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From research to action: enhancing crop yield through wild pollinators

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Recent evidence highlights the value of wild-insect species richness and abundance for crop pollination worldwide. Yet, deliberate physical importation of single species (eg European honey bees) into crop fields for pollination remains the mainstream management approach, and implementation of practices to enhance crop yield (production per area) through wild insects is only just beginning. With few exceptions, studies measuring the impacts of pollinator-supporting practices on wild-insect richness and pollination service success – particularly in relation to long-term crop yield and economic profit – are rare. Here, we 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, including some benefits detected only through long-term monitoring. We argue for integrating the promotion of wild-insect species richness with single-species management to benefit farmers and society.

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Farmland covers more than 35% of Earth's ice-free terrestrial area, and agriculture is expanding and intensifying in many regions to meet the growing demands of human populations (FAO 2013). This trend threatens biodiversity and the ecosystem services on which agriculture depends, including crop pollination (Garibaldi *et al.* 2011a). Indeed, recent reviews have highlighted how multiple anthropogenic pressures lead to a decline in wild pollinators such as bees, flies, beetles, and butterflies (Vanbergen and the Insect Pollinators Initiative 2013). However, practices to enhance wild pollinators in agroecosystems are still in development (Kremen *et al.* 2007;

FAO 2008; Menz *et al.* 2011), and considerable uncertainty remains regarding their effects on crop yield (production per area) and farmers' profits. Here we review recent research on the topic, including the impacts of certain practices on wild pollinators, crop pollination, yield, and profits (WebFigure 1). We focus on practices that enhance the carrying capacity of habitats for wild-insect assemblages that may then provide crop pollination services; practices to conserve or manage a particular pollinator species are outside our scope although they have received attention elsewhere (eg Bohart 1972). We offer general science-based advice to land managers and policy makers and highlight knowledge gaps. Throughout, we emphasize the need to consider population-level processes, rather than just short-term behavioral responses of pollinators to floral resources.

In a nutshell:

- Farms with greater numbers of wild-insect species (richness) exhibit higher abundance of flower visitors and enhanced crop pollination; however, the effectiveness of practices to enhance both pollinator richness and crop yield is unclear
- We offer examples of practices (eg wildflower plantings) that promote pollinator “success” – including species richness and abundance – and discuss where and when such methods are expected to be effective for crop pollination
- Our review provides a general framework for increasing wild-insect pollinator richness and abundance for improved pollination quality and quantity
- Introduction of such methods to complement current single-species management (eg the use of European honey bees) can lead to higher and more stable crop yields

■ Diverse assemblages of wild insects improve pollination

Plant–pollinator interactions are typically very general, with many pollinators being rewarded with pollen, nectar, or other resources from several plant species (WebPanel 1), and with most angiosperms being pollinated by multiple insect species (Waser *et al.* 1996). Humans benefit from this generalized nature of pollination systems, as exotic crops brought far from their ancestral ranges can find effective pollinators within native insect assemblages (Garibaldi *et al.* 2013). Accordingly, a synthesis of 600 fields from 41 crop systems showed that only two of the 68 most frequent pollinators globally were specialist species: the weevil *Elaeiodobius kamerunicus* pollinating oil palm and the squash-bee *Peponapis pruinosa* pollinating pumpkin (Table S2 in Garibaldi *et al.* 2013).

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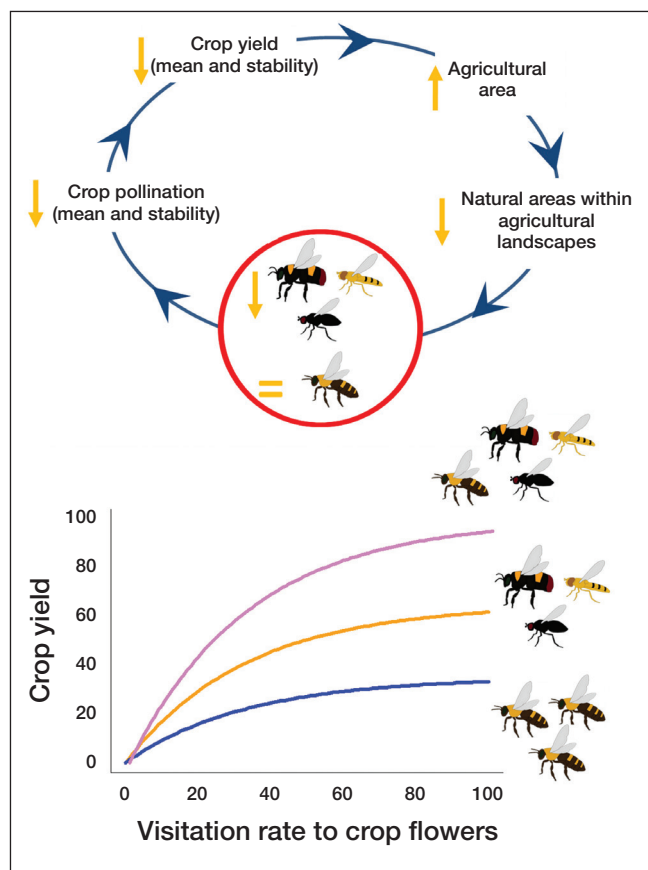


Figure 1. Cycle of wild pollinator decline in agricultural systems and global consequences. Pollen limitation hinders yield (metric tons per hectare) of pollinator-dependent crops, decreasing temporal stability of production and promoting compensatory land conversion to agriculture at the expense of (semi-)natural areas. These land-use changes decrease wild pollinator richness/abundance and crop pollination, but do not affect honey bee abundance. However, increasing the abundance of only honey bees does not compensate for the pollination losses from fewer wild insects (see references in main text). Drawings courtesy of A Hudewenz. Note that both variables (crop yield and visitation rate) in the lower panel are expressed in relative terms, where 0 and 100 are the minimum and maximum values, respectively.

Because of differences in species functional traits, greater pollinator richness can lead to foraging complementarity or synergy, improving the quantity and quality of pollination (Blüthgen and Klein 2011) and therefore increasing both the proportion of flowers setting fruits (or seeds) and product quality (eg fruit size and shape). Across crop species, insects with contrasting mouthpart (eg tongue) lengths may be needed for the pollination of flowers not only with easily accessible rewards but also with rewards hidden at the bottom of a tubular corolla (Fontaine *et al.* 2006). Within a crop species, social and solitary bees visited flowering radish plants at different times of day, suggesting temporal complementarity among these pollinator groups (Albrecht *et al.* 2012). Flower visiting behavior also differs among pollinators of different body sizes, and visits by a range of differently

sized pollinator species increase pumpkin pollination (Hoehn *et al.* 2008). In addition to functional traits, interspecific differences in response traits to climate and land-use change (Winfree *et al.* 2009; Williams *et al.* 2010) can increase resilience of pollination services (Brittain *et al.* 2013).

The role of diverse assemblages of wild insects in crop pollination is also evident from recent global analyses. Worldwide, incomplete and variable animal pollen delivery decreases the growth and stability of yields for pollinator-dependent crops (Garibaldi *et al.* 2011a). This lower yield growth has been compensated for by greater land cultivation to sustain production growth (Figure 1). The consequent reduction in (semi-)natural areas within agricultural landscapes decreases the richness and abundance of wild pollinators, including bees, syrphid flies, and butterflies (Williams *et al.* 2010; Winfree *et al.* 2011a), further diminishing crop pollination (Garibaldi *et al.* 2011b). A possible solution to this “vicious cycle” is to increase pollinator abundance through single-species management, most commonly European honey bees (*Apis mellifera*), which are not greatly affected by isolation from natural areas (Winfree *et al.* 2009; Garibaldi *et al.* 2011b). However, increasing the abundance of one species may complement but not replace the pollination services provided by diverse assemblages of wild insects, and wild insects pollinate some crops more efficiently than honey bees (Garibaldi *et al.* 2013). Moreover, during the past 50 years, the fraction of animal-pollinator-dependent agriculture and the number of managed honey bee hives have increased 300% and 45%, respectively, and honey bees have suffered from major health problems such as colony collapse disorder (Aizen and Harder 2009). All of these factors point to the potential benefit of practices that boost the species richness and abundance of wild pollinators. Indeed, richness and visitation rate (a proxy for abundance) of wild pollinators are strongly correlated across agricultural fields globally (Garibaldi *et al.* 2013). Therefore, practices that enhance habitats to promote species richness are also expected to improve the aggregate abundance of pollinators, and vice versa (WebFigure 1).

■ Off-field practices

Below we describe practices that diversify and improve the abundance of resources for wild insects (WebPanel 1) outside the crop field, without affecting crop management. Practices are ranked from less-to-more required area, with practices covering less area likely to be less costly (WebTable 1).

Nesting resources – such as reed internodes (stem segment between nodes) and muddy spots for cavity nesters, and bare ground for soil nesters – can be enhanced at crop field edges without affecting much of the crop area. Although providing such resources can promote the recruitment of certain bee species (Steffan-Dewenter and

Schiele 2008), evidence of its effects on crop yield is lacking (WebTable 1).

Hedgerows and flower strips are woody or herbaceous vegetation, respectively, planted at the edge of a crop field, and generally covering only a small area. If appropriate plant species are chosen and adequately managed through time (eg proper sowing depth, mowing of perennials), hedgerows and flower strips can provide suitable food and nesting resources for, and enhance species richness and abundance of, bees and syrphid flies (Figure 2). These practices also enhance pollinators in adjacent fields – rather than simply concentrating pollinators at dense flower-rich regions (Figure 2) – and therefore increase crop yield (WebTable 1). Regional programs that augment the quality and availability of seeds from native flowering plants are important for the success of these practices (Isaacs *et al.* 2009).

Conserving or restoring (semi-)natural areas within landscapes dominated by crops often provides habitat for wild pollinator populations (Figure 3; Garibaldi *et al.* 2011b; Winfree *et al.* 2011a). In addition, pollinators depend on various types of resources (WebFigure 2), which are difficult to provide in ways other than by enhancing natural areas. Consequently, these areas also enhance pollination services for nearby crops (WebTable 1).

Enhancing farmland heterogeneity (richness of habitats) increases pollinator richness because plant species provide complementary resources over time and space, and insect species use different resource combinations (Blüthgen and Klein 2011; Kremen and Miles 2012; Shackelford *et al.* 2013). Also, insects usually require resources for periods longer than crop flowering (Mandelik *et al.* 2012). In fact, a synthesis of 605 fields from 39 crop systems in different biomes found that diversity of habitats (mixed crop types, presence of hedgerows and flower strips) within 4 ha enhanced bee abundance by 76% as compared with bee abundance in monoculture fields (Kennedy *et al.* 2013).

Smaller crop fields increase land-use heterogeneity, and also benefit pollinators because most species forage at distances less than 1 km from their nests (Zurbuchen *et al.* 2010b, a). Thus, crops in small fields are more likely to benefit from pollinator enhancements such as nearby field margins and hedgerows (Figure 2). Indeed, pollinator richness, visitation rate, and the proportion of flowers setting fruits (or seeds) decreased by 34%, 27%, and 16%, respectively, at 1 km from (semi-)natural areas across 29 studies worldwide (Garibaldi *et al.* 2011b).

■ On-field practices

In contrast to off-field methods that can be ordered from smaller to larger scale (costs), on-field practices are all applied at a similar spatial scale, ie that of the crop field. Here we discuss practices that (1) reduce the use of insecticides and machinery, (2) enhance the richness of flowering plants, and (3) require greater effort because of

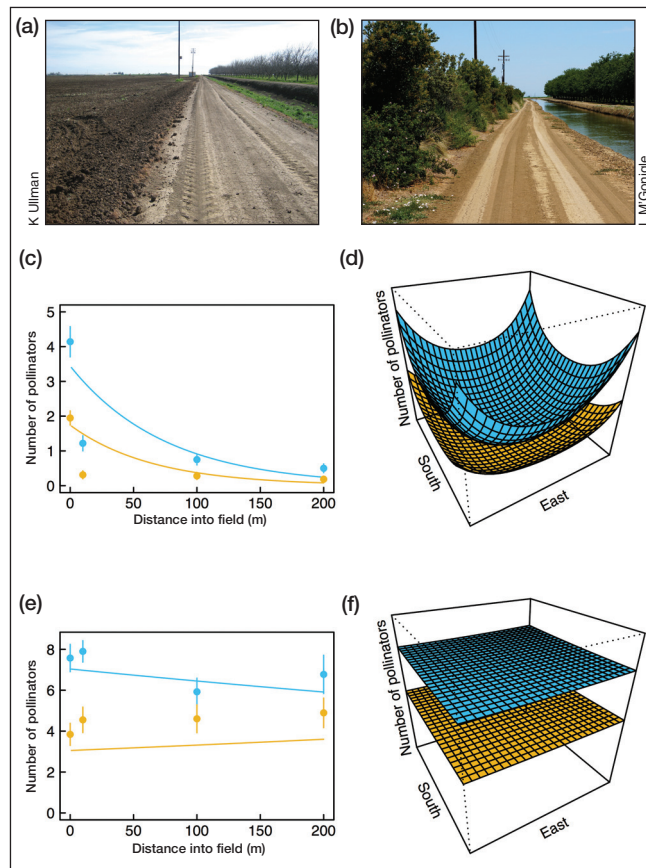


Figure 2. Hedgerows adjacent to crop monocultures enhance wild pollinators in California. Study site (a) before planting in 2007 and (b) 5 years later. (c) Tomato fields next to hedgerows (blue) have more pollinators than those without hedgerows (gold), but pollinator abundance declines with increasing distance from the field edge into the field. (e) Canola attracts pollinators farther into the field. Regression lines with Poisson error distribution are depicted; closed circles and vertical bars indicate means and standard errors, respectively, across sites (Morandin and Kremen 2013). Panels (d) and (f) provide a three-dimensional, additive extrapolation, with hedgerows on four sides of a field.

changes in the crop species or system (eg organic versus conventional).

Reducing the use of synthetic insecticides that are toxic to pollinating insects should provide an important benefit (Tuell and Isaacs 2010). For example, in South Africa, insecticides adversely affected pollinators, impairing rather than enhancing mango yield (WebTable 1). Insecticides with low toxicity to pollinators, with non-dust formulations, applied locally through integrated pest management practices, and applied during the non-flowering season are less likely to be detrimental to pollinators than highly toxic, systemic insecticides that are broadly sprayed from airplanes (Vaughan *et al.* 2007).

No-tillage farming may enhance populations of ground-nesting bees given that many species place their brood cells <30 cm below the surface (Roulston and Goodell 2011). Tillage timing, depth, and method probably have

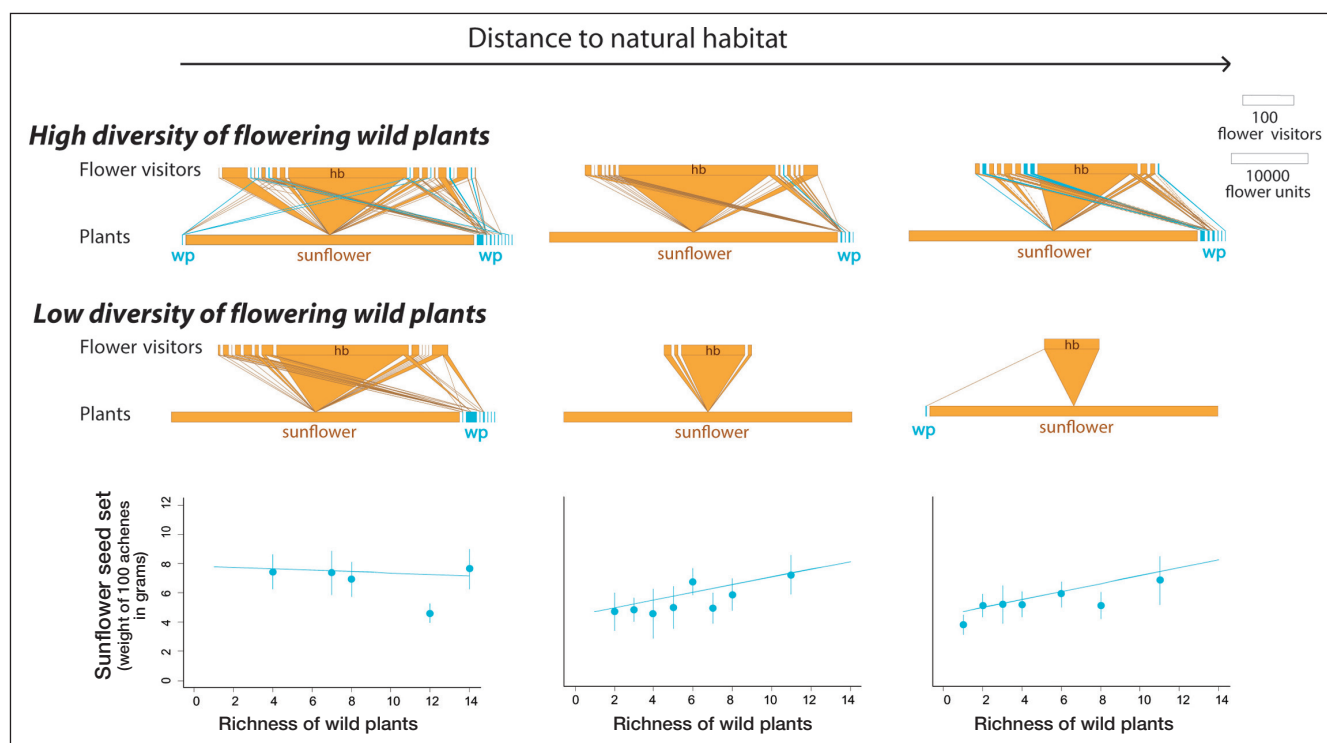


Figure 3. Richness of wild plants (*wp*) improves sunflower visitation and seed set far from natural areas in South Africa. (top panel) From left to right, flower visitation webs within farms located near (28–108 m), at medium distance (280–652 m), or far (683–1120 m) from natural habitat. Sunflower and its flower visitors are in orange (*hb*: honey bee), while other species are in blue. Each species is represented by a rectangle, scaled to species abundance. Line widths represent visitation frequency. (bottom panel) Mean \pm standard deviation seed set as a function of plant richness across twenty 4-m \times 4-m plots (Carvalho *et al.* 2011).

differential impacts on pollinators and pollination, but further studies are required to verify this expectation (WebTable 1). Similarly, *flood irrigation* may be detrimental in comparison to *drip irrigation* because of the increased likelihood of flooding pollinator nests but, particularly in arid systems, irrigation in general can promote wild-insect abundance through higher productivity of flowering plants or by making the soil easier to excavate (Julier and Roulston 2009).

Enhancing flowering plant richness within crop fields can benefit pollinator richness (Nicholls and Altieri 2013) and crop pollination, as demonstrated for mango (WebTable 1) and sunflower (Figure 3; WebTable 1) in South Africa. Similar results were found for wild plants within watermelon and muskmelon fields in the US (Winfree *et al.* 2008). In Ghana, banana intercropping with cocoa boosted pollinator (ceratopogonid midge) abundance and cocoa pod set (Frimpong *et al.* 2011). A diverse set of flower species (crop or non-crop) with different phenologies is likely to increase resource stability for pollinators (Blüthgen and Klein 2011; Mandelik *et al.* 2012) and thus the resilience of pollination services. Herbicides and mowing can negatively affect pollinators by reducing floral resources provided by weeds (Figure 3), but can be useful for reducing the abundance of invasive grasses that could otherwise displace native flowering plants (Isaacs *et al.* 2009).

Organic farming combines some of the practices

described above and can enhance wild pollinator populations in comparison to conventional farming (Kennedy *et al.* 2013), probably because of the absence of synthetic insecticides and/or greater non-crop floral resources. Farmland heterogeneity can also be increased by organic management practices, which account for less than 1% of global agriculture (FAO 2013). When the extent of organic farming was expanded in a German agrolandscape from 5% to 20%, bee richness rose by 50%, while the density of solitary bees and bumble bees increased by 60% and 150%, respectively (Holzschuh *et al.* 2008). Pollination-related benefits of organic practices were also found for strawberry in Sweden (Andersson *et al.* 2012) and canola in Canada (Morandin and Winston 2005).

Sowing flowering crops, instead of crops that do not offer floral resources for pollinators, may enhance wild pollinators in heterogeneous landscapes (Holzschuh *et al.* 2013). In western France, solitary-bee richness and abundance were higher in margins of canola fields than in fields of other crops (Le Féon *et al.* 2013). In the UK, bumble bee abundance was higher in areas adjacent to bean fields than to wheat fields but only during crop flowering (Hanley *et al.* 2011), suggesting a short-term behavioral response to flower abundance rather than a long-term population enhancement. Similarly, in Germany, canola improved bumble bee early-colony growth but not whole-season sexual reproduction (Westphal *et al.* 2009), and greater land cover of mass-flowering crops increased the number of bum-

ble bee workers but not colony numbers (Herrmann *et al.* 2007). Therefore, although crops can provide abundant resources, the short duration of floral availability, the low diversity of resources, the application of insecticides, and the presence of tillage may limit the capacity of one crop species to support wild pollinator populations on its own (Vanbergen and the Insect Pollinators Initiative 2013). Furthermore, large monocultures of flowering crops can suffer from pollination deficit and trigger indirect negative effects on pollinators (Figure 1). Sowing crops that bloom in different periods may therefore increase wild-insect populations; in Sweden, bumble bee reproduction was improved in landscapes with both late-season flowering red clover and early-season mass-flowering crops (Rundlöf *et al.* 2014). Moreover, managing crop phenology (eg through breeding) to better match the availability of efficient pollinators should enhance pollination, but we found no studies on this practice (WebTable 1).

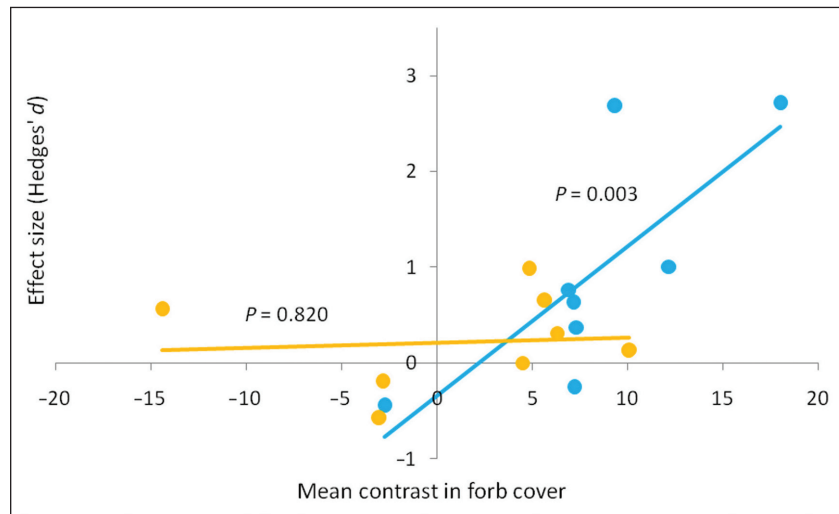


Figure 4. Agri-environmental schemes in Europe enhance bee species richness (d values above zero) in croplands (blue circles) and grasslands (gold circles). The magnitude of this enhancement (effectiveness) increases with the contrast in resource availability (percentage of forb cover) between fields with and without schemes in croplands (blue regression line), but not in grasslands (gold regression line). Effect size for richness indicates Hedges' unbiased weighted standardized mean difference (Hedges' d), which is the difference between environment scheme and control field means corrected by their pooled standard deviation. Regression lines and P values are shown for meta-regressions (Scheper *et al.* 2013).

■ Which practices are more effective in space and time?

The effectiveness of pollinator-supporting practices is influenced by interactive effects between large (landscape) and small (within-field) scale factors. For example, the effects of landscape composition (the proportion of different habitats) on bee richness are greater on farms with low habitat diversity than on farms with high habitat diversity (Kennedy *et al.* 2013). Similarly, in Argentina, the importance of wildflower strips as pollinator sources for sunflower increased in the absence of large remnants of natural habitats nearby (Sáez *et al.* 2012). In South Africa, the importance of weed richness for enhancing sunflower seed set increased with larger distances from natural areas (Figure 3).

Throughout Europe, extensive programs aim to mitigate biodiversity loss on farmland through practices such as organic farming or wildflower strips, thereby offering a unique opportunity to understand interactions among these methods. A meta-analysis showed that these (small-scale) practices enhanced pollinator richness (Figure 4), but their effectiveness varied with (1) the magnitude of increase in flowering plant cover resulting from the practices, (2) farmland type, and (3) landscape context (Scheper *et al.* 2013). Because intensively managed croplands are generally devoid of flowering plants, pollinator-supporting practices in these landscapes result in the largest increase in floral resources and thus pollinator richness (Figure 4). On the other hand, conventionally managed grasslands generally contain more flowering plant species than arable fields,

making it more difficult to enhance floral resources and pollinators (Scheper *et al.* 2013). Finally, local effects were more positive in structurally simple landscapes (1–20% semi-natural habitat) than in cleared (<1% semi-natural habitat) or complex (>20% semi-natural habitat) landscapes, presumably because cleared landscapes lack sources of pollinator colonists and complex landscapes have less need of restoration.

Recently, researchers have begun to explore the relative effectiveness of different pollinator-supporting practices. In Europe, flower strips were more effective than grass-sown or naturally regenerated strips (Scheper *et al.* 2013). Globally, the effect of landscape composition and farm management (within-farm habitat diversity and organic versus conventional) was more important for improving bee richness than the effect of landscape configuration (the arrangement in space and time of different habitats; Kennedy *et al.* 2013). Interestingly, conventional farms with high in-field habitat diversity maintained similar pollinator abundance as organic farms with low in-field habitat diversity, across the gradient of heterogeneity in surrounding land use. Thus, different combinations of local and landscape practices can result in similar outcomes in terms of promoting pollinator richness, providing alternative solutions suited to different agricultural settings.

The importance of small-scale practices is likely greater for insects with short flight ranges foraging from a fixed nest, such as small- to medium-sized bees, which usually forage within an area of a few hundred meters and comprise the greatest fraction of bee species (Murray *et al.*

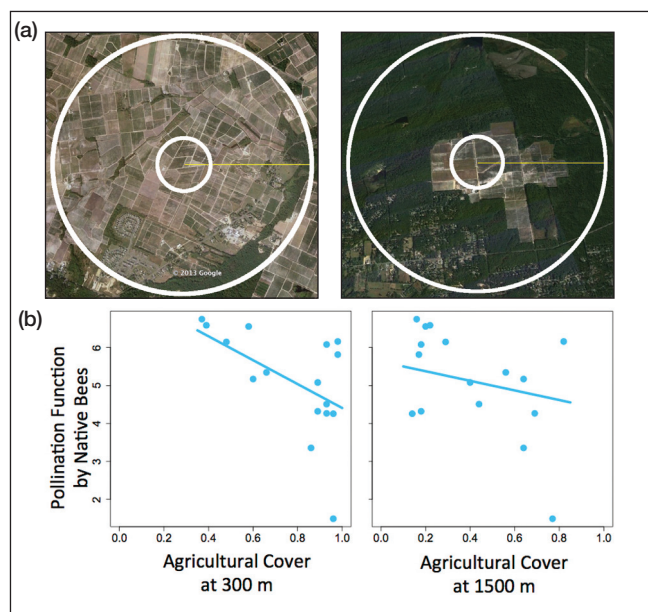


Figure 5. Land use immediately surrounding blueberry fields exerts the strongest effect on pollination services in New Jersey. (a) Study sites were selected so that the proportion of agricultural land cover at the local (300 m, inner circles) and landscape (1500 m, outer circles) scales was uncorrelated across study sites; two representative sites are shown. (b) Land use at the local scale had a stronger effect on pollination services than at the landscape scale. Pollination services are measured as the log-transformed number of blueberry pollen grains deposited on blueberry stigmas by wild pollinators (Benjamin *et al.* 2014).

2009; Zurbuchen *et al.* 2010b). Consistent with the idea that small-scale practices alone can have high impact, a study designed to separate the effects of local- versus landscape-scale habitat on pollination services delivered to blueberries found that the local scale had stronger positive effects (Figure 5). Indeed, farmers acting individually are more likely to improve the quality of their own fields and the immediate surroundings than to be able to manage complete landscapes for pollinators. Assuming a foraging range of 200 m from the nest for small bee species (Zurbuchen *et al.* 2010b, a), diverse and high-quality habitats need to be provided within 13 ha (ie the surface of a 200-m-radius circle).

■ Costs and benefits of practices

Understanding the socioeconomic consequences of pollinator-supporting practices is essential to effectively enhancing wild pollinator richness in “real-world” (as opposed to modeled) landscapes (Grieg-Gran and Gemmill-Herren 2012). Farmers generally face implementation costs, such as those for planting hedgerows, and opportunity costs, such as those for setting aside natural habitats that could otherwise be cultivated (Olschewski *et al.* 2006). Off-field practices have the advantage that land owners do not need to change their typical crop management; however, they still entail

implementation and opportunity costs. On the other hand, on-field practices generally necessitate changes in how farmers manage their crops, which may reduce implementation costs (eg lower insecticide use) but potentially increase opportunity costs (eg because of a positive effect of insecticide on crop yield).

Occasionally, the costs of implementing these pollinator-supporting practices are higher than the income derived from their implementation (Olschewski *et al.* 2006), resulting in a low likelihood of adoption. However, such practices can generate other benefits for society, such as the enhancement of biodiversity; mitigation of soil erosion; and improvements in pest control, nutrient cycling, and/or water use efficiency (Kremen and Miles 2012; Wratten *et al.* 2012; Shackelford *et al.* 2013). Many countries have therefore developed government-sponsored programs (Figure 4; see also the Conservation Reserve Program in the US or Australia’s Landcare program) that compensate farmers for enhancing biodiversity and ecosystem services, which are essential for human well-being but have no market value.

In other situations, pollinator-supporting practices are profitable to farmers independent of government payments (Carvalho *et al.* 2012). Some of these practices imply lower costs (eg a more targeted use of herbicides or mowing) or fewer additional costs (eg setting aside a small area in soils with intrinsic limitations where crop yield is low). In the US state of Michigan, plantings of native wildflowers gradually increased wild bee and syrphid abundance as well as blueberry yield in fields adjacent to the plantings, as compared with fields with a standard grassy perimeter (Figure 6). While the cost of establishing the plantings resulted in negative profit in the first year, the gain from pollinator-enhanced yield outpaced the costs of the establishment and maintenance by the fourth year, and growers made cumulative profits (Figure 6). The plantings were on land that could not be cropped with blueberry because of soil or topography limitations, so there was no opportunity cost of “lost” crop production. The perennial wildflower plantings, if properly managed, will likely provide this benefit for many years. Furthermore, such practices have the added benefit of supplying habitat for natural enemies and enhancing biological control of pests in fields adjacent to the plantings. Although economic valuations of pollination services exist (eg Winfree *et al.* 2011b), studies that consider both the costs and benefits of pollinator-supporting practices are rare (WebTable 1). We highlight the importance of estimating the marginal profits of implementing such practices (Fisher *et al.* 2008), because management usually only partially increases or decreases ecosystem services (rather than maximizing or eliminating them).

■ General science-based advice to land managers and policy makers

Our consensus, based on the reviewed evidence, indicates that:

- Pollinator richness (and associated aggregate abundance of wild insects) contributes to crop pollination even when honey bees are present in high abundance (Figure 1).
- Pollinator richness increases with the diversity of floral resources (WebTable 1).
- Effectiveness of pollinator-supporting practices (eg flower strips) is context-dependent, and usually more successful in situations where background floral resources are scarce. In cases where abundant floral resources are available, these should be preserved (Figure 4).
- Effectiveness of large-scale practices (eg natural or organic area) varies according to the smaller-scale practices carried out (eg plant diversity within fields), and vice versa (Figure 3). Different combinations of local and landscape practices can result in similar outcomes in terms of promoting pollinator richness, providing alternative solutions suited to different agricultural settings.
- Small-scale practices can have major effects on pollinators and pollination services (Figures 2 and 5). The relative importance of such smaller-scale initiatives is likely greater for pollinators with shorter flight ranges.
- Enhancement of wild pollinators can take several years but still be cost-effective (Figure 6). However, the generality of this conclusion is uncertain and more studies are needed in a variety of crop, landscape, and economic contexts (WebTable 1).
- On the basis of current evidence (WebTable 1), we propose that a practical way to start transforming pollinator-limiting landscapes into more suitable ones is to carry out more targeted use of insecticides, and to employ marginal land to establish and maintain flower strips and hedgerows, as well as to restore (semi-)natural areas adjacent to crops (less than 200 m away). These changes will also increase farmland heterogeneity, benefiting the sustainability of agriculture.

■ Conclusions

Single-species bee management (eg *A mellifera*, *Bombus* spp, *Osmia* spp) is the mainstream approach to crop pollination. Despite providing acceptable yields in some systems, this form of management does not replace the contribution of rich assemblages of wild pollinators (Figure 1), and carries the risks associated with facilitating pathogen, disease, and predator incidence. Therefore, we argue for integrated management of single species and wild pollinator assemblages (WebTable 1; WebFigure 1). Indeed, practices that enhance wild pollinators will likely also increase resources for managed species and help to sustain, for instance, honey bee colony health.

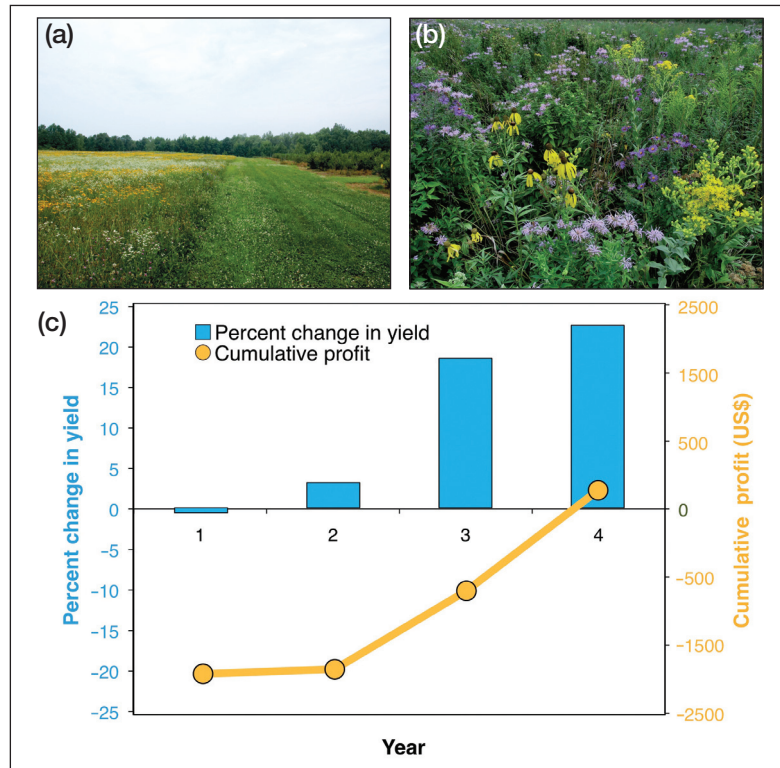


Figure 6. Plantings of native wildflower species selected for support of pollinators enhance blueberry yield and profit in Michigan. (a) Planting in midsummer with blueberry on the right. (b) Close-up of a mature planting with a mix of flower forms, species, and colors, with blueberry in the background. (c) Percent change in blueberry yield (blue bars) between fields adjacent to wildflower plantings and fields without plantings. The gold line (cumulative profit) shows that the initial cost of establishment in the first year was paid for by the fourth year when higher yield resulted in a profit (Blaauw and Isaacs 2014).

Promotion of biodiversity within agricultural landscapes is essential for sustaining associated ecosystem services. This paper provides a general framework to enhance wild insects and associated pollination services, which resource managers and policy makers can adapt to specific landscape conditions, crop varieties, and crop management strategies. These practices will have additional benefits to crop pollination, including the enhancement of scenic values, cultural values, plant and insect diversity, and other ecosystem services. Transdisciplinary work is essential to implement pollinator-supporting practices in real-world landscapes and support long-term yields of pollinator-dependent crops.

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References

- Aizen MA and Harder LD. 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr Biol* **19**: 915–18.
- Albrecht M, Schmid B, Hautier Y, and Müller CB. 2012. Diverse pollinator communities enhance plant reproductive success. *P Roy Soc B–Biol Sci* **279**: 4845–52.
- Andersson GKS, Rundlöf M, and Smith HG. 2012. Organic farming improves pollination success in strawberries. *PLoS ONE* **7**: 2–5.
- Benjamin FE, Reilly JR, and Winfree R. 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. *J Appl Ecol* **51**: 440–49.
- Blaauw BR and Isaacs R. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J Appl Ecol* **51**: 890–98.
- Blüthgen N and Klein AM. 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl Ecol* **12**: 282–91.
- Bohart GE. 1972. Management of wild bees for the pollination of crops. *Annu Rev Ecol Evol S* **17**: 287–312.
- Brittain C, Kremen C, and Klein AM. 2013. Biodiversity buffers pollination from changes in environmental conditions. *Glob Change Biol* **19**: 540–47.
- Carvalho LG, Seymour CL, Nicolson SW, and Veldtman R. 2012. Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study. *J Appl Ecol* **49**: 1373–83.
- Carvalho LG, Veldtman R, Shenkute AG, *et al.* 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecol Lett* **14**: 251–59.
- FAO (UN Food and Agriculture Organization). 2008. Tools for conservation and use of pollination services: initial survey of good pollination practices. Rome, Italy: FAO.
- FAO (UN Food and Agriculture Organization). 2013. FAOSTAT <http://faostat.fao.org/site/377/default.aspx#ancor>. Viewed 05 Oct 2013.
- Fisher B, Turner K, Zylstra M, *et al.* 2008. Ecosystem services and economic theory: integration for policy-relevant research. *Ecol Appl* **18**: 2050–67.
- Fontaine C, Dajoz I, Meriguet J, and Loreau M. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol* **4**: e1.
- Frimpong EA, Gemmill-Herren B, Gordon I, and Kwabong PK. 2011. Dynamics of insect pollinators as influenced by cocoa production systems in Ghana. *J Pollination Ecol* **5**: 74–80.
- Garibaldi LA, Aizen MA, Klein AM, *et al.* 2011a. Global growth and stability of agricultural yield decrease with pollinator dependence. *P Natl Acad Sci USA* **108**: 5909–14.
- Garibaldi LA, Steffan-Dewenter I, Kremen C, *et al.* 2011b. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol Lett* **14**: 1062–72.
- Garibaldi LA, Steffan-Dewenter I, Winfree R, *et al.* 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**: 1608–11.
- Grieg-Gran M and Gemmill-Herren B. 2012. Handbook for participatory socioeconomic evaluation of pollinator-friendly practices. Rome, Italy: FAO.
- Hanley ME, Franco M, Dean CE, *et al.* 2011. Increased bumblebee abundance along the margins of a mass flowering crop: evidence for pollinator spill-over. *Oikos* **120**: 1618–24.
- Herrmann F, Westphal C, Moritz RFA, and Steffan-Dewenter I. 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. *Mol Ecol* **16**: 1167–78.
- Hoehn P, Tschamtk T, Tylianakis JM, and Steffan-Dewenter I. 2008. Functional group diversity of bee pollinators increases crop yield. *P Roy Soc B–Biol Sci* **275**: 2283–91.
- Holzschuh A, Dormann CF, Tschamtk T, and Steffan-Dewenter I. 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* **172**: 477–84.
- Holzschuh A, Steffan-Dewenter I, and Tschamtk T. 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* **117**: 354–61.
- Isaacs R, Tuell J, Fiedler A, *et al.* 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Front Ecol Environ* **7**: 196–203.
- Julier HE and Roulston TH. 2009. Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behavior and landscape effects. *J Econ Entomol* **102**: 563–73.
- Kennedy CM, Lonsdorf E, Neel MC, *et al.* 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol Lett* **16**: 584–99.
- Kremen C and Miles A. 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecol Soc* **17**: 40.
- Kremen C, Williams NM, Aizen MA, *et al.* 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol Lett* **10**: 299–314.
- Le Féon V, Burel F, Chifflet R, *et al.* 2013. Solitary bee abundance and species richness in dynamic agricultural landscapes. *Agr Ecosyst Environ* **166**: 94–101.
- Mandelik Y, Winfree R, Neeson T, and Kremen C. 2012. Complementary habitat use by wild bees in agro-natural landscapes. *Ecol Appl* **22**: 1535–46.
- Menz MHM, Phillips RD, Winfree R, *et al.* 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends Plant Sci* **16**: 4–12.
- Morandin LA and Kremen C. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol Appl* **23**: 829–39.
- Morandin LA and Winston ML. 2005. Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecol Appl* **15**: 871–81.
- Murray TE, Kuhlmann M, and Potts SG. 2009. Conservation ecology of bees: populations, species and communities. *Apidologie* **40**: 211–36.
- Nicholls CI and Altieri MA. 2013. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agron Sustain Dev* **33**: 257–74.
- Olschewski R, Tschamtk T, Benitez PC, *et al.* 2006. Economic evaluation of pollination services comparing coffee landscapes in Ecuador and Indonesia. *Ecol Soc* **11**: 7.
- Roulston TH and Goodell K. 2011. The role of resources and risks in regulating wild bee populations. *Annu Rev Entomol* **56**: 293–312.
- Rundlöf M, Persson AS, Smith HG, and Bommarco R. 2014. Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biol Conserv* **172**: 138–45.
- Sáez A, Sabatino M, and Aizen MA. 2012. Interactive effects of large- and small-scale sources of feral honey-bees for sunflower in the Argentine Pampas. *PLoS ONE* **7**: e30968.
- Scheper J, Holzschuh A, Kuussaari M, *et al.* 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecol Lett* **16**: 912–20.
- Shackelford G, Steward PR, Benton TG, *et al.* 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape

- and local effects on abundance and richness in crops. *Biol Rev Camb Philos* **88**: 1002–21.
- Steffan-Dewenter I and Schiele S. 2008. Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology* **89**: 1375–87.
- Tuell JK and Isaacs R. 2010. Community and species-specific responses of wild bees to insect pest control programs applied to a pollinator-dependent crop. *J Econ Entomol* **103**: 668–75.
- Vanbergen AJ and the Insect Pollinators Initiative. 2013. Threats to an ecosystem service: pressures on pollinators. *Front Ecol Environ* **11**: 251–59.
- Vaughan M, Shepherd M, Kremen C, and Black SH. 2007. Farming for bees: guidelines for providing native bee habitat on farms. Portland, OR: The Xerces Society for Invertebrate Conservation.
- Waser NM, Chittka L, Price MV, *et al.* 1996. Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043–60.
- Westphal C, Steffan-Dewenter I, and Tschamtkke T. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *J Appl Ecol* **46**: 187–93.
- Williams NM, Crone EE, Roulston TH, *et al.* 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol Conserv* **143**: 2280–91.
- Winfree R, Aguilar R, Vázquez DP, *et al.* 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* **90**: 2068–76.
- Winfree R, Bartomeus I, and Cariveau DP. 2011a. Native pollinators in anthropogenic habitats. *Annu Rev Ecol Evol S* **42**: 1–22.
- Winfree R, Gross BJ, and Kremen C. 2011b. Valuing pollination services to agriculture. *Ecol Econ* **71**: 80–88.
- Winfree R, Williams NM, Gaines H, *et al.* 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J Appl Ecol* **45**: 793–802.
- Wratten SD, Gillespie M, Decourtye A, *et al.* 2012. Pollinator habitat enhancement: benefits to other ecosystem services. *Agr Ecosyst Environ* **159**: 112–22.
- Zurbuchen A, Cheesman S, Klaiber J, *et al.* 2010a. Long foraging distances impose high costs on offspring production in solitary bees. *J Anim Ecol* **79**: 674–81.
- Zurbuchen A, Landert L, Klaiber J, *et al.* 2010b. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol Conserv* **143**: 669–76.

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