

Combined effects of global change pressures on animal-mediated pollination

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Pollination is an essential process in the sexual reproduction of seed plants and a key ecosystem service to human welfare. Animal pollinators decline as a consequence of five major global change pressures: climate change, landscape alteration, agricultural intensification, non-native species, and spread of pathogens. These pressures, which differ in their biotic or abiotic nature and their spatiotemporal scales, can interact in nonadditive ways (synergistically or antagonistically), but are rarely considered together in studies of pollinator and/or pollination decline. Management actions aimed at buffering the impacts of a particular pressure could thereby prove ineffective if another pressure is present. Here, we focus on empirical evidence of the combined effects of global change pressures on pollination, highlighting gaps in current knowledge and future research needs.

Animal-mediated pollination under global change

Pollination is an essential process in the sexual reproduction of angiosperm species, more than 260 000 of which (88%) rely on animals for pollen transfer [1]. In turn, approximately 300 000 animal species are attracted to visit angiosperm flowers by pollen and nectar rewards [2]. Besides the critical role of this mutualism for the maintenance of biodiversity, animal-mediated pollination also provides a key ecosystem service to society. Approximately 70% of the major crop species worldwide are at least partly reliant on animal pollination (mainly by insects) for yield production, accounting for 35% of global food production [3].

Pollinator declines have been attributed to different global change pressures [4–7]. Climate change [8,9], landscape alteration [10,11], species invasions [12,13], agricultural

intensification [14–16], and spread of pathogens [17] have been identified as the main causes of declines in pollinator abundances and extinctions, with the latter causing shifts in pollinator community composition [18], disruption of plant–pollinator interactions [19], and loss or destabilisation of pollination services to wild [19] and crop plants [10,20,21].

Terrestrial ecosystems are currently impacted by multiple pressures and, thus, knowledge of the interactive effects between them is essential for both biodiversity conservation and the maintenance of the ecosystem services provided by pollinators [22]. Indeed, the effects of one pressure can be amplified or buffered by the effects of another pressure [22,23]. The management implication of such interactive effects is that action plans aimed at buffering the effects of a particular pressure can become ineffective if another pressure is present, potentially resulting in a waste of resources devoted to mitigation (e.g., [24]).

In this paper, we focus on the empirical evidence of combined effects of multiple global change pressures on animal-mediated pollination, and discuss both the consequences for pollination services and the potential implications for management. We draw attention to the spatiotemporal scales of impact, the experimental approaches used to study them, the gaps in current knowledge, and future research needs.

From single effects of global change pressures to interactions between them

Single global change pressures have characteristic spatiotemporal scales of action and generate impacts at different rates and at different levels of ecological organisation, from individuals to ecosystems (Boxes 1 and 2). It is important to consider the contrasting biotic or abiotic nature of these pressures to understand their interactive impacts on animal-mediated pollination; environmental pressures can shape the distribution of species, but the presence of

Box 1. The global change pressures and their spatiotemporal scales of action

Climate change

Climate change, mostly warming, typically occurs at broad spatial and temporal scales. However, increased climatic variability can result in climatically anomalous seasons and/or years at a regional scale, whereas anomalous weather events can occur locally during a short time period. Climate change entails changes in community composition through shifts in the geographical range and/or phenology of species.

Landscape alteration

Landscape alteration comprises the degradation (including diffuse pollution), destruction, and fragmentation of natural habitats, resulting in associated changes in landscape configuration, habitat diversity, and community composition. Although landscape alteration occurs at local and landscape scales, shared environment (e.g., orography) and policies can lead to similar alteration regimes at broader spatiotemporal scales.

Agricultural intensification

Intensive agriculture is characterised by an increase in input of pesticides and fertilisers, farm size, monocultures, and simplified crop rotations. Agricultural intensification and landscape alteration are usually difficult to separate because the highest levels of

intensification generally occur in the most altered landscapes. Thus, agricultural intensification shares similar spatiotemporal scales with landscape alteration, but also comprises processes (e.g., ploughing and herbicide and/or pesticide application) that occur at the narrowest scales (plots and days).

Invasive species

The effects of biological invasions on animal-mediated pollination have usually been addressed considering non-native plants and non-native pollinators (but see [12] for a study considering an invasive predator). Whereas non-native plants can require long lag-times until significant representation in the wild, non-native managed pollinators (mainly honeybees *Apis mellifera* and bumblebees *Bombus* spp.) can achieve huge abundances at short spatiotemporal scales after the introduction of hives.

Pathogens

The huge increase during the past decades in the trade of managed pollinators has promoted pathogen transmission to wild pollinators, and vice versa. Pathogen transmission occurs at landscape scales and during the first weeks after the release of managed hives. However, large-scale trends in the use of managed pollinators can lead to widespread transmission across a region.

Box 2. Main documented impacts of single global change pressures on animal-mediated pollination

Climate change

Climate change is predicted to cause spatial and temporal mismatches between pollinators and their food plants owing to differential shifts in the distribution ranges and phenology of interacting species, respectively ([8,9,23], but see [61]). Mismatches can cause pollen limitation to plants and gaps in food supply to pollinators, and both processes are expected to be particularly detrimental in specialist species [8]. Overall, the more generalist the relations (i.e., multiple pollinator species for a plant or broad diet in pollinators), the more resilient the interactions are under climate change. Consequently, non-random novel communities overrepresented by generalist species are expected after the spatial and phenological shifts of species distributions imposed by climate change [8,23].

Landscape alteration

Landscape alteration generally involves the reduction of floral and nesting resources, isolation of populations, and shifts of biotic interactions. Landscape alteration results in significant reductions in species richness and abundance of pollinators, particularly of habitat- and food-specialist insect taxa that locate their nests above ground [11,62]. As a consequence, habitat fragmentation produces strong negative effects on plant pollination and fecundity [63]. The compatibility system of plants, which reflects the degree of dependence on pollinator mutualism, explains the differences among species in their response to fragmentation [63].

Agricultural intensification

Agricultural intensification is thought to be a major driver of loss of pollinators [14,15,24] and, thus, of pollination services [21]. Mechanical and chemical (herbicides) practices result in the loss of field margins and weeds that provide nest sites and forage resources for pollinators. Pesticides can directly affect the fitness of pollinators, leading to declines, particularly of wild species [6,27,64]. Increased use of inorganic fertilisers might also result in pollinator losses via

homogenisation of floral communities [65].

Invasive species

Many non-native plants are ornamental entomophilous plants with floral displays attractive to native pollinators. These non-native plants integrate well within local pollination networks, receiving on average more pollinator visits than coexisting native plant species and, thus, acting as super-generalists [30,34]. Competition with native plants seems to prevail over facilitation [66], although the sign and magnitude of such effects are likely density dependent. Non-native pollinators can change the composition of local pollinator assemblages as a result of their high abundance [38] and their direct competition with native pollinators. Furthermore, non-native pollinators can disrupt pollination patterns of native plants [66]. Managed honeybees can reduce both fecundity and progeny performance through pollen limitation and inbreeding depression [37–39]. Some short-tongue bumblebees (e.g., *Bombus terrestris*) can bite a hole in the corolla of long-tube flowers [20,31], which can also be used by subsequent visitors, leading to illegitimate visits and reduction of plant fitness.

Pathogens

Pathogen transmission from managed to wild pollinators, and vice versa, has resulted in widespread pollinator declines [6,17]. The best-known cases are the transmissions (mainly the *Varroa* mite and intestinal protozoans *Nosema* spp. and *Crithidia* spp.) between native Asiatic honeybee (*Apis cerana*) and non-native and managed European honeybees (*Apis mellifera*; [6,67]), and between managed (mainly originating from Europe) and wild bumblebees [40,41,44,58]. Although some of these pathogens can be transferred between phylogenetically more distant species (e.g., bumblebees and honeybee), there is a lack of studies on infection of wild pollinators not belonging to the *Apis* or *Bombus* genera. Transfer of RNA viruses has also been found among honeybees, bumblebees, and other non-*Apis* taxa of wild bees [43].

species cannot (normally) change the magnitude of the environmental changes.

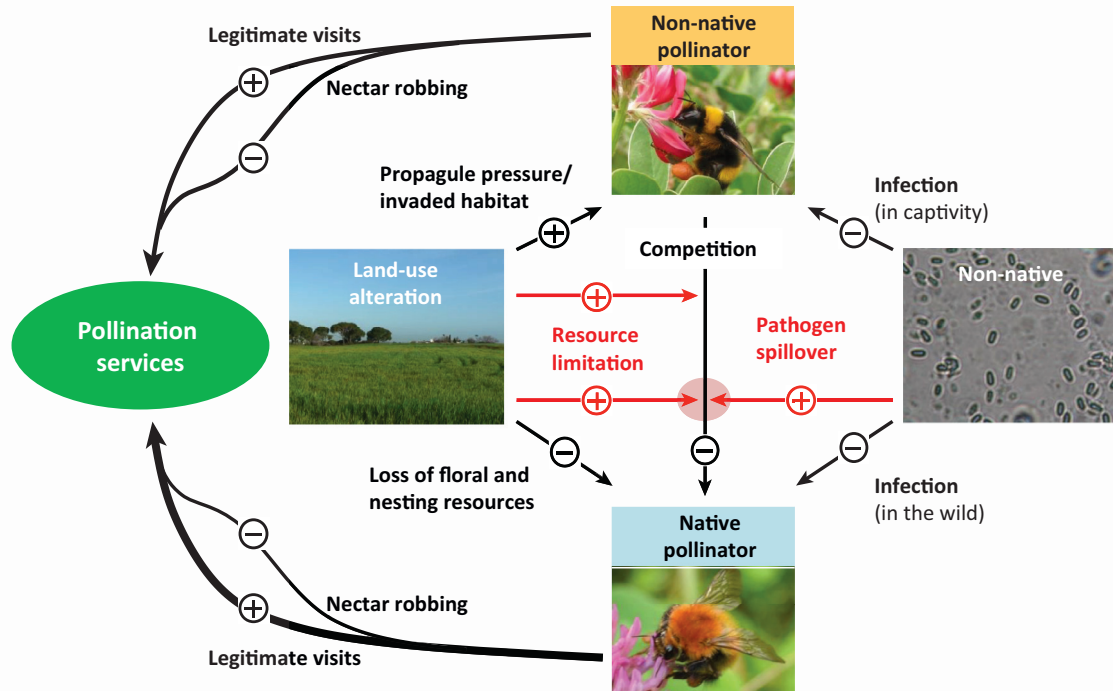
A given pressure can impact animal-mediated pollination directly by disrupting the occurrence, abundance and phenology of partner species. However, a pressure can also impact pollination indirectly, by interacting with other pressures, either additively or nonadditively. Nonadditive

effects occur if the effect of a given pressure is amplified or buffered when it occurs in combination with another pressure. Many interactive effects are indirect effects in which a pressure modifies the magnitude (quantity) of another pressure (i.e., interaction chain effects) and/or its impact per capita (quality; i.e., interaction modification effects [22]). Indirect effects are expected to be particularly

Box 3. Complex interactive effects in real-world ecosystems

In the real world, animal-mediated pollination is impacted by more than one pair of global change pressures, so that multi-pressure complex interactive effects are probably the norm rather than the exception [23,52]. Figure 1 represents the possible combined negative effects of three pressures on native bumblebees and their pollination services: landscape alteration, invasion by a non-native bumblebee, and spread of non-native pathogens (based on [17,20,31,40,41,58]). Landscape alteration might impact native bumblebees directly by reducing floral and nesting resources. Indirect impacts include: (i) ‘interaction chain effects’ favouring the

abundance of the non-native bumblebee; and (ii) ‘interaction modification effects’ increasing its per capita impact through resource limitation, which additionally would increase the probability of pathogen spillover [22]. Cascading effects on plant pollination are expected if the non-native bumblebee is less efficient than the native pollinator or if it visits flowers illegitimately, for example by nectar robbing [31]. Nectar robbing is expected to be more frequent in the commercially traded bumblebee *Bombus terrestris* owing to its shorter tongue length compared with other bumblebee species [20,31].



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Figure 1. Scheme showing possible synergistic effects between landscape alteration, invasion by a non-native pollinator, and pathogen spread impacting native pollinators and their pollination services. Black arrows represent direct effects, whereas red arrows represent (indirect) interactive effects by which a pressure (landscape alteration or pathogens) change the per capita impact of the non-native pollinator on the native pollinator [22]. Positive or negative signs in the arrows denote an increase or a decrease, respectively, in the variable of study, whereas the text close to each arrow denotes the mechanism(s) responsible for its effects. The shaded ellipse denotes a higher probability of pathogen spillover due to flower resource limitation in altered landscapes. The pollination services provided by both pollinators will depend on whether they perform legitimate visits or nectar robbing. Photo reproduced with permission from A. Montero-Castaño (top), H. Szentgyorgyi (right), and J.P. González-Varo (bottom and left).

common in interactions between environmental (climate change, landscape alteration, or agricultural intensification) and biotic pressures (such as invasion of non-native species, or spread of pathogens), because the former can potentially affect both the abundance and the per capita impact of the latter (Box 3, Figure 1).

Only a few empirical studies have explicitly explored the interactive effects of multiple global change pressures on pollinators and pollination (Table 1). In the following sections, we summarise studies focusing on the paired combinations of these pressures, aiming to identify gaps in current knowledge and priorities for future research.

Landscape alteration and agricultural intensification

The interactive effect between agricultural intensification and landscape alteration is the most commonly assessed interaction, largely motivated by evaluations of the context dependent effects of agri-environmental schemes on

biodiversity (Table 1). A common experimental approach is a factorial design with two levels within each factor. Levels for landscape alteration are usually ‘simple versus complex’, ‘homogeneous versus heterogeneous’ [25] or ‘close to versus far from’ edges of semi-natural habitats [26], whereas levels for agricultural intensification usually are ‘conventional versus organic’ farming, although some studies have compared farms with and without pesticide application [27].

In general, the negative effects of agricultural intensification on pollinator species richness and abundance are stronger in simple (i.e., low cover of semi-natural habitats) than in complex landscapes, indicating synergistic effects between both pressures [24]. A plausible explanation is that farms in complex landscapes are more likely to have higher pollinator diversity than are those in simple landscapes. Therefore, the effects of organic farming are weak in the former and stronger in the latter [24]. Although most

Table 1. Summary of studies that have simultaneously addressed the effects of two global change pressures on animal-mediated pollination^{a,b}

Global change pressures	Climate change	Landscape alteration	Non-native species	Agricultural intensification
Landscape alteration	Positive C: [19] Negative I: [52]			
Non-native species	Negative R: [23]	Positive I: [30,32–34] C: [29,31]		
Agricultural intensification	Negative I: [53]	Positive M: [24] I: [25–27,60,68] C: [14,69]	Positive C: [40,41]	
Spread of pathogens	Positive R: [23,56] C: [57]	–	Positive C: [40,41,70]	Positive I: [48–51] C: [40,41]

^a‘Positive’ and ‘Negative’ denote the type of combined effect between pairs of pressures on diverse response variables related to pollinators (assemblages, species, populations, and individual fitness) and/or pollination-associated processes (visitation rates, pollen limitation, mating patterns, and fecundity).

^bI, studies that explicitly tested for interactive effects between pressures; C, studies that assessed simultaneously the effects of two pressures but not the interaction; R, review studies; M, meta-analytical studies.

studies have only focused on pollinators, changes in their abundance and composition are expected to have consequences on the magnitude and stability of the pollination service needed for fruit and seed production of wild plants [19,28] and agricultural crops [10,14,21]. The implication for management of this relatively well-studied interactive effect is that certain policy actions aimed at buffering the negative effects of agricultural intensification can be more efficient in moderate to highly altered landscapes compared with little altered landscapes [24].

Landscape alteration and non-native species

Several studies have considered the effect of landscape type in combination with the occurrence of non-native pollinators or plants (Table 1). In these studies, the degree of landscape alteration has been accounted for either categorically; for example, ‘continuous versus fragmented’ or ‘disturbed versus undisturbed’ [29,30], or continuously along a gradient of landscape naturalness [31,32]. Invasion is assessed at the local plot level (‘invaded versus non-invaded’). In general, both non-native plants and pollinators are disproportionately more abundant in highly altered landscapes, such as in disturbed habitats, or in small remnant patches of semi-natural habitat [29,31,33,34]. Thus, it is difficult to disentangle the causal effects of landscape alteration from those of invasion.

With regard to non-native pollinators, only a few case studies exist. Ishii *et al.* [31] studied the distribution of non-native (*Bombus terrestris*) and native (*Bombus* spp.) bumblebees as well as their foraging behaviour visiting flowers along transitions from open farmland habitats to forests in central Hokkaido, Japan. They found that *B. terrestris* occupied deforested areas, where they had displaced native *Bombus* spp. to forest habitats, which seem to act as barriers against the expansion of *B. terrestris*. Given that *B. terrestris* is a short-tongued pollinator, the consequence for many plants is an increase in nectar robbing (i.e., illegitimate visits performed by biting a hole in the corolla tube) on long-tube flowers in the most deforested landscapes. In another study, Dick *et al.* [29] examined the mating patterns

and pollen dispersal distances of *Dinizia excelsa* trees in fragmented versus continuous rainforests in Brazil. Whereas flower visits in continuous forests were performed almost exclusively by native pollinators, introduced honeybees were the main flower visitor on remnant *D. excelsa* trees located in pastures. For this self-incompatible tree, honeybees provide genetic rescue by promoting long-distance mating events that connect continuous and fragmented populations. Managed honeybees can also reduce pollen limitation of self-compatible plants through high flower visitation rates [35]. Nevertheless, because they tend to forage on many flowers of the same individual plant [36], honeybees usually promote geitonogamous crossings, particularly in those that bear large numbers of flowers [35,37], which can reduce fecundity [38] and plant progeny performance through self-incompatibility and/or inbreeding depression [39].

With regard to non-native plants, Williams *et al.* [33] studied bee visits to non-native and native plants in transformed and semi-natural habitats of California and New Jersey (USA). They found a positive interaction between landscape alteration and non-native plants on bee-plant interactions; bee visits (species richness and abundance) to non-native plants were greater in transformed than in semi-natural habitats. However, bees foraged on different flower species according to their local abundance, denoting a lack of preference for non-native flowers.

Additionally, non-native pollinators and plants can form ‘invader complexes’; that is, groups of introduced species interacting more with each other than expected by chance, which might have positive feedbacks facilitating the invasion of undisturbed habitats [34]. For example, in temperate forests of the southern Andes, non-native visitors, mainly *Apis mellifera* and *Bombus ruderatus*, visited flowers of non-native plants more frequently in disturbed than in undisturbed habitats; however, there was no interaction between habitat disturbance and plant origin (native or non-native) [34]. As in the case of Williams *et al.* [33], this result could be explained by the greater abundance of non-native plants in disturbed habitats.

Pathogens and non-native species

The interactive effects of non-native species and pathogen transmission have been examined in terms of pathogen spillover from commercially reared honeybees and bumblebees to wild pollinators. In a case study in southern Ontario (Canada), three bumblebee pathogens (two microsporidia and a tracheal mite) infected native bumblebees via shared flowers more frequently in landscapes with greenhouses than in those lacking them [40]. A follow-up study found a sharp decline in infection rates by the microsporidian *Crithidia bombi* in wild bumblebees with distance from greenhouses with commercial bumblebee hives (*Bombus impatiens*) [41]. In addition, the most infected wild bumblebee species were those with a high similarity with the commercial bumblebee in the use of plant species. Pathogen spillover to wild bee taxa not belonging to the genera *Apis* and *Bombus* is likely to also be important [42,43], and there is a huge knowledge gap on this issue [44].

Pathogens and landscape alteration or agricultural intensification

The impact of pathogens on pollinators is expected to be higher in altered and intensively cultivated landscapes, where pollinator nutrition and, thus, health (immune system [45]), relies on poor flower communities. This positive interaction is supported by significant correlations between the honeybee colony loss suffered by the states in the USA and the extent of their main land-use types [46].

Although the combined effects of pathogen spread and landscape alteration have not been assessed directly so far (Table 1), available evidence suggests that pathogen spillover from commercial pollinators should be much greater (positive interaction) in altered landscapes, where floral resources are usually scarcer and mean foraging distances are larger (e.g., [31,40,41,47]) (Box 3, Figure I). Similarly, a positive interactive effect is also expected between pathogen spillover and agricultural intensification, because both insecticides and pathogens have detrimental effects on the health of wild pollinators. Indeed, Pettis *et al.* [48] recently found that microsporidia infections (*Nosema* sp.) increased significantly in honeybees exposed to a widely used pesticide; thus, the authors demonstrated experimentally an indirect positive effect of pesticides on pathogen spread. Moreover, several tests on joint effects between infection by a microsporidian (*Nosema ceranae*) and exposure to a neonicotinoid insecticide on honeybee performance, show that several fitness parameters decreased only by the combination of both factors [49–51]. These results provide strong evidence of synergistic effects between pathogen infection and pesticide use. As noted, agricultural intensification is typically associated with the presence of managed, and often non-native, pollinators used to provide pollination services to intensively produced crops (e.g., [14,21,40]). There is, however, a lack of studies assessing whether native pollinators are more impacted by such synergistic effects than the non-natives.

Climate change and landscape alteration or agricultural intensification

Landscape alteration and climate change are expected to affect animal-mediated pollination synergistically, causing spatiotemporal mismatches between interacting species [19] (Box 2). Only one study has experimentally assessed the interactive effect of climate change and landscape alteration on animal-mediated pollination [52]. Pollinator visits and seed production were examined in experimental patches of native flowers. Pots with wild mustard (*Sinapsis arvensis*) grown with ‘normal’ and ‘advanced’ flowering phenology were placed both ‘close’ and ‘distant’ to semi-natural grasslands. Advanced flowering simulated a phenological shift in flowering due to global warming, and distance to grasslands represented landscape alteration. A negative interaction between flowering phenology and proximity to grasslands was found: the difference in the number of flower visits by wild bees to ‘distant’ (>500 m) and ‘close’ (0 m) flower islands was higher under normal than under advanced flowering phenology. This result could be explained by more similar local flower abundance between close and distant experimental islands in the advanced phenology scenario as compared with the normal one.

Recently, Hoover *et al.* [53] examined interactive effects between warming, increased CO₂ and nitrogen (N) deposition in laboratory trials on several plant and flower traits of pumpkin (*Cucurbita maxima*) as well as on domestic bumblebee (*B. terrestris*) foraging preferences and longevity. To our knowledge, this is the only study that has examined interactive effects between climate change and agricultural intensification, because N deposition can be linked to agricultural intensification [54]. There was an antagonistic effect between warming and N deposition in that both nectar production (by plants) and nectar consumption (by bumblebees) in the N-enriched treatment were higher under normal than under elevated temperatures. Although such experiments are valuable because they provide insights into the mechanisms underlying plant and pollinator responses, they often represent an oversimplification of the real world. For example, the studies by Parsche *et al.* [52] and Hoover *et al.* [53] considered climate change effects (phenological shifts and alterations in nectar composition, respectively) in a single plant species. However, climate change tends to impact on entire communities, which means that generalisations based on microcosm studies should be made with caution [23].

Climate change and non-native species or pathogens

There is a lack of empirical studies testing interactive effects of climate change and non-native species on animal-mediated pollination. Schweiger *et al.* [23] compiled literature concerning both global change pressures and developed hypotheses about their possible interactive effects. The authors hypothesised that atypical flowering phenology of non-native species might buffer (antagonistic effect) the detrimental effects of temporal mismatches between interacting species caused by climate change [8]. In temperate regions, many non-native plants are from warmer areas and exhibit a high tolerance to a wide range of climatic conditions; therefore, they have the potential to fill gaps and curtailments in food supply to native

pollinators [8]. In support of this hypothesis, Stelzer and collaborators [55] recently observed that ornamental plant species of urban areas in southern England provide food to bumblebees (*B. terrestris*) that are increasingly active during warmer winters. In addition, features of non-native pollinators, mainly *A. mellifera* and *Bombus* spp., such as sociality, long foraging seasons, broad diets, and long flight ranges, might buffer spatiotemporal mismatches between flowering plants and their native partners.

There is also potential for a positive interactive effect between climate change and pathogen virulence, because there could be changes in the geographical distribution and severity of those diseases whose pathogens respond positively to expected climatic changes [23,56]. In fact, Martín-Hernández *et al.* [57] found that *N. ceranae* (the microsporidian intestinal parasite of the Asiatic honeybee *Apis cerana* that has been transferred to the European honeybee *A. mellifera* worldwide) can develop at a wider temperature range than its congener *Nosema apis* and lacks epidemiological seasonality.

Concluding remarks and future directions

Despite advances in understanding the single effects of global change pressures on animal-mediated pollination, studies simultaneously considering multiple pressures are scarce (Table 1), highlighting that knowledge is still limited. Overall, there is evidence of synergistic effects between agricultural intensification and landscape alteration affecting pollinators negatively. In the case of synergistic effects, the reduction of one pressure will ultimately lead to the reduction in the combined effect. Accordingly, the positive effects of organic farming on pollinators can be negligible in complex or well-preserved landscapes but highly beneficial in simple or highly altered landscapes. Similarly, conserving and restoring (semi-) natural habitats and increasing landscape heterogeneity can be beneficial within intensive croplands. Synergistic effects also occur between agricultural intensification and pathogen virulence, demonstrating that both infection rates and damage caused by pathogens are higher in pollinators exposed to pesticides. In addition, infection rates are higher in landscapes with intensive cropping systems that typically use commercial beehives for pollination. Taken together, such positive interactions, either synergistic or additive, are evidence of multi-pressure effects being common mechanisms underlying the declines of both pollinators and pollination services (Box 3).

That said, many interactions are still unexplored (Table 1). For example, given that pathogen spillover is considered a major driver for observed bumblebee declines in North America [17,44,58], more attention should be paid to pathogen spread under contrasting scenarios of landscape alteration. Also unexplored are interactions between climate change and landscape alteration, agricultural intensification, or non-native species. Climate change is expected to cause phenological mismatches in the poor plant–pollinator communities of altered and intensively cultivated landscapes, jeopardising both plant reproduction and pollinator feeding. However, non-native plants and pollinators could provide food and pollination function, respectively, to native partners in periods where native plants and pollinators have curtailed their phenology. In the case of this potentially, and

unexplored, antagonistic interaction between climate change and non-native species, the reduction of one pressure will lead to an increase in the severity of the other pressure (even if this pressure is held constant).

In summary, the outstanding challenges are to combine observational and manipulative experimental designs to analyse explicitly pair-wise, and further multiple (Box 3), interactions between pressures [59]. For this purpose, it is important to consider the spatiotemporal scales of action of the pressures as well as their hierarchical differences for the combined effects. As mentioned above, environmental pressures can potentially shape the distribution of species (and their per capita impact; Box 3), but the spread of species cannot shape the magnitude of the environmental changes. With such approaches, we will be able to understand the sign and magnitude of multi-pressure effects, which are essential to guide the most appropriate mitigation and adaptation options to conserve plant and pollinator biodiversity and, ultimately, to manage pollination services.

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