on native ecosystems of commercial bumblebee deployment, escape, establishment, and invasion. We discuss impacts associated with competition for resources, pathogen co-introduction, genetic introgression and hybridization, and changes in pollination networks by the three species with best documented invasions (*Bombus impatiens*, *Bombus ruderatus*, and *Bombus terrestris*). We then briefly discuss the main drivers of invasion and finalize by discussing the ecological cost/benefit of supplementing pollination services with commercial bumblebee colonies and the main alternatives to their use.

Invasive bumblebee species and invasion events

Several of the approximately 250 described species of *Bombus* bumblebees [8] have been translocated through history, but only three have shown enough range expansion outside of their native distribution to be considered invasive [1]: the North American *Bombus impatiens* and the European *Bombus ruderatus* and *Bombus terrestris*. While *B. ruderatus* was translocated only through wild-caught fertilized queens released to form feral colonies, most invasion events for *B. impatiens* and *B. terrestris* were driven by trading of commercially reared queens and colonies.

Bombus (Pyrobombus) impatiens is a species native to eastern North America, where it is the most frequently found bumblebee. After commercial breeding of captive *B. terrestris* started in Europe in the late 1980s, both Canada and the US banned its import, prompting the development of the native *B. impatiens* instead [1]. Commercial production of *B. impatiens* from wild queens started in eastern Canada in 1990; later, queens of *B. impatiens* were translocated to Europe between 1992 and 1994 to develop this species for commercial rearing in the same facilities used to develop *B. terrestris*, and the resulting colonies were brought back to the US [9]. During the 1990's, deployment of commercial colonies of this species was restricted to areas within its native distribution; in western North America, *Bombus (Bombus) occidentalis*, a species native to that region, had been developed instead. However, commercial colonies of this species crashed in 1999, likely due to *Nosema bombi* infections; in response, importation of *B. impatiens* colonies was permitted to western Canada first and soon to western US states [10] (Fig. 1A). Presumptively, feral individuals of *B. impatiens* were found in British Columbia in 2003 [12] and have since then been expanding in the Pacific Northwest [10]. Starting in the mid-90s, commercial colonies have also been imported to Mexico in large numbers for exclusive greenhouse use [5, 13]; escaped individuals have been observed from Baja California to Querétaro [11] (Fig. 1A). Habitat suitability modeling for the species suggests it has a low chance of establishing feral populations in northern México (including Baja California) [10]; however, some invasive species have been known to expand their ecological niches upon arrival to new habitats [14–16].

Bombus (Megabombus) ruderatus is a species native to Western and Central Europe, and is declining in parts of its native range, but abundant where it was introduced [1, 17]. Although *B. ruderatus* has never been commercially reared, it was translocated from its European range to two separate continents in the Southern Hemisphere (Fig. 1B) to enhance the reproduction of another introduced European species, the red clover *Trifolium repens*: first to New Zealand over 130 years ago and more recently to southern South America. In both cases, invasion required just a few introductory events [5]. In New Zealand, UK-caught *B. ruderatus* queens were introduced in 1885 and 1906, along with at least six other bumblebee species [18, 19]. By 1960, *B. ruderatus* had already spread over large areas of the Southern Island—concurrently with *B. terrestris* and *B. hortorum* [20]—and by 1995, it had become, along with *B. terrestris*, ubiquitous throughout New Zealand [21]. In South America, about 300 *B. ruderatus* queens brought from New Zealand were released in December 1982 and November 1983 in two regions of south-central Chile, representing the first introduction of European bumblebees into South America [22]. *Bombus ruderatus* rapidly spread and invaded southward at both sides of the Andes. Although in some areas of New Zealand and Argentina *B. ruderatus* seems to have declined compared to the initial invasion stage (especially after *B. terrestris* introduction, see below), this species is still abundant in its non-native ranges [23, 24].

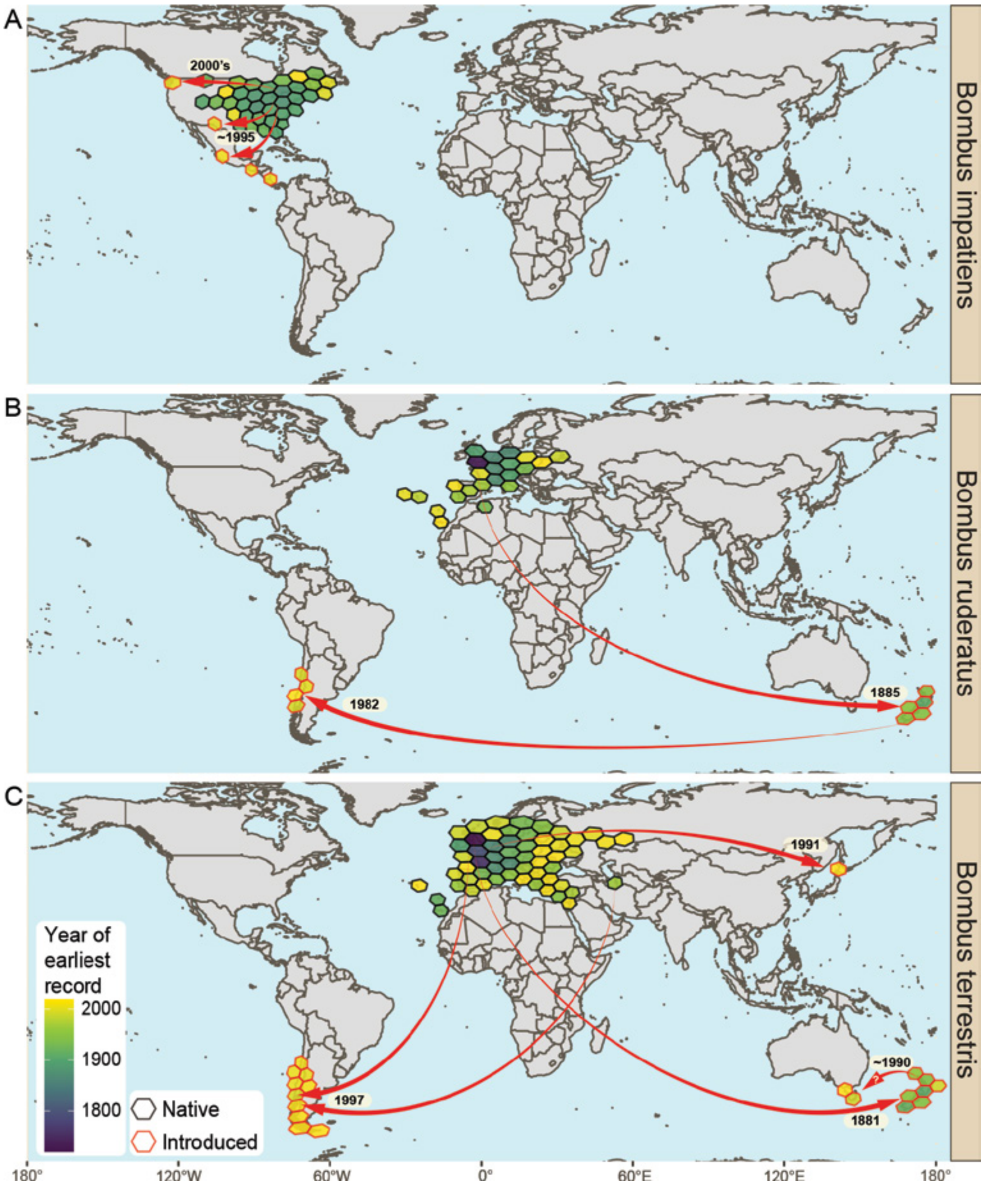

Figure 1. Global distribution of the three main invasive bumblebee species. Occurrences of each species were downloaded from GBIF [11], projected on a global grid of approximately 520-km radius hexagonal cells, and each cell was color-coded according to the year of the earliest reported occurrence within the cell; cells within invaded ranges have red outlines. Red arrows indicate the approximate origin and date of the initial translocation event (the "?" indicates a non-confirmed translocation of *Bombus terrestris* to Tasmania from New Zealand). Only cells with more than five records were retained; some reports of *B. terrestris* in Canada were removed since they actually refer to *Bombus terricola* records. (A) *Bombus impatiens.* (B) *Bombus ruderatus*. (C) *Bombus terrestris.*

Bombus (Bombus) terrestris is a species native to temperate Eurasia [25] that is a matter of concern worldwide due to its invasiveness and impacts [26] (Fig. 1C). Besides its rearing within its native range, it has been exported to Israel, New Zealand, Tasmania, China, South Korea, Japan, México and Chile [27]. In Europe, commercial rearing of *B. terrestris* began in the late 80's for pollination of many crops (particularly tomato), replacing manual pollination and faring even better than honeybee pollination [28]. The species comprises several subspecies with distinct distribution across the continent, and commercial rearing is somewhat customized to different regions [5]: while in continental Europe mostly *B. terrestris terrestris*, *B. t. sassaricus* and *B. t. dalmatinus* are used for pollination efforts, only the local subspecies *B. terrestris audax* in the United Kingdom and *B. terrestris canariensis* in the Canary Islands are allowed for outdoor pollination. Despite these practices, among European countries, only Norway, Turkey, and the Canary Islands (Spain) have actually imposed restrictions on the import of exotic bumblebees [5]. *B. terrestris* has also shown invasive behavior in Israel, but whether this resulted from early introduction of commercial colonies [27] or range expansion is unclear, since this region is at the margins of the natural distribution of the species [29]: although a local subspecies was present as early as 1930 at northern Galilee, its distribution has been expanding south since then, probably fueled by the expansion of irrigated land [30]. Agricultural use of *B. terrestris dalmatinus* started in the country in 1991 [5], and 10 years later it was the predominant species in Mt. Carmel, where it was previously absent [30]. Importing of *B. terrestris* to the country is presently prohibited, and commercial rearing is based on local populations of the subspecies *B. t. dalmatinus* [5].

B. terrestris was imported to New Zealand in 1881 for pollination of red clover, and five years later, feral populations could already be found in the wild [5, 31]. Since then, it became naturalized, rapidly expanding its range at maximum rates of approximately 90 km/yr [18] and replacing previously introduced *Bombus* species as the main pollinating bumblebees. It is currently reared commercially for tomato pollination.After being introduced in 1990 likely in Hobart, Tasmania, *B. terrestris* became feral and expanded its range at a rate of up to 25 km/yr [32]. Import of *B. terrestris* is banned in Australia and alternative native buzz-pollinating bees are being explored [26]. In Japan, *B. terrestris* was introduced in 1992 for greenhouse crop pollination with almost immediate ecological impacts [33–37]. Therefore, after the Japanese government enacted its Invasive Alien Species Act in 2004 [38], *B. terrestris* was categorized as an invasive species and its introduction was banned in the country nearly 20 years later [39]. In North America, *B. terrestris* import has been prohibited in the USA and Canada, but was briefly allowed into Jalisco, Mexico, in 1995 and 1996; detection of the pathogen *Nosema bombi* in a batch of colonies intended for shipment to that locality led to the destruction of the batch and removal of import permits, stopping further introductions of this European species and prompting importation of *Bombus impatiens* (see above) instead [40]. Feral colonies of *B. terrestris* have not been reported in Mexico to date. In South America, import of colonies of *B. terrestris* from Belgium and Israel began in central Chile in 1997; by 2006, they had been already detected across the Andes on the Argentinian side, where its range continues to expand South and East [7]. Although in neighboring countries import of *B. terrestris* is forbidden, it remains legal in Chile in spite of efforts to impose a ban [41]; consequently, thousands of queens are imported yearly to this day.

Impacts of invasive bumblebees due to competition with native bees

When resources are limited, competition between species sharing these resources is likely. Negative effects of introducing exotic bees on native bee fauna can be mediated by competition for floral resources and competition for nesting sites [1, 3].

The main approach to assess potential competition for floral resources is the analysis of the foraging habits of each species to determine the extent of overlap in flower visitation. In Patagonia, both *Bombus ruderatus* and *Bombus terrestris* show a significant overlap with the native bumblebee *Bombus dahlbomii* in visited plant species: 17 out of 20 plant species for *B. ruderatus* [42] and 15 out of 20 plant species for *B. terrestris* [24]. In Japan, Inoue and Yokoyama [37] found significant foraging overlap between *B. terrestris* with *Bombus hypocrita sapporoensis* and *Bombus pseudobaicalensis*. Besides overlap, foraging efficiency and mechanical interference also contribute to competition for floral resources: a study in the UK found that imported *B. terrestris dalmatinus* can collect more nectar per hour and achieve higher reproductive success than the native subspecies *B. terrestris audax* [43], and Hingston and McQuillan [44] found in Tasmania that when *B. terrestris* foraged concurrently with native bees, these native bees spent less time at each flower. Demonstrating niche overlap is necessary but not sufficient to prove competition [1]; even in extreme cases, like the precipitous decline of the native species *B. dahlbomii* concomitant to the arrival of introduced *B. terrestris* to Patagonia [24], the role of interspecific competition for floral resources remains a hypothesis.

Competition for nesting sites with native bees is even harder to demonstrate, since *Bombus* nests are notoriously hard to locate [3]; thus, less evidence for it is currently available. Studies in Japan—where native bumblebees have declined coincidently with *B. terrestris* invasion—found overlap in nest site preferences between *B. terrestris* and Japan's native bumblebee species [34, 36]. Evidence of more direct competition for sites came from laboratory experiments that found that queens of *B. terrestris* succeeded in usurping the nests of native bumblebees within artificial nest boxes [45], and reports of dead queens of native bumblebee species found in and around *B. terrestris* nests in the field in Japan [37]. Differences in phenology can also impose an asymmetry to competition: *Bombus terrestris* not only benefits from an earlier emergence from hibernation in comparison with its native competition [34], but is also more flexible regarding nesting selection, thriving on artificial nests, rodent cavities, and even anthropic debris [34, 46] .

Impacts of invasive bumblebees due to pathogen co-introduction

There is strong evidence that introduced bumblebees bring with them a significant array of pathogenic parasites with large potential to spill over to native bee species [1, 47]. On the one hand, introduced bumblebees can harbor pathogenic species or strains that are novel to native species populations and for which they lack adequate immune defenses; on the other hand, the high demographic densities implied by commercial scale rearing often promote both high levels of parasite infection and promotes selection of highly parasite-tolerant genotypes

[48, 49]. Native populations can be exposed to novel pathogens as a result of contact with introduced exotic species [13, 50–52], or by contact with conspecific colonies that have been translocated to rearing facilities outside their native range, infected there by pathogens, and taken back to their native range [5, 9, 49, 53]. The susceptibility to decline is phylogenetically structured within the *Bombus* genus, with some clades more prone to decline than others, with non-declining species harboring internal parasites with rather small fitness costs, probably because highly lethal parasites act as strong ecological filters [54]. The impact of each pathogen on different species is still under investigation, but it is clear that pathogens can have synergistic impacts on bumblebee health [6].

Pathogens have been shown to regulate, to a large extent, the fate of bumblebee colonies [55]. To understand their impact on colony development, it is important to understand their roles, their routes of infection, how infection affects each individual bee, and which stages in the colony cycle are most affected by the pathogen. Most species of *Bombus* native to cold and temperate regions are univoltine (i.e., produce a single colony cycle per season), although recent observations suggest that climate change-driven warmer and longer summers might be resulting in bivoltine populations [56, 57]. The colony cycle begins as fertilized queens that have been overwintering emerge, feed, and start looking for suitable nesting sites to found a new colony. Once a site is found, the queen lays the eggs for the first workers and looks after them until they emerge from the pupal case. Until this point, the queen is the only foraging member of the new colony, but after the first workers emerge, they take over foraging first and then start helping with brooding the next batch of eggs and larvae. As the season proceeds, the number of workers increases, until the colony begins to generate reproductive individuals: gynes (future queens) and males, which will leave the nest to mate. Past this point, the colony enters into a senescent phase, in which the dominance of the queen over the workers debilitates as the founder queen ages and eventually dies, and the colony degenerates quickly as parasites and commensals take over the nest [1].

Emergence from hibernation and nest initiation is probably the most critical stage of the bumblebee life cycle: finding a suitable place for colony foundation, including wax production and egg laying, finding flowers to feed, and gathering pollen to supply brood [1, 25]. Several pathogens strongly impact queens at this stage. The nematode *Sphaerularia bombi* induces complex changes in bumblebee's gene expression and behavior, described as mixed and disorientated, with characteristic flight behavior and sound production [58, 59]. Infected new emerging queens search for overwintering sites instead of seeking for a suitable place for nesting, after which the nematode reproduces, killing the host and leaving infective progeny waiting for the next generation of new fertilized queens that are looking for hibernation sites [58]. The apicomplexan *Apicystis bombi* and the microsporidian *Nosema bombi* also can preclude infected queens from founding a colony [60]. The effects of infection by the trypanosomatid *Crithidia bombi* on hibernation are less clear: studies showed that hibernating infected queens lost more body mass and were less likely to initiate a colony than control ones, but there was no difference in survival of each group; survival varies strongly among families, and evidence of reduction in hibernation success is only indirect [61–63].

After finding a nesting site, founder queens lay the first batch of eggs and brood them. *Nosema bombi* can travel through ovaries to the offspring and cause their death; healthy *B. terrestris* colonies can also be infected from outside sources, with younger bees showing higher susceptibility to infection [60, 64, 65]. *Crithidia bombi* has lethal and sublethal effects on different *Bombus* species. They are not vertically transmitted, but acquired from spore-contaminated flowers by foragers, which can pass spores to larvae and in turn infect brooding workers. The impact of this parasite is very context-dependent, particularly with diet, and includes behavioral and cognitive impairments (e.g., reduced ability to learn the color of rewarding flowers) [62, 66, 67]. Single infections with the neogregarine *Apicystis bombi* cause moderate mortality (<20% of queens), but reduce fat reserves, which might hamper overwintering [68]. Viruses also affect colony startup: infection with Kashmir bee virus (KBV) and Israeli acute paralysis virus (IAPV) causes slower offspring production and/or delayed colony startup [69]. In contrast to the previous pathogens, viral infections by KBV and IAPV seem to be sourced from honeybee colonies, with little evidence for secondary propagation within the bumblebee community [70, 71].

A final point for impact is at the reproductive stage of the colony; most pathogens affect reproductive output indirectly, by causing the colony to produce lower-quality reproductive individuals or fewer of them. *Nosema bombi* lowers colony fitness mainly through lower male life span and fertility [55, 72]. Colonies infected with *Crithidia bombi* produced fewer males and thus had lower fitness than healthy colonies [62, 63]. Viral infections by KBV and IAPV also reduce the production of males [69].

Impacts of invasive bumblebees due to introgression and hybridization

Bumblebee males are prone to rather indiscriminate mating behaviors and in laboratory settings will readily mate females of other subspecies or even distantly related species [3]; although natural settings might alleviate these tendencies, there are numerous anecdotal reports of interspecific mating attempts in the wild. Thus, bumblebee trade and translocation that create new areas of contact between geographically distant and genetically different populations imply a risk of hybridization and genetic introgression.

Even though nine *Bombus terrestris* subspecies, differing in morphology, genetics, behavior, resistance to pathogens, and/or phenology, have been described throughout Europe, commercial lines traded within and outside the continent are mainly derived from two: *B. terrestris terrestris* and *B. terrestris dalmatinus* [5, 73–75]. This reduced representation promotes genetic homogenization and introgression of non-local (and probably non-adaptive) alleles into endemic populations [76]. Evidence of interbreeding between the native *B. terrestris lusitanicus* and the commercial *B. terrestris* strains has been reported throughout the entire Iberian Peninsula [77–79]. In Spain, only 19% of wild-caught bumblebees were identified as genetically pure individuals, while more than 45% showed signs of interbreeding with commercial bumblebees; introgressing alleles were found at distances greater than 60 km from managed colonies [79]. In Poland, commercial bumblebees frequently escape and mate with wild *B. terrestris* populations [80]. In contrast, in England no signs of introgression from commercial *B. terrestris lusitanicus* into native *B. terrestris audax* were found [81]. Interestingly, population genetic studies on eastern North American *Bombus impatiens* (for which no subspecies are described) found no widespread introgression from commercial to wild individuals [82].

While the consequences of genetic introgression within species are difficult to measure and predict, the impact of hybridization among species is more evident. Both in the field and in the laboratory, reproductive individuals from commercial *Bombus terrestris* and the native Japanese and Korean species *Bombus ignitus* and *Bombus hypocrita* (*hypocrita* and *sapporoensis* subspecies) mate readily [35, 83, 84]. About 20% of *B. h. hypocrita* and 30% of *B. h. sapporoensis* wild queens had sperm from *B. terrestris* males in their spermathecas [84], and 70% of the *B. ignitus* queens copulated with *B. terrestris* males in laboratory conditions [35]. Viability of diploid (worker) hybrid eggs between native bumblebee queens and *B. terrestris* males after experimental mating gave variable results, and hybrid genetic background of the workers was not confirmed for apparently successful crosses [35, 83, 85, 86]. However, reduced fecundity due to the high frequency of nonviable diploid hybrid eggs could be a significant threat to these native bumblebee species [35, 84, 87]. Although bumblebees are generally monandrous (queens mate once in their life) [88–90], *B. terrestris* males in some regions of Japan outnumber native males by a factor of more than 50 to 1 [36] and might have evolved a higher mating frequency [87]. Thus, the mating opportunities of local bumblebees with their conspecifics are substantially diminished. Interestingly, recent studies found that *B. h. sapporoensis* and *B. terrestris* queens were more likely to show polyandry in regions of Japan where the latter are more abundant (*unpublished data* in [35]). Polyandry in both bumblebee species (which increases the probability of mating with their conspecifics) could thus be an adaptive response to among-species reproductive interference [35, 87].

Impacts of invasive bumblebees due to changes in pollination networks

Plant-pollinator interactions established during or after a bee invasion can range from beneficial to detrimental to native plant communities and even for cultivated plants [91]. For example, although the native Patagonian bumblebee *Bombus dahlbomii* is the most efficient pollinator of *Alstroemeria aurea* in terms of pollen quantity and quality deposited per visit, the high-visit frequency of invasive *Bombus ruderatus* compensates for this lack and outperforms *B. dahlbomii* when cumulative visits per flower are considered [92, 93]. Similarly, after the drastic decline of *B. dahlbomii*, invasive *B. terrestris* and *B. ruderatus* became the main pollinators of two Andean orchids [94]. In an experimental setup, when seven Japanese native plant species were exposed only to *B. terrestris* pollination, five species whose flowers the invasive bumblebees could only access through nectar robbing showed decreased fruit set or fruit quality or both, but when the same plants were exposed to a mix of *B. terrestris* and native bumblebees, pollination success varied unpredictably [95–97]. This difference in pollination success suggests that native plants are relatively specialized to native bumblebees, and therefore, invasive bumblebees could be poor substitutes for local ones, and that even at medium invasion densities, the fertility of native plants is compromised. Invasive bumblebees also show patterns of pollen transport different to those of native pollinators, potentially altering the genetic structure of plant populations—as it was reported in pollination networks invaded by honeybees [98–100]. For raspberry crops in northwestern Patagonia, disproportionate abundance of invasive *B. terrestris* relative to flowers altered the historical cost-benefit balance of pollination interactions and drove this mutualism toward antagonism by decreasing fruit yields [101, 102]. Overall, current data show that impacts of invasive pollinators on plants are predominantly negative for native species, mixed for crops, and positive for invasive species [91].

Drivers and facilitators of bumblebee invasions

While most arthropod biological invasions are usually related to undesirable species, like pests or disease vectors, that are accidentally translocated out of their home range, there are no known reports of unintentional bumblebee translocations across continents. Instead, the main driver of *Bombus* invasions has been the provision of pollination services—whether needed or unneeded—to augment yield of plant species of economic value, like crops. Climate change might also be driving invasions within continents through ecological niche range shifts of native species, and facilitating establishment and range expansion of intentionally translocated species. Introduction of species happen most often as a single translocation event in which only a few members of a given species are brought into a novel environment. Feral populations resulting from such events will inevitably have a reduced genetic pool and will be particularly vulnerable to stochastic events [103, 104]. Thus, most introduction events fail to establish naturalized populations, and the relatively few that achieve critical numbers can take decades to become invasive. Despite this difficulty, even a single introduction event can result in successful invasion, as shown by the point release of fertilized queens that primed the invasion of Patagonia by *Bombus ruderatus* [22]. However, in most recent pollinator invasions, driven by commercial provision of pollination services, the foreign species is introduced in great numbers over a prolonged period of time. Each year, hundreds of thousands of bumblebee hives are brought into new environments to provide pollination services for crops [5, 7]. Because of this, alien bumblebees are mostly safe from stochastic forces, harbor more genetic diversity, and are also actively catered by human care [105, 106]. Such constant subsidies ensure that if a species has any invasive potential at all, then it will eventually become established. Even without invasive potential, introduced pollinators can impact native ecosystems if sustained through human care. For example, honeybees can outcompete local pollinators within environments in which they would not thrive on its own [107]. As long as the pollinator is domestically bred, it might not matter if a natural ecosystem acts as a population sink: the foreign species could exploit resources, displace local species, and spread diseases, as an invasive species would.

Climate change is a driving force of many ecological invasions since climate is one of the main factors defining species distribution [108, 109]. As the thermal landscape of the world is altered, species can venture into previously inaccessible ecosystems where they might become invasive. Climate change can also displace species from their original habitats, liberating niches that foreign species can exploit and, even when not displaced, species can experience a loss of fitness as a result of suboptimal climatic conditions, which can allow low-fitness foreign species to outcompete the native ones, leading to invasion events. The Brazilian bumblebee *Bombus bellicosus*, for example, is slowly being displaced toward colder latitudes to the southernmost regions of Brazil and further into Argentina as a consequence of heat stress suffered in its historical range [110]; this southern shift could potentially make it invasive within the novel range, while facilitating invasions from other species after abandoning parts of its historical range. Other examples of potential invasion driven by climate change are the spread of *Bombus terrestris* and *Bombus lapidarius* above the Arctic Circle [111], the expansion of *B. terrestris* over northern Israel [30], or the arrival to the British islands of *Bombus hypnorum* from mainland Europe [112, 113]. Climate change can also worsen ongoing invasion events, by introducing additional stress on native species and enabling invaders to advance further and faster.

Since organisms are not passive subjects to their environment, but instead regulate their development and behavior in response to climate change and other external challenges [114], it is fundamental to incorporate perspectives that take into account the differential ability of bumblebees to adapt and respond through both phenotypic plasticity and adaptive evolution [115]. This can result in complex interactions with other drivers, like changes in land use: in North America, average bumblebee worker size, measured from museum specimens of four *Bombus* species, decreased from historical (1897–1926) to recent (1978–2016) collections, a change associated with increasingly unfavorable environmental conditions [116]. In contrast, studies in Belgium and Germany have found trends toward an increasing body size of queens and workers [117, 118]; such increase in size does not seem to be a direct response to warmer temperatures, but is instead associated with changes in land use such as agricultural intensification and urbanization. The direction and intensity of these documented trends of size change are species-specific [116–118] and thus can potentially impact overall pollination networks by altering size-dependent plant-pollinator interactions and changing the composition of local pollinator communities. Additionally, invasive species have been shown to shift and expand their climatic niches within their invaded ranges [119], as described for example for the Asian giant resin bee *Megachile sculpturalis* [120, 121] or the bull-headed dung beetle *Onthophagus taurus* [15]. Such examples demonstrate the plasticity and adaptability of invasive species in the face of environmental challenges, and the complex network of interactions between environmental drivers and biological capabilities that need to be traced to be able to predict species invasive potential and introduction and invasion outcomes. In other words, our current state of knowledge is often still insufficient to fully and confidently ascertain the risks of species translocation.

Concluding remarks: do we really need to keep importing bumblebees?

Deployment of commercially reared bumblebee colonies is often portrayed as a biological, or "green," eco-friendly solution to missing or deficient pollination services for crops. However, worldwide implementation has repeatedly resulted in biological invasions that are now near impossible to revert. As we summarized above, these invasions are taking a heavy toll on native ecosystems. Just as it happened with other examples of "biological" solutions (e.g., the worldwide importation of the Asian harlequin ladybeetle *Harmonia axyridis* for pest control [122]), translocation of bumblebees has proven to be far from environmentally friendly. Some countries, like Australia, have thus chosen to ban the importation of bumblebees, despite discontent from the agricultural sector [26]. But what are the alternatives?

A first answer would be the local rearing of native species. Commercial rearing of *Bombus impatiens, Bombus* *vosnesenskii*, and *Bombus huntii* in North America, and *Bombus ignitus* in Japan is ongoing [5, 123, 124]. In South America, commercial rearing of *Bombus pauloensis* (= *B. atratus*) and/or *Bombus bellicosus* is ongoing or being developed in Colombia, Argentina, and Uruguay [125–130]. In Pakistan, *Bombus haemorrhoidalis* is being explored as an option to replace *B. terrestris* [131]. However, rearing conditions favor the growth of *Bombus* pathogens and select for a small fraction of genotypes, leading to potential erosion of genetic diversity of wild populations and pathogen spillover, as mentioned above. Other buzz-pollinating bee species have been explored as viable options in crops that require this specific type of pollination (like tomatoes). For example, a number of native species such as *Examalopsis* spp. and *Augochloropsis* spp. have been explored in Mexico to avoid import of *B. impatiens* [132]. In Brazil, breeding of two stingless bee species (*Tetragonisca angustula* and *Melipona fasciculata*) is widely established but not at the scale needed for crop pollination [133]. Import of *Melipona quadrifasciata* from Brazil to Japan has been suggested, given the very low risk of this tropical species becoming invasive in temperate and cold environments [134]. In Australia, potential native crop pollinators such as *Xylocopa lestis*, *Amegilla* spp., *Austroplebeia australis*, *Tetragonula carbonaria*, and even the introduced syrphid hoverfly *Eristalis tenax* have been explored [135–141]. However, in many cases, the biology of native pollinator species does not allow for cost-efficient, profitable rearing at commercial scale [5].

The well-proven risks of commercial-scale deployment of managed pollinators have prompted a search for technological rather than biological alternatives [142]. Asian engineers developed a proof-of-concept pollination system based on flying drones blowing pollen-laden soap bubbles over flowers [143]. In Israel, two companies (Edete and Arugga) are developing robotic arrays that use optic sensing and artificial intelligence to deliver automated pollen collection and pollination (https://www.edetepta.com, https://www.arugga.com); these technologies are being marketed as eco-friendly alternatives to managed pollinators when wild pollination services are insufficient, although they still need to be benchmarked against them for efficiency and cost-effectiveness. There is always a low-tech fallback: hand-pollination by humans is still widespread [144], especially when labor costs are low [145]. Although this approach is largely unsustainable in the long term, it provides an alternative to ameliorate losses of wild or managed pollination services, or sudden changes in the cost-benefit balance of certain crops [144].

A last and probably best alternative is increasing local pollinator diversity (especially native wild pollinators) instead of (or, at least, in addition to) import of commercially reared bees. In an assemblage of pollinators, behavioral and physiological differences between species can provide a more complete pollination service, covering more hours of the day of flower visitation or providing the crop with a collection of functional traits that can not only increase pollination in some crops such as pumpkin or tomatoes, but also create crops more capable to endure future threats such as climate change and land-use transformations [146–148]. Besides actions and measures to protect overall landscape integrity and species conservation, visitation and pollination by wild species can be locally boosted through a variety of strategies [149]. Boosting pollinator diversity is a necessary move toward ecological intensification of agricultural production and will positively challenge not only the business-as-usual of food production stakeholders but also the current low diversity of crops [150].

Any alternative solutions to importing managed pollinators are meaningless if they never reach the stakeholders requesting them. In many cases, established invasive species are so abundant that deploying commercial colonies might lower rather than enhance crop yields. Since farming stakeholders are often prone to follow advice from their peers, or biased consulting from producers of commercial pollinators, expecting a bottom-up approach to change might result in a change too slow to avoid irreversible ecosystem damage. Therefore, we suggest encouraging a top-down approach in which national and regional regulators take action to stop importation and promote development of alternative approaches, while demanding that trade regulations are fair and reciprocal, unlike the current unbalanced scenario in which countries that would not authorize importation of invasive exotic species to their own territory have no problem exporting native species with invasive potential to other countries [7]. Moreover, it will be of great importance to keep sharing information with stakeholders on the real environmental costs of some apparently "green" eco-friendly solutions and setting an example by asking for (and heeding) expert advice.

Acknowledgments

The authors thank the editor, David Hemming, for his kind invitation to write this review. J.L. is supported by an Internal Doctoral Fellowship awarded by CONICET (National Council for Scientific and Technical Research); N.R.C. is supported by an Internal Postdoctoral Fellowship awarded by CONICET. All authors declare no competing interests. This work was partially funded by the International Cooperation Project SURPASS-RD 2019-1984 awarded by CONICET and the SURPASS2 project under the Newton Fund Latin America Biodiversity Programme: Biodiversity - Ecosystem services for sustainable development, awarded by the UKRI Natural Environment Research Council (NERC) NE/S011870/2.

Author contributions: J.L., N.R.C., N.A., and M.P.A. contributed to conceptualization, writing—original draft, writing—review & editing; E.E.Z contributed to conceptualization, supervision, writing—original draft, and writing—review & editing.

References

1. Goulson D. Bumblebees: behaviour, ecology, and conservation. Oxford: Oxford University Press; 2010. 330 p.
2. Crichton M. Jurassic park. London: Random House; 1991.
3. Goulson D. Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution, and Systematics 2003;34:1–26.
4. Schneider SS, DeGrandi-Hoffman G, Smith DR. The African honey bee: factors contributing to a successful biological invasion. Annual Review of Entomology 2004;49:351–76.
5. Velthuis HHW, van Doorn A. A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. Apidologie 2006;37(4):31.
6. Goulson D, Nicholls E, Botías C, Rotheray EL. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 2015;347(6229):1255957.
7. Aizen MA, Smith-Ramírez C, Morales CL, Vieli L, Sáez A, Barahona-Segovia RM, et al. Coordinated species importation policies are needed to reduce serious invasions globally: the case of alien bumblebees in South America. Journal of Applied Ecology 2019;56:100–6.
8. Williams PH, Cameron SA, Hines HM, Cederberg B, Rasmont P. A simplified subgeneric classification of the bumblebees (genus Bombus). Apidologie 2008;39(1):46–74.
9. Cameron SA, Lim HC, Lozier JD, Duennes MA, Thorp R. Test of the invasive pathogen hypothesis of bumble bee decline in North America. PNAS 2016;113(16):4386–91.
10. Looney C, Strange JP, Freeman M, Jennings D. The expanding Pacific Northwest range of Bombus impatiens Cresson and its establishment in Washington State. Biological Invasions 2019;21(6):1879–85.
11. GBIF.org. Bombus Occurrences Structured Query [Internet]. 2021. DOI: 10.15468/dl.7dvysa. Available from: https://www.gbif.org/occurrence/download/0347458-200613084148143
12. Ratti CM, Colla SR. Discussion of the presence of an eastern bumble bee species (Bombus impatiens Cresson) in western Canada. The Pan-Pacific Entomologist. 2010;86(2):29–31.
13. Sachman-Ruiz B, Narváez-Padilla V, Reynaud E. Commercial Bombus impatiens as reservoirs of emerging infectious diseases in central México. Biological Invasions 2015;17(7):2043–53.
14. Fernández M, Hamilton H. Ecological niche transferability using invasive species as a case study. PLoS One 2015;10(3):e0119891.
15. Silva DP, Vilela B, Buzatto BA, Moczek AP, Hortal J. Contextualized niche shifts upon independent invasions by the dung beetle Onthophagus taurus. Biological Invasions 2016;5:1–12.
16. Liu C, Wolter C, Xian W, Jeschke JM. Most invasive species largely conserve their climatic niche. PNAS 2020;117(38):23643–51.
17. Kosior A, Celary W, Olejniczak P, Fijał J, Król W, Solarz W, et al. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. Oryx 2007;41(1):79–88.
18. Hopkins I. History of the bumblebee in New Zealand: its introduction and results. New Zealand Department of Agriculture, Industry and Commerce). Report No.: 46; 1914. p. 29.
19. Lye GC, Lepais O, Goulson D. Reconstructing demographic events from population genetic data: the introduction of bumblebees to New Zealand. Molecular Ecology 2011;20(14):2888–900.
20. Gurr L. The distribution of bumblebees in the South Island of New Zealand. New Zealand Journal of Science 1964;7(4):625–42.
21. Macfarlane RP, Gurr L. Distribution of bumble bees in New Zealand. New Zealand Entomologist 1995;18(1):29–36.
22. Arretz PV, Macfarlane RP. The introduction of Bombus Ruderatus to Chile for red clover pollination. Bee World 1986;67(1):15–22.
23. Goulson D, Hanley ME. Distribution and forage use of exotic bumblebees in South Island, New Zealand. New Zealand Journal of Ecology 2004;28(2):225–32.
24. Morales CL, Arbetman MP, Cameron SA, Aizen MA. Rapid ecological replacement of a native bumble bee by invasive species. Frontiers in Ecology and the Environment 2013;11(10):529–34.
25. Heinrich B. Bumblebee Economics. Harvard University Press; 2004. 296 p.
26. Cooley H, Vallejo-Marín M. Buzz-pollinated crops: a global review and meta-analysis of the effects of supplemental bee pollination in Tomato. Journal of Economic Entomology 2021;114(2):505–19.
27. Dafni A. The threat of Bombus terrestris spread. Bee World 1998;79(3):113–4.
28. Banda HJ, Paxton RJ. Pollination of greenhouse tomatoes by bees. Acta Horticulturae 1991;(288):194–8.
29. Potts SG, Willmer P, Dafni A, Ne'eman G. The utility of fundamental ecological research of plant-pollinator interactions as the basis for landscape management practices. Acta Horticulturae 2001;(561):141–4.
30. Dafni A, Shmida A. International Bee Research Association, & Linnean Society of London. The possible ecological implications of the invasion of Bombus terrestris (L.) (Apidae) at Mr Carmel, Israel. In: Conservation of bees. Vol. 18. Cambridge: Academic Press; 1996. pp. 183–200. ISBN: 0124797407.
31. Dafni A, Kevan P, Gross CL, Goka K. *Bombus terrestris,* pollinator, invasive and pest: an assessment of problems associated with its widespread introductions for commercial purposes. Applied Entomology and Zoology 2010;45(1):101–13.
32. Hingston AB, Marsden-Smedley J, Driscoll DA, Corbett S, Fenton J, Anderson R, et al. Extent of invasion of Tasmanian native vegetation by the exotic bumblebee Bombus terrestris (Apoidea: Apidae). Austral Ecology 2002;27(2):162–72.
33. Goka K. Influences of invasive species on native species. Will the European Bumble Bee, Bombus terrestris, bring genetic pollution into the Japanese native species? Bulletin of Biogeographical Society of Japan 1998;53(2):91–101.
34. Matsumura C, Yokoyama J, Washitani I. Invasion status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in southern Hokkaido, Japan. Global Environmental Research 2004;8(1):51–66.
35. Tsuchida K, Yamaguchi A, Kanbe Y, Goka K. Reproductive interference in an introduced Bumblebee: polyandry may mitigate negative reproductive impact. Insects 2019;10(2):59.

36. Inoue MN, Yokoyama J, Washitani I. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). Journal of Insect Conservation 2008;12(2):135–46.
37. Inoue MN, Yokoyama J. Competition for flower resources and nest sites between *Bombus terrestris* (L.) and Japanese native bumblebees. Applied Entomology and Zoology 2010;45(1):29–35.
38. Mizutani T, Goka K. Japan's *Invasive Alien Species Act*. Applied Entomology and Zoology 2010;45(1):65–9.
39. Goka K. Introduction to the special feature for ecological risk assessment of introduced bumblebees: status of the European bumblebee, *Bombus terrestris*, in Japan as a beneficial pollinator and an invasive alien species. Applied Entomology and Zoology 2010;45(1):1–6.
40. Winter K, Adams L, Thorp RW, Inouye D, Day L, Ascher J, et al. Importation of non-native bumble bees into North America: potential consequences of using *Bombus terrestris* and other non-native bumble bees for greenhouse crop pollination in Canada, Mexico, and the United States [Internet]. North American Pollinator Protection Campaign; 2006. p. 33. Available from: http://cues.cfans.umn.edu/old/pollinators/pdf-BBcolony/2006nonativebee.pdf
41. Smith-Ramírez C, Vieli L, Barahona-Segovia RM, Montalva J, Cianferoni F, Ruz L, et al. Las razones de por qué Chile debe detener la importación del abejorro comercial Bombus terrestris (Linnaeus) y comenzar a controlarlo. Gayana (Concepción) 2018;82(2):118–27.
42. Morales CL, Aizen MA. Does invasion of exotic plants promote invasion of exotic flower visitors? A case study from the temperate forests of the Southern Andes. Biological Invasions 2002;4(1):87–100.
43. Ings TC, Ward NL, Chittka L. Can commercially imported bumble bees out-compete their native conspecifics? Journal of Applied Ecology 2006;43(5):940–8.
44. Hingston AB, McQuillan PB. Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? Australian Journal of Ecology 1998;23(6):539–49.
45. Ono M. Ecological implications of introducing *Bombus terrestris*, and significance of domestication of Japanese native bumblebees (Bombus spp.). In: Proc Int Workshop on Biological Invasions of Ecosystem by Pests and Beneficial Organisms. Tsukuba: National Institute of Agro-Environmental Sciences; 1997. p. 244–52.
46. Prŷs-Jones OE, Corbet SA. Bumblebees. Exeter: Pelagic Publishing; 2011. 130 p.
47. Otterstatter MC, Thomson JD. Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? PLoS One 2008;3(7):e2771.
48. Meeus I, Brown MJF, Graaf DCD, Smagghe G. Effects of invasive parasites on bumble bee declines. Conservation Biology 2011;25(4):662–71.
49. Graystock P, Blane EJ, McFrederick QS, Goulson D, Hughes WOH. Do managed bees drive parasite spread and emergence in wild bees? International Journal for Parasitology: Parasites and Wildlife 2016;5(1):64–75.
50. Arbetman MP, Meeus I, Morales CL, Aizen MA, Smagghe G. Alien parasite hitchhikes to Patagonia on invasive bumblebee. Biological Invasions 2012;15(3):489–94.
51. Maharramov J, Meeus I, Maebe K, Arbetman M, Morales C, Graystock P, et al. Genetic variability of the Neogregarine Apicystis bombi, an etiological agent of an emergent bumblebee disease. PLoS One 2013;8(12):e81475.
52. Schmid-Hempel R, Eckhardt M, Goulson D, Heinzmann D, Lange C, Plischuk S, et al. The invasion of southern South America by imported bumblebees and associated parasites. The Journal of Animal Ecology 2014;83(4):823–37.
53. Goka K, Okabe K, Yoneda M, Niwa S. Bumblebee commercialization will cause worldwide migration of parasitic mites. Molecular Ecology 2001;10(8):2095–9.
54. Arbetman MP, Gleiser G, Morales CL, Williams P, Aizen MA. Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. Proceedings of the Royal Society B 2017;284(1859):20170204.
55. Otti O, Schmid-Hempel P. A field experiment on the effect of Nosema bombi in colonies of the bumblebee *Bombus terrestris*. Ecological Entomology 2008;33(5):577–82.
56. Skyrm KM, Rao S, Stephen WP. A scientific note on a trend towards bivoltinism in Western North American bumblebees. Apidologie 2012;43(1):82–4.
57. Potapov G, Kolosova Y, Bolotov IN. Possible bivoltine development of several bumblebee species in Europe. Arctic Environmental Research 2018;18(1):45–51.
58. Lundberg H, Svensson BG. Studies on the behaviour of Bombus Latr. species (Hym., Apidae) parasitized by Sphaerularia bombi Dufour (Nematoda) in an alpine area. Norwegian Journal of Entomology 1975;22(2):129–34.
59. Colgan TJ, Carolan JC, Sumner S, Blaxter ML, Brown MJF. Infection by the castrating parasitic nematode *Sphaerularia bombi* changes gene expression in *Bombus terrestris* bumblebee queens. Insect Molecular Biology 2020;29(2):170–82.
60. Rutrecht ST, Brown MJF. The life-history impact and implications of multiple parasites for bumble bee queens. International Journal for Parasitology 2008;38(7):799–808.
61. Shykoff JA, Schmid-Hempel P. Incidence and effects of four parasites in natural populations of bumble bees in Switzerland. Apidologie 1991;22(2):117–25.
62. Brown MJF, Schmid-Hempel R, Schmid-Hempel P. Strong context-dependent virulence in a host–parasite system: reconciling genetic evidence with theory. Journal of Animal Ecology 2003;72(6):994–1002.
63. Yourth CP, Brown MJF, Schmid-Hempel P. Effects of natal and novel *Crithidia bombi* (Trypanosomatidae) infections on Bombus terrestris hosts. Insectes Sociaux 2008;55:86–90. DOI: 10.1007/s00040-007-0974-1
64. Rutrecht ST, Klee J, Brown MJF. Horizontal transmission success of *Nosema bombi* to its adult bumble bee hosts: effects of dosage, spore source and host age. Parasitology 2007;134(12):1719–26.
65. van der Steen JJM. Infection and transmission of *Nosema bombi* in *Bombus terrestris* colonies and its effect on hibernation, mating and colony founding. Apidologie 2008;39(2):273–82.
66. Gegear RJ, Otterstatter MC, Thomson JD. Bumble-bee foragers infected by a gut parasite have an impaired ability to utilize floral information. Proceedings of the Royal Society of London B: Biological Sciences 2006;273(1590):1073–8.
67. Folly AJ, Koch H, Stevenson PC, Brown MJF. Larvae act as a transient transmission hub for the prevalent bumblebee

parasite *Crithidia bombi*. Journal of Invertebrate Pathology 2017;148:81–5.

68. Graystock P, Meeus I, Smagghe G, Goulson D, Hughes WOH. The effects of single and mixed infections of *Apicystis bombi* and deformed wing virus in *Bombus terrestris*. Parasitology 2016;143(3):358–65.
69. Meeus I, de Miranda JR, de Graaf DC, Wäckers F, Smagghe G. Effect of oral infection with Kashmir bee virus and Israeli acute paralysis virus on bumblebee (*Bombus terrestris*) reproductive success. Journal of Invertebrate Pathology 2014;121:64–9.
70. Singh R, Levitt AL, Rajotte EG, Holmes EC, Ostiguy N, van Engelsdorp D, et al. RNA viruses in hymenopteran pollinators: evidence of inter-taxa virus transmission via pollen and potential impact on non-apis hymenopteran species. PLOS ONE 2010;5(12):e14357.
71. Fürst MA, McMahon DP, Osborne JL, Paxton RJ, Brown MJF. Disease associations between honeybees and bumblebees as a threat to wild pollinators. Nature 2014;506(7488):364–6.
72. Otti O, Schmid-Hempel P. *Nosema bombi*: a pollinator parasite with detrimental fitness effects. Journal of Invertebrate Pathology 2007;96(2):118–24.
73. Rasmont P, Coppee A, Michez D, De Meulemeester T. An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). Annales de la Société entomologique de France (NS). 2008;44(2):243–50.
74. Moreira AS, Horgan FG, Murray TE, Kakouli-Duarte T. Population genetic structure of *Bombus terrestris* in Europe: isolation and genetic differentiation of Irish and British populations. Molecular Ecology 2015;24(13):3257–68.
75. Lecocq T, Rasmont P, Harpke A, Schweiger O. Improving international trade regulation by considering intraspecific variation for invasion risk assessment of commercially traded species: the *Bombus terrestris* case. Conservation Letters 2015;9(4):281–9.
76. Todesco M, Pascual MA, Owens GL, Ostevik KL, Moyers BT, Hübner S, et al. Hybridization and extinction. Evolutionary Applications 2016;9(7):892–908.
77. Seabra SG, Silva SE, Nunes VL, Sousa VC, Martins J, Marabuto E, et al. Genomic signatures of introgression between commercial and native bumblebees, *Bombus terrestris*, in western Iberian Peninsula—Implications for conservation and trade regulation. Evolutionary Applications 2019;12(4):679–91.
78. Cejas D, López-López A, Muñoz I, Ornosa C, Rúa PD la. Unveiling introgression in bumblebee (*Bombus terrestris*) populations through mitogenome-based markers. Animal Genetics 2020;51(1):70–7.
79. Bartomeus I, Molina FP, Hidalgo-Galiana A, Ortego J. Safeguarding the genetic integrity of native pollinators requires stronger regulations on commercial lines. Ecological Solutions and Evidence. 2020;1(1):e12012.
80. Kraus FB, Szentgyörgyi H, Rożej E, Rhode M, Moroń D, Woyciechowski M, et al. Greenhouse bumblebees (*Bombus terrestris*) spread their genes into the wild. Conservation Genetics 2011;12(1):187–92.
81. Hart AF, Maebe K, Brown G, Smagghe G, Ings T. Winter activity unrelated to introgression in British bumblebee *Bombus terrestris audax*. Apidologie 2021;52(2):315–27.
82. Suni SS, Scott Z, Averill A, Whiteley A. Population genetics of wild and managed pollinators: implications for crop pollination and the genetic integrity of wild bees. Conservation Genetics 2017;18(3):667–77.
83. Kanbe Y, Okada I, Yoneda M, Goka K, Tsuchida K. Interspecific mating of the introduced bumblebee *Bombus terrestris* and the native Japanese bumblebee Bombus hypocrita sapporoensis results in inviable hybrids. Die Naturwissenschaften 2008;95(10):1003–8.
84. Kondo NI, Yamanaka D, Kanbe Y, Kunitake YK, Yoneda M, Tsuchida K, et al. Reproductive disturbance of Japanese bumblebees by the introduced European bumblebee *Bombus terrestris*. Die Naturwissenschaften 2009;96(4):467–75.
85. Mitsuhata M, Ono M. Hybridization between Japanese and European bumblebees (Bombus spp.). Summaries of the 7th International Pollination Symposium, Lethbridge, Albarta, Canada, 1996. 1996. Available from: https://ci.nii.ac.jp/naid/10012498064/
86. Yoon H-J, Kim S-Y, Lee K-Y, Lee S-B, Park I-G, Kim I-S. Interspecific hybridization of the Bumblebees *Bombus ignitus* and *B. terrestris*. International Journal of Industrial Entomology 2009;18(1):41–8.
87. Inoue MN, Saito F, Tsuchida K, Goka K. Potential increase in mating frequency of queens in feral colonies of *Bombus terrestris* introduced into Japan. Die Naturwissenschaften 2012;99(10):853–61.
88. Schmid-Hempel R, Schmid-Hempel P. Female mating frequencies in Bombus spp. from Central Europe. Insectes Sociaux 2000;47(1):36–41.
89. Payne CM, Laverty TM, Lachance MA. The frequency of multiple paternity in bumble bee (Bombus) colonies based on microsatellite DNA at the B10 locus. Insectes Sociaux 2003;50(4):375–8.
90. Takahashi J, Itoh M, Shimizu I, Ono M. Male parentage and queen mating frequency in the bumblebee *Bombus ignitus* (Hymenoptera: bombinae). Ecological Research 2008;23(6):937–42.
91. Morales CL, Sáez A, Garibaldi LA, Aizen MA. Chapter 13. Disruption of pollination services by invasive pollinator species. In: Vilà M, Hulme PE, editors. Impact of biological invasions on ecosystem services. Basel: Springer; 2017. p. 203–20. (Invading Nature - Springer Series in Invasion Ecology).
92. Aizen MA. Flower sex ratio, pollinator abundance, and the seasonal pollination dynamics of a protandrous plant. Ecology 2001;82(1):127–44.
93. Madjidian JA, Morales CL, Smith HG. Displacement of a native by an alien bumblebee: lower pollinator efficiency overcome by overwhelmingly higher visitation frequency. Oecologia 2008;156(4):835–45.
94. Sanguinetti A, Singer RB. Invasive bees promote high reproductive success in Andean orchids. Biological Conservation 2014;175:10–20.
95. Kenta T, Inari N, Nagamitsu T, Goka K, Hiura T. Commercialized European bumblebee can cause pollination disturbance: an experiment on seven native plant species in Japan. Biological Conservation 2007;134(3):298–309.
96. Dohzono I, Kunitake YK, Yokoyama J, Goka K. Alien bumble bee affects native plant reproduction through interactions with native bumble bees. Ecology 2008;89(11):3082–92.
97. Graham M. Efecto del robo de néctar por el abejorro invasor Bombus terrestris sobre la polinización y el éxito reproductivo de la arvejilla nativa Vicia nigricans (Fabaceae) [Tesis para optar al grado de licenciado en ciencias biológicas.]. Bariloche: Universidad Nacional del Comahue; 2015.

98. Dick CW, Etchelecu G, Austerlitz F. Pollen dispersal of tropical trees (Dinizia excelsa: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest. Molecular Ecology 2003;12(3):753–64.
99. Dupont YL, Hansen DM, Valido A, Olesen JM. Impact of introduced honey bees on native pollination interactions of the endemic Echium wildpretii (Boraginaceae) on Tenerife, Canary Islands, Biological Conservation 2004;118(3):301–11.
100. Whelan RJ, Ayre DJ, Beynon FM. The birds and the bees: pollinator behaviour and variation in the mating system of the rare shrub Grevillea macleayana. Annals of Botany 2009;103(9):1395–401.
101. Aizen MA, Morales CL, Vázquez DP, Garibaldi LA, Sáez A, Harder LD. When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. The New Phytologist 2014;204(2):322–8.
102. Sáez A, Morales CL, Ramos LY, Aizen MA. Extremely frequent bee visits increase pollen deposition but reduce drupelet set in raspberry. Journal of Applied Ecology 2014;51(6):1603–12.
103. May RM. Stability in multispecies community models. Mathematical Biosciences 1971;12(1):59–79.
104. Lande R. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 1993;142(6):911–27.
105. Simberloff D. The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics 2009;40(1):81–102.
106. Fauvergue X, Vercken E, Malausa T, Hufbauer RA. The biology of small, introduced populations, with special reference to biological control. Evolutionary Applications 2012;5(5):424–43.
107. Herrera CM. Gradual replacement of wild bees by honeybees in flowers of the Mediterranean Basin over the last 50 years. Proceedings of the Royal Society B: Biological Sciences 2020;287(1921):20192657.
108. Walther G-R, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, et al. Alien species in a warmer world: risks and opportunities. Trends in Ecology & Evolution 2009;24(12):686–93.
109. Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F. Will climate change promote future invasions? Global Change Biology 2013;19(12):3740–8.
110. Martins AC, Silva DP, Marco PD, Melo GAR. Species conservation under future climate change: the case of Bombus. Journal of Insect Conservation 2014;19(1):33–43.
111. Martinet B, Rasmont P, Cederberg B, Evrard D, Ødegaard F, Paukkunen J, et al. Forward to the north: two Euro-Mediterranean bumblebee species now cross the Arctic Circle. Annales de la Société entomologique de France (NS) 2015;51(4):303–9.
112. Goulson D, Williams P. *Bombus hypnorum* (L.) (Hymenoptera: Apidae), a new British bumblebee? British Journal of Entomology and Natural History. 2001;14(3):129–31.
113. Crowther LP, Hein P-L, Bourke AFG. Habitat and forage associations of a naturally colonising insect pollinator, the tree bumblebee *Bombus hypnorum*. PLoS One 2014;9(9):e107568.
114. Sultan SE, Moczek AP, Walsh D. Bridging the explanatory gaps: what can we learn from a biological agency perspective? BioEssays. 2022;n/a(n/a):2100185.
115. Maebe K, Hart AF, Marshall L, Vandamme P, Vereecken NJ, Michez D, et al. Bumblebee resilience to climate change, through plastic and adaptive responses. Global Change Biology 2021;27(18):4223–37.
116. Nooten SS, Rehan SM. Historical changes in bumble bee body size and range shift of declining species. Biodiversity and Conservation 2020;29(2):451–67.
117. Gérard M, Martinet B, Maebe K, Marshall L, Smagghe G, Vereecken NJ, et al. Shift in size of bumblebee queens over the last century. Global Change Biology 2020;26(3):1185–95.
118. Theodorou P, Baltz LM, Paxton RJ, Soro A. Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. Evolutionary Applications 2021;14(1):53–68.
119. Hill MP, Gallardo B, Terblanche JS. A global assessment of climatic niche shifts and human influence in insect invasions. Global Ecology and Biogeography 2017;26(6):679–89.
120. Lanner J, Huchler K, Pachinger B, Sedivy C, Meimberg H. Dispersal patterns of an introduced wild bee, Megachile sculpturalis Smith, 1853 (Hymenoptera: Megachilidae) in European alpine countries. PLoS One 2020;15(7):e0236042.
121. Polidori C, Sánchez-Fernández D. Environmental niche and global potential distribution of the giant resin bee *Megachile sculpturalis*, a rapidly spreading invasive pollinator. Global Ecology and Conservation 2020;24:e01365.
122. Brown PMJ, Thomas CE, Lombaert E, Jeffries DL, Estoup A, Lawson Handley L-J. The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. BioControl 2011;56(4):623–41.
123. Koppert. Quad [Internet]. [cited 2021 Nov 21]. Available from: https://www.koppertus.com/quad/
124. Biobest. Hive types | Biobest [Internet]. [cited 2021 Nov 21]. Available from: https://www.biobestgroup.com/en/biobest/pollination/things-to-know-about-bumblebees-7052/hive-types-6683/
125. Cruz P, Escobar A, Almanza MT, Cure JR. Implementación de mejoras para la cría en cautiverio de colonias del abejorro nativo Bombus pauloensis (= B. atratus) (Hymenoptera: Apoidea). Revista Facultad de Ciencias Básicas 2008;4(1–2):70–83.
126. Salvarrey S, Arbulo N, Santos E, Invernizzi C. Cría artificial de abejorros nativos Bombus atratus y Bombus bellicosus (Hymenoptera, Apidae). Agrociencia (Uruguay). 2013;17(2):75–82.
127. Padilla SC, Cure JR, Riaño DA, Gutierrez AP, Rodriguez D, Romero E. Gyne and drone production in bombus atratus (Hymenoptera: Apidae). Journal of Apicultural Science 2017;61(1):55–72.
128. Cavigliasso P, Bello F, Rivadeneira MF, Monzon NO, Gennari GB, Basualdo M. Pollination efficiency of managed bee species (*Apis mellifera* and *Bombus pauloensis*) in highbush blueberry (*Vaccinium corymbosum*) productivity. Journal of Horticultural Research. 2020;28(1):57–64. Available from: http://yadda.icm.edu.pl/yadda/element/bwmeta1.element.agro-4c159450-3fa9-449d-b0a9-276493ae4e70

129. Estravis-Barcala MC, Palottini F, Macri I, Nery D, Farina WM. Managed honeybees and South American bumblebees exhibit complementary foraging patterns in highbush blueberry. Scientific Reports 2021;11(1):8187.

130. Salvarrey S, Antúnez K, Arredondo D, Plischuk S, Revainera P, Maggi M, et al. Parasites and RNA viruses in wild and laboratory reared bumble bees *Bombus pauloensis* (Hymenoptera: Apidae) from Uruguay. PLoS One 2021;16(4):e0249842.

131. Sharma HK, Thakur S, Rana K, Thakur M. Small scale rearing of Bombus haemorrhoidalis Smith. Pharma Innovation 2018;7(11):41–5.

132. Torres-Ruiz A, Jones RW, Barajas RA. Present and potential use of bees as managed pollinators in Mexico. Swen 2013;38(1):133–48.

133. Giannini TC, Alves DA, Alves R, Cordeiro GD, Campbell AJ, Awade M, et al. Unveiling the contribution of bee pollinators to Brazilian crops with implications for bee management. Apidologie 2020;51(3):406–21.

134. Hikawa M, Miyanaga R. Effects of pollination by *Melipona quadrifasciata* (Hymenoptera: Apidae) on tomatoes in protected culture. Applied Entomology and Zoology 2009;44(2):301–7.

135. Hogendoorn K, Steen Z, Schwarz MP. Native Australian carpenter bees as a potential alternative to introducing bumble bees for tomato pollination in greenhouses. Journal of Apicultural Research 2000;39(1–2):67–74.

136. Hogendoorn K, Gross CL, Sedgley M, Keller MA. Increased tomato yield through pollination by native Australian Amegilla chlorocyanea (Hymenoptera: Anthophoridae). Journal of Economic Entomology 2006;99(3):828–33.

137. Bell MC, Spooner-hart RN, Haigh AM. Pollination of greenhouse tomatoes by the Australian Bluebanded Bee Amegilla (Zonamegilla) holmesi (Hymenoptera: Apidae). Journal of Economic Entomology 2006;99(2):437–42.

138. Halcroft M. Investigations into the biology, behaviour and phylogeny of a potential crop pollinator: the Australian stingless bee, Austroplebeia australis [Internet]. Sydney: University of Western Sydney; 2012. Available from: https://researchdirect.westernsydney.edu.au/islandora/object/uws%3A14329/

139. Switzer CM, Hogendoorn K, Ravi S, Combes SA. Shakers and head bangers: differences in sonication behavior between Australian Amegilla murrayensis (blue-banded bees) and North American Bombus impatiens (bumblebees). Arthropod-Plant Interactions 2016; 10(1):1–8.

140. Howlett BG, Gee M. The potential management of the drone fly (*Eristalis tenax*) as a crop pollinator in New Zealand. New Zealand Plant Protection 2019;72:221–30.

141. Garcia Bulle Bueno F. Native bees as alternative crop pollinators: reproductive behaviour of *Tetragonula carbonaria* [Internet] [Thesis]. 2021. Available from: https://ses.library.usyd.edu.au/handle/2123/25582

142. Kimbrough L. Bubbles, lasers and robo-bees: the blossoming industry of artificial pollination [Internet]. Mongabay Environmental News. 2020. Available from: https://news.mongabay.com/2020/07/bubbles-lasers-and-robo-bees-is-artificial-pollination-here-to-stay/

143. Yang X, Miyako E. Soap bubble pollination. iScience. 2020;23(6):101188.

144. Wurz A, Grass I, Tscharntke T. Hand pollination of global crops—a systematic review. Basic and Applied Ecology. 2021. Available from: https://www.sciencedirect.com/science/article/pii/S1439179121001286

145. Partap U, Ya T. The human pollinators of fruit crops in Maoxian County, Sichuan, China. Mountain Research and Development 2012;32(2):176–86.

146. Albrecht M, Schmid B, Hautier Y, Müller CB. Diverse pollinator communities enhance plant reproductive success. Proceedings of the Royal Society B: Biological Sciences 2012;279(1748):4845–52.

147. Hoehn P, Tscharntke T, Tylianakis JM, Steffan-Dewenter I. Functional group diversity of bee pollinators increases crop yield. Proceedings of the Royal Society B: Biological Sciences 2008;275(1648):2283–91.

148. Brittain C, Kremen C, Klein A-M. Biodiversity buffers pollination from changes in environmental conditions. Global Change Biology 2013;19(2):540–7.

149. Garibaldi LA, Carvalheiro LG, Leonhardt SD, Aizen MA, Blaauw BR, Isaacs R, et al. From research to action: enhancing crop yield through wild pollinators. Frontiers in Ecology and the Environment 2014;12(8):439–47.

150. Aizen MA, Aguiar S, Biesmeijer JC, Garibaldi LA, Inouye DW, Jung C, et al. Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. Global Change Biology 2019;25(10):3516–27.