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 agro-ecosystems 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 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.

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 (e.g., 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 (e.g., the use of European honey bees) can lead to higher and more stable crop yields

Introduction of such methods to complement current single-species management (e.g., the use of European honey bees) can lead to higher and more stable crop yields.
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 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
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 (Winfrey 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).

### 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) farm-land type, and (3) landscape context (Schepet 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 (Schepet 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 (Schepet 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. 2013).
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 (Carvalheiro 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 (e.g., 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 (e.g., natural or organic area) varies according to the smaller-scale practices carried out (e.g., 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 (e.g., 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.

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.

Acknowledgements
F Benjamin, I Bartomeus, B Gemmill-Herren, and CL Morales provided insightful comments that improved the manuscript. The authors declare no competing financial interests. This research was funded by Universidad Nacional de Río Negro (PL 40-B-259), EU FP7 project “Status and Trends of European Pollinators” (244090, www.STEP-project.net), EU FP7 project “Securing the...
Conservation of biodiversity across Administrative Levels and spatial, temporal, and Ecological Scales” (www.scales-project.net), and the US Department of Agriculture’s Sustainable Agriculture Research and Education program.

References


1Department of Tropical Biology and Animal Ecology, University of Würzburg, Würzburg, Germany; 2Laboratorio Ecotono, INIBIOMA, Universidad National del Comahue–CONICET, Río Negro, Argentina; 3Department of Entomology, Michigan State University, East Lansing, MI; 4Department of Life Sciences, Terrestrial Invertebrates Division, Natural History Museum, London, UK; 5Alterra, Animal Ecology Team, Wageningen, The Netherlands; 6Resource Ecology Group, Wageningen University, Wageningen, The Netherlands; 7Chair of Nature Conservation and Landscape Ecology, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany; 8Environmental Sciences Policy and Management, University of California – Berkeley, Berkeley, CA; 9Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ.