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Towards an integrated species and habitat management of crop pollination

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Pollination deficits are widespread in current agriculture, so improving management for crop pollination is critical. Here we review the two most common management approaches to enhance crop pollination, species and habitat management, by providing referenced lists of successful examples. We pinpoint that these approaches have been studied in isolation from each other, with little discussion on potential synergies and trade-offs between them. The potential costs of species management (e.g., loss of biodiversity due to biological invasion), as well as the potential benefits to managed pollinator species from habitat restoration, are rarely quantified. An integrative approach to crop pollination should be implemented, accounting for the cost and benefits (including those beyond crop production) and interactions of species and habitat management.

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Introduction

The expansion of urban and agricultural land, and the intensification of agricultural practices during the past century have caused widespread environmental degradation and biodiversity loss [1••]. These changes affect the ecosystem services on which human well-being depends, including crop pollination by wild insects [1••]. To counteract the decrease in crop pollination, two main approaches have been proposed: (1) the management of pollinator species, which is the most widespread, and (2) the management of pollinator habitats. Here we review successful examples of these approaches, their associated costs and benefits for biodiversity and crop yield, and briefly discuss impacts on other socio-economic and environmental aspects. As a recent study provides a detailed discussion of practices for biological conservation [2], we will focus on management approaches directed to improve crop pollination.

Management of pollinator species and habitats

The European honey bee (*Apis mellifera*) is the most widely managed species (Table 1), and builds large perennial colonies of 20–60 thousand workers performing more than 10 thousand foraging trips per day [3]. Honey bees are usually managed in open pollination systems (fields), but sometimes in enclosed systems (greenhouses) (Table 1). The most common practice is to increase the number of honey bee colonies per hectare (i.e., management by saturation), however, it does not necessarily result in higher fruit production [4•]. Conversely, managing the spatial arrangement of honey bee colonies, with lower density, can reduce pollination deficits [5•] (Box 1).

Other social bees are also employed for crop pollination, such as bumble bees (Table 1), whose commercialization have expanded in the 1990s from Europe to North America, Australasia, Asia, Africa, and South America, especially for tomato pollination [6]. The bumble bee *Bombus terrestris* has been recognized to be more efficient than honey bees for pollinating greenhouse tomatoes [7]. This has been attributed to their longer tongues, which better match the deeper corollas of tomato flowers, and their buzzing pollination behavior, where pollen is released through vibration of poricidal anthers by shivering the flight muscles. Commercialized bumble bee colonies contain one queen and 50–500 workers, depending on the species [6], and are managed by saturation (like honey bees) to perform pollination during less than two months, after which they begin to produce male bees and new queens.

In tropical and subtropical regions, various stingless bee species are domesticated (Table 1). Stingless bees are social species living in perennial colonies from which they forage year-round, with 50–10,000 workers. Species of the genus *Melipona* are, like bumble bees, capable of buzz pollination, and *Melipona quadrifasciata* have been shown to pollinate tomatoes efficiently (Table 1). Other species, especially of the genus *Trigona*, are also managed to pollinate several crops such as avocado, coconut, coffee, macadamia, and mango (Table 1).

The management of some solitary bees has also expanded over the last decades (Table 1), such as various species of *Osmia* for almond, apple, berries, cherry, pear, and prune, in open and enclosed pollination systems, but also *Nomia melanderi* and *Megachile rotundata* in several countries for alfalfa pollination (Table 1). The orchard pollinator, *Osmia lignaria lignaria*, is commercialized in North America and Europe [8]. Populations of these bees are hosted in orchards within nesting shelters consisting of wood with cavities or paper tubes, with a single female bee occupying each cavity during 20–25 days. Still only a few species of solitary bees are produced on a commercial basis (Table 1).

Although incipient, some studies propose to jointly manage multiple pollinator species. Successful examples include honey bees and bumble bees [9], honey bees and solitary bees [10], honey bees and stingless bees [4•], several stingless bee species [11], and several solitary bee species [12]. However, the vast majority of pollinator species are wild, including more than 20,000 species of bees, together with thousands of species of flies, butterflies, moths, wasps, beetles, trips, birds, bats and other vertebrates. Proper management of pollinator habitat is needed to support these species. The majority of habitat management practices focus on foraging resources [13•], by sowing particular plant species or conserving natural plant communities (Table 2). Some also enhance artificial or natural nesting sites to promote wild pollinator populations (Table 2).

Box 1 Pollinator dependence and pollination deficits

- Animal pollination enhances the reproduction of 90% of all angiosperms [58,59]. Similarly, it enhances the yield (tons ha^{-1}) of 85% of 264 European crops [60], 70% of 1330 tropical crops [61], and 75% of the 115 most important global crops as measured by food production [62,63] and economic value [64], including crops with a high domestication investment, such as soybean, sunflower, and canola [38,65,66]. Such estimates consider crops to be of two kinds: completely unaffected by animal pollination or at least partially dependent on animal pollination.

- However, crops differ greatly in the extent to which animal pollinators increase yield, ranging from little or no improvement (e.g., wind-pollinated or self-pollinated cereals) to complete dependence (e.g., Brazil nut, cocoa, kiwi, melon, and papaya) [62]. The contribution of animal pollination to global agriculture was estimated based on the pollinator dependence of the 87 most important crops, using yearly data for 1961–2006 provided by the Food and Agriculture Organization of the United Nations [63]. Crops were classified into five dependency categories: 0, 5, 25, 65, and 95% (extremely high dependence) according to the extent of yield reduction in the absence of pollinators compared to potential yield [62]. With no animal pollination, the estimated reduction in total agricultural production is 3 to 8%, depending on the year and global region [63]. These estimates are lower than previous ones of about 30%, which were derived without considering the degree of pollinator dependence [62]. However, the extra cultivated area needed to compensate the <10% production loss, under a hypothetical scenario of complete pollinator collapse, is much higher. It ranges from 15 to 42%, with the largest estimates for developing countries, where two-thirds of global agricultural land is farmed [63]. Furthermore, analyses of temporal trends for cultivated area and production reveal that agriculture has steadily become more pollinator dependent (>50% increase) during 1961–2006 [63].

- Pollination deficit is a shortfall in the yield of crops that could be alleviated by improved pollination, and can be expressed as the difference between potential and realized yield [67]. Crop yield increases asymptotically with the delivery of resources in general, as with the pollen delivered to the stigmas [51,68]. Pollen quality, resulting for example from enhanced cross pollination, can also affect pollination deficits through changes in ovule fertilization and embryo development [39,69], and increase both potential yield and the rate of increase in crop yield with increasing pollen quantity. Thus, reducing the quantitative component of the pollination deficit will not maximize yield unless pollinators deliver a sufficient pollen quality.

- Pollination deficits occur frequently in wild communities [70], just as crops can be nutrient limited even in non-degraded soils [71]. Pollination deficits are further aggravated in agricultural landscapes for several reasons. First, intensively-managed agricultural landscapes usually provide poor habitat for pollinators [35,72] (Table 2). Second, unlike crop loss due to herbivores, weeds, pathogens, and their vectors, which are usually highly regulated by agricultural practices, pollination is often subject to little deliberate management and occurs mostly naturally, as an ecosystem service [73]. Third, pollinator diversity is declining in many agricultural landscapes [35,74,75], further reducing the quantity and quality of pollen delivered to flowers [47]. Finally, current agricultural practices often involve cultivation of extensive and massively flowering monocultures, increasing pollination demands for brief periods [61,76], which cannot be satisfied by the local pollinator pool, itself diminished by the practice.

Integrative management of crop pollination

Surprisingly, among the practices reviewed in this study, none were designed to benefit from both species and habitat management. However, there seems to exist a clear interaction between the two approaches (Figure 1). For instance, managed pollinator species can affect the surrounding landscape (risk of biological invasion and competition with wild pollinators), and habitat management can provide supplemental pollination through wild and diversified pollinators. Therefore, we propose an integrative management of crop pollination that considers synergies and trade-offs between species and habitat management (Figure 1), and should integrate costs and benefits from the promotion of biotic pollination to crop production. It can be applied in different systems, such as open or enclosed, with particular attention to the risk of biological invasion, but also in different levels of agricultural intensification and landscape simplification (Figure 1). This systemic concept supports the idea of managed pollinators at low density to be complemented by wild species. Future evaluation of how to implement this integrative approach is important both to increase

Table 1

Most common bee species managed for crop pollination. Some key examples of crop systems are provided for each pollinator species.

Pollinator	Crop-system	Crop	References
Bumble bees			
Bombus hypocrita	Enclosed	Tomato	[6,95]
Bombus ignitus	Enclosed	Tomato	[6]
Bombus impatiens	Enclosed	Sweet pepper, tomato	[6,9,26]
Bombus lucorum	Enclosed	Tomato	[6]
Bombus occidentalis	Open	Pear	[6]
Bombus patagiatus	Enclosed	Peach	[12]
Bombus ruderatus	Open & enclosed	Red clover	[26,101]
Bombus terrestris	Open & enclosed	Apple, avocado, pear,pepper, raspberry, strawberry, tomato	[6,7,25,26•]
Bombus vosnesenskii	Enclosed	Tomato	[77]
Honey bees			
Apis cerana	Open	Carrot, coriander, cumin, fennel, onion	[78]
Apis dorsata	Open	Caccao, carrot, coriander, coffee, cumin, fennel, onion	[78,79]
Apis florea	Open	Carrot, coriander, cumin, fennel, onion	[78,80]
Apis mellifera	Open & enclosed	Alfalfa, almond, apple, apricot, blueberry, buckwheat, cotton, cherry, coffee, grapefruit, kiwifruit, longan, macadamia, mango, melon, muskmelon, oilseed rape, onion, passion fruit, peach, pear, pigeonpean, pumpkin, red clover, strawberry, sunflower, watermelon	[5•,8,12,27,81]
Apis mellifera scutellata	Open	Apple	[4•]
Solitary bees			
Habropoda laboriosa	Open	Blueberry	[82]
Megachile rotundata	Enclosed	Alfalfa	[3,83]
Nomia melanderi	Enclosed	Alfalfa	[3,83]
Osmia aglaia	Open & enclosed	Alfalfa, blackberries, raspberries	[3,84]
Osmia cornifrons	Open	Apple	[85]
Osmia cornuta	Open	Almond, apple, pear	[10,86–88]
Osmia lignaria lignaria	Open	Almond, apple, cherry, prune	[8,89,90,91•]
Osmia lignaria propinqua	Open	Almond, apple	[85,92]
Osmia rufa	Open	Cherry	[93•]
Osmia sanrafaelae	Enclosed	Alfalfa	[3]
Peponapis limitaris	Open	Pumpkin	[94]
Peponapis pruinosa	Enclosed	Pumpkin	[9]
Xylocopa virginica	Open	Blueberry	[96]
Stingless bees			
Melipona favosa	Enclosed	Sweet pepper	[97]
Melipona melanoventer	Open	Annato	[98]
Melipona quadrifasciata	Open	Apple, tomato	[4•]
Nanotrigona testaceicornis	Enclosed	Cucumber, strawberry	[11,99]
Partamona cupira	Open	Chayote	[98,100]
Trigona spp.	Open	Avocado, carambola, chayote, coconut, coffee, macadamia, mango, mapati, cupuaçu	[94,98,100]

farmers willingness to adopt it and to provide multi-functional landscapes by optimizing the provision of ecosystem services.

Effects on pollinator diversity

Evaluations of costs and benefits of pollinator species and habitat management are scarce [13•]. The increase of honey bee density to saturate crop flowers with foragers can have detrimental effects on wild pollinators, such as decreasing their flower visitation, reproductive success, abundance, and diversity [14–20] (Figure 1). However, effects can vary among wild species, environments with contrasting floral diversity and abundance, and types of honey bee managements [18,21–23]. In addition, because pollinators are globally commercialized, many species are used outside their native distribution areas, which increase the risk of biological invasion, contributing to biodiversity loss and threatening human well-being. While there has been a focus on the negative effects on biodiversity by the introduction of honey bees [24], attention should be also payed to other managed species (Table 1). For instance, the bumble bee *B. terrestris* was imported to Chile for tomato pollination in greenhouses, invading large areas of South America, with negative consequences for native bumble bee species [25,26•]. Consequently, crop pollination practices need also to consider wild pollinators and their habitats at different spatial and temporal scales and not only the dominant crop pollinator (Figure 1).

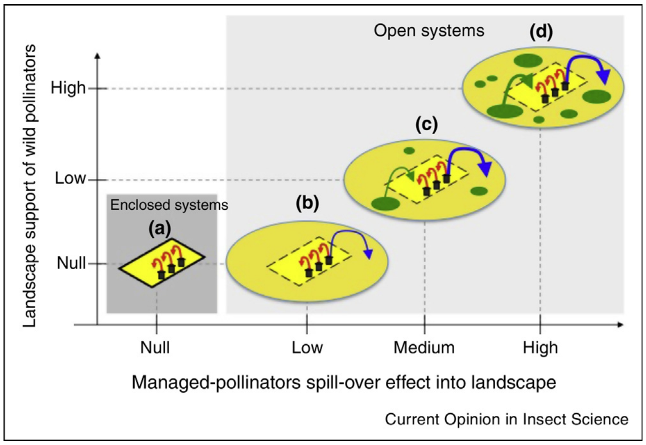
Habitat management can benefit pollinator diversity (Table 2), which suggests that degraded agricultural land

Table 2

Synthetic list of habitat managements with evidences of positive effects on wild pollinator abundance and (or) diversity in agricultural landscapes.

Type of management	Habitat	References
Protect and restore favorable habitats		
Natural or semi-natural habitats	Natural and semi-natural habitats	[35,129]
Set-aside areas	Uncropped areas	[130,131]
Burning and grazing to promote species-rich vegetation communities	Grasslands, steppe	[132]
Hedgerows	Hedgerows	[34,133,134••]
Increase quality and quantity of floral resources		
Increase the quantity of floral resources	Floral strip, grassland	[135,136••]
Intercropping	Crops	[137•]
Sow uncropped arable field margins with agricultural mix of legumes	Field margins	[30,102–107]
Sow uncropped arable field with a native wild flower seed mix	Field margins, grassland	[30,105,108,109••,110,111]
Leave arable field margins uncropped with natural regeneration	Field margins	[105,108]
Provide grass strips at field margins	Field margins	[30,112]
Reduce intensive mechanical practices		
Reduce the intensity of farmland meadow management	Crops	[113•,114]
Reduce grazing intensity on pasture	Grasslands	[115,116]
Reduce tillage	Crops	[117]
Reduce chemical inputs		
Reduce spraying frequency	Crops	[118,119]
Convert to organic farming	Crops	[66,118,120–123]
Restrict certain pesticides	Crops	[124]
Provide nest sites		
Increase areas of rough grassland for bumblebee nesting	Grasslands	[125]
Create patches of bare ground for ground nesting bees	Uncropped areas	[126]
Provide artificial nest sites for solitary bees	Artificial resources	[127,128]

Figure 1



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A summarized conceptual framework of potential costs and benefits of the management of species and habitats for greater crop pollination. Four crop systems are depicted: **(a)** greenhouses, **(b)** simplified intensive open systems, **(c)** complex intensive open systems, **(d)** complex extensive open systems. The red arrows represent a managed species pollinating a crop (yellow rectangle). The large yellow circle shows the surrounding landscape habitat where managed pollinator species can forage (blue arrow) if the system is open, with potential benefits (e.g., pollination of wild plants) and costs (e.g., competition with wild pollinators and risk of biological invasion). When open systems are not too simple, the surrounding landscape can provide additional pollination with wild insects (green arrow). Lines widths represent possible effect sizes.

can be partially recoverable. Given that pollinator species richness and flower visitation rate (a proxy for pollinator abundance) correlate strongly across agricultural fields [27], practices that enhance species richness may also increase aggregate wild pollinator abundance (Table 2). However, studies show contrasting results for bee populations, where some practices have benefits only for certain functional groups [28,29]. For example, the use of plants with deep corollas such as perennial leguminous herbs (e.g., white clover *Trifolium repens*, alfalfa *Medicago sativa*, or *Phacelia tanacetifoila*) often promotes long-tongued bees, like *Bombus* spp. [30]. In addition, the effectiveness of large-scale practices (e.g., restoration of semi-natural areas) depends on smaller-scale practices (e.g., increasing plant diversity within fields), and vice versa [13•]. In general, habitat management is relatively more successful when and where forage and nesting resources are scarce [31]. Furthermore, effects depend on how far the pollinators will fly from their nests, which is poorly studied, where larger pollinators are expected to fly longer distances [32]. However, strong fidelity to small habitats has been documented for large, solitary bees [33]. Therefore, small-scale practices can strongly affect pollinators [34], and the preservation of diverse floral resources, where available, is likely to be the most cost-effective practice (Table 2) [13•]. To integrate species management in a sustainable way, native pollinators should be chosen, reducing the risks associated to biological invasions. Much research is still needed to understand how to breed and manage most of the native pollinator species around the world.

Effects on crop yield

Land conversion to agriculture reduces natural and semi-natural areas, which increasingly isolates crop plants from wild pollinators, aggravating pollination deficits (Box 1). A synthesis of data from 29 studies with contrasting biomes, crop species, and pollinator communities revealed that 1 km separation from natural and semi-natural areas reduced flower-visitor richness, visitation rate to crop flowers by wild insects, and fruit set by 34%, 27%, and 16%, respectively [35]. Moreover, spatial stability decreased by 25%, 16%, and 9% for richness, visitation, and fruit set, respectively, whereas temporal stability decreased by 39% and 13% for richness and visitation, respectively [35].

Increasing the abundance of honey bees cannot compensate for these losses of wild insects [27]. A global synthesis revealed that wild insects pollinate most crops more effectively than honey bees [27]. Fruit set varied positively with flower visitation by honey bees in only 14% of the sampled crops, while flower visitation by wild insects increased fruit set in all the studied crops. Positive effects of wild insects on fruit set occur regardless of geographic location, sample size of the study, relative proportion of honey bees in the pollinator assemblage, pollinator dependence of the crop, or whether the crop species is herbaceous, woody, native, or exotic [27]. Such consistency is expected from the generalized nature of plant-pollinator interactions, where several pollinator species can profit from pollen and nectar of the same plant species [36]. This does not mean that all pollinators interacting with a given crop are equally effective, but rather that various pollinators can have comparable pollination efficiencies. The relatively weak influence of honey bees may reflect their tendency to limit foraging bouts to small flower patches, and sometimes the flowers of a single plant [37,38], limiting cross pollination and increasing self-pollen interference and inbreeding depression [39].

Even for crops pollinated by honey bees, their current commercial availability may not suffice. The global increase of about 50% in hive numbers during the past five decades, does not compensate for the three times larger increase in the fraction of agriculture that depends on animal pollination [40], suggesting an expanding demand for the pollination services provided by wild fauna. Furthermore, honey bee numbers have increased unevenly, with strong growth in major honey-producing countries, such as Argentina, China, and Spain, but declines elsewhere, including the United States, and many western European countries [40,41]. The growth of honey bee numbers in some countries are unlikely to contribute to the pollination of crops in countries where honey bees are in decline. Moreover, in most countries, except the United States, beekeepers profit more from producing honey than from renting colonies for pollination, so the use of honey bees as crop pollinators is commonly not encouraged.

Pollinator species diversity can increase the mean and the stability of crop yield through several mechanisms [42]. First, a diverse pollinator fauna displays more niche complementarity providing greater pollination overall, such as when different pollinators are active during different periods, climatic conditions, flower patches, or a crop's flowering season [21,43,44]. Diversity plays an important role in stabilizing crop pollination, as pollinator species also respond differently to environmental change [44], such as global warming [45] or wind conditions [46]. Second, different pollinator species can act synergistically. For example, wild insects enhance pollination behavior of honey bees by displacing them from flowers, thus potentially enhancing outcrossing [37,38,47]. Third, more diverse pollinator assemblages are more likely to include an efficient pollinator for a given crop than species-poor assemblages [48]. By these, and other mechanisms [49,50], pollinator diversity plays a relevant role in improving the yield of both small-holdings and large-holdings worldwide [51], and its importance will increase in the future. Management practices mostly ignore the quality component of the pollination deficit (Box 1), but encouraging pollinator diversity by habitat management in addition to species management could improve pollen quality [37,38]. Future studies should evaluate whether the integrative approach can improve the quality as well as the quantity component of crop production over time.

Beyond crop pollinators and yield

Crop pollination practices can promote multi-functional benefits to the society (Figure 1), including those of a recreational, cultural, and health value [52•]. These were summarized in a recent assessment from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [1••,53,54••], for example: (1) many of the fruits, berries, and other non-cultivated plants that we enjoy in gardens, parks, and semi-natural habitats depend on wild pollinators for their propagation; (2) the nutritional content of many pollinator-dependent fruits and berries can benefit peoples health; (3) there are cultural heritages or traditions that depend on pollinators, such as the symbolic meaning and use of many pollinator species in different cultures around the world; and (4) the enhancement of other taxonomic groups, such as natural enemies and detritivores, which also may act as ecosystem service providers. The conservation of emblematic pollinator species could then protect the habitat as a whole, acting as an umbrella species ([55] but see [56]).

These values are however seldom conveyed and paid to farmers, making them hesitant to implement pollination conservation practices, where they may incur considerable cost and the direct benefits, such as increased crop yield, may not compensate for these costs [57]. Furthermore, while the individual manager experience the costs, the benefits may be distributed beyond the farm to neighbors who did not change their practices (a type of 'tragedy of the ecosystem service common') [57]. Therefore, policies for crop pollination practices need to take into account the benefits to society [52•] and compensate farmers for those benefits if management practices are to be effectively implemented. Future research should examine how to integrate the species and habitat management approaches to improve the values beyond crop pollination .

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- • of special interest
- •• of outstanding interest

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This review updates the list of current drivers of the worldwide declines of wild and managed pollinators, and shows the wide range of benefits from pollinator conservation to the society. In an applied perspective, this study syntheses and recommends many effective policy and management responses that can be implemented to safeguard pollinators and sustain pollination services.

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This study is one the first to investigate the density of Africanised honey bee hives required to increase the apple yield in Brazil, with the complementary contribution of stingless bees. In a large study area of apple orchard from the Eva variety, they show that supplementation with both stingless bees and Africanised honey bees provided higher seed and fruit production than supplementation with honey bees alone.

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Few studies measure the impacts of pollinator-supporting practices on wild-insect richness and pollination service success. This study provide a general framework and examples of approaches for enhancing pollinator richness and abundance, quantity and quality of pollen on stigmas, crop yield, and farmers' profit. Furthermore, the study includes benefits detected only through long-term monitoring. The study finds benefits of promoting wild-insect species richness combined with single-species management to both farmers and society.

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