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A dual role for farmlands: food security and pollinator conservation

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Summary

1. We briefly review current understanding of wild pollinators and pollination services on farmlands.
2. We consider how concepts in plant ecology – community assembly and functional trait diversity – may be applied to create diverse, wild pollinator communities across scales in agroecosystems.
3. We also make recommendations for best practices to enhance pollination services and create more sustainable food production systems under changing environmental conditions, including creating greater landscape connectivity, embracing pollinator dynamics, and providing incentives and other motivations to support these practices.
4. *Synthesis.* We highlight the opportunity for agricultural lands to serve a dual role for both food production and pollinator conservation, and conclude by posing unanswered questions and top priorities for future studies.

Key-words: agroecosystems, bees, floral resources, native plants, nesting habitat, sustainability, wild pollinators

Introduction

Wild pollinators provide essential ecosystem services to crops (Klein *et al.* 2007) in agricultural landscapes. Although primarily honeybees (*Apis mellifera*) are relied upon for crop pollination, their recent increases in mortality highlight the importance of wild pollinators (e.g. Allen-Wardell *et al.* 1998; Potts *et al.* 2010). Furthermore, agricultural reliance on one managed species (i.e. the honeybee) with a prevalence of known pathogens is risky, especially when wild bees are often superior pollinators (Garibaldi *et al.* 2011, 2013). Alone, wild bees can sufficiently pollinate certain crops (Kremen, Williams & Thorp 2002; Winfree *et al.* 2007), and their diversity is a positive predictor of the magnitude and temporal stability of pollination even when honeybees are also present (Kremen, Williams & Thorp 2002; Klein 2009; Garibaldi *et al.* 2011). Despite global declines in honeybee health (Potts *et al.* 2010; Wilfert *et al.* 2016), when many colonies are stocked locally, honeybees can usurp floral resources critical to wild pollinators, reducing their fitness (Elbgami *et al.* 2014) and potentially lowering their abundance and diversity (Cane & Tepedino 2016).

Local farm management practices (e.g. organic farming, on-farm habitat heterogeneity; Benton, Vickery & Wilson

2003) as well as the quality and structure of the surrounding landscape are important to the abundance and richness of wild pollinators on farms (Kremen, Williams & Thorp 2002; Kremen *et al.* 2007). Wild pollinators require floral resources and nesting habitat that are frequently limited in agricultural landscapes, and are often provided by adjacent or integrated natural and semi-natural areas (Westrich 1996; Williams & Kremen 2007). Visitation rates, richness and population stability of wild pollinators decline with increasing distance from these habitats (Ricketts *et al.* 2008; Garibaldi *et al.* 2011), but landscape configuration has not been shown to have strong effects (Kennedy *et al.* 2013). In truly isolated agroecosystems (i.e. organic farm 'islands' surrounded by species-poor conventional farms), farm management practices are not able to rescue pollinator communities or pollination services (Brittain *et al.* 2010).

Given these issues, as well as other known contributors to pollinator declines (Goulson *et al.* 2015), implementing management practices that increase pollinator populations and enhance diverse community membership in agroecosystems is paramount to maintain and ensure food security. In this review, we (i) consider how basic concepts in plant ecology – community assembly and functional trait diversity – can be applied to create agricultural landscapes that support dynamic wild pollinator communities and (ii) explore the opportunity for agricultural lands to serve a dual role in both food

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production and pollinator conservation. Throughout, we highlight the types of conservation goals most compatible with feasible practices in agroecosystems and raise caveats concerning circumstances in which this dual role is less likely to succeed.

Shifting towards greater incorporation of non-managed pollinators in agroecosystems provides an exciting opportunity to encourage wild pollinator conservation and restoration globally. Long-term pollinator conservation (i.e. pollinator production) need not be seen as a goal competing with food production. Investments in wild pollinator resources could benefit food producers, reduce our dependence on managed bees, and make more efficient use of available funds (Kremen, Williams & Thorp 2002; Blaauw & Isaacs 2014). We develop these ideas in the context of fundamental concepts in plant ecology, including community assembly and functional trait diversity, which are useful frameworks for considering the scales at which different factors restrict – or could be manipulated to enhance – recruitment and success of diverse pollinator communities (Fig. 1), especially with changing environmental conditions. While the ecological understanding of community assembly is derived mainly from research of plant communities (reviewed in Götzenberger *et al.* 2012), we apply a similar framework to pollinators here. By combining consideration of both community assembly and functional trait variation, we can ‘build up’ plant assemblages such that they contain suites of traits that will support existing, local pollinator communities while also incorporating the functional trait redundancy necessary to buffer against natural community dynamics (Fig. 1). We highlight how the application of these concepts in plant ecology can assist with food security by supporting pollinators and pollination services in agroecosystems. For our recommendations to have future longevity, we also consider best practices in the context of global climate change.

Consideration of community assembly and disassembly processes

Community assembly and disassembly describe the processes of species addition or loss, respectively, operating at different spatiotemporal scales to form local, interacting communities (e.g. Ostfeld & LoGiudice 2003; HilleRisLambers *et al.* 2012). We can apply these concepts to agroecosystems to better understand existing plant–pollinator communities as well as manage for biodiversity conservation and sustained pollination services. At the landscape level, agricultural intensification has replaced once continuous, heterogeneous, native habitat with large, often isolated, monocultures (Saunders, Hobbs & Margules 1991; DeFries, Foley & Asner 2004). This reduction in and homogenization of floral diversity is often accompanied by intensive pest management practices and creates highly disturbed environments, which can hinder the success of and disassemble resident pollinator communities (Kevan 1999; Kremen, Williams & Thorp 2002). The resulting on-farm wild pollinator communities are those that remain (i.e. are environmentally filtered;

HilleRisLambers *et al.* 2012) or have naturally recruited since conversion to agriculture (Fig. 1). Thus, unless they bring in honeybees or other managed bees, growers currently have little direct control over the pollinator communities in agroecosystems.

While plant community assembly in agroecosystems is rapid (i.e. we grow the desired floral species), the speed of pollinator community assembly is poorly understood. Pollinator assembly may be slow because ample time may be needed for pollinators to colonize from the surrounding fragmented landscape (Aizen & Feinsinger 1994; Dorchin *et al.* 2013). Alternatively, if there are flowers and other resources available in the landscape, dispersal may not be limiting and expansion could be rapid (López-Urbe *et al.* 2016). Both scenarios emphasize the potential importance of corridors or ‘stepping stones’ of floral resources and nesting habitat at the landscape scale. There is evidence, however, that pollinators respond consistently to the availability of floral resources after land-use change (Winfree, Bartomeus & Cariveau 2011), highlighting the applicability of the ‘if you build it, they will come’ adage. On-farm management practices can therefore help to enhance resident pollinator communities and to recruit new, sustainable pollinator populations from surrounding natural areas. However, the degree to which these practices provide resources necessary for viable pollinator communities (e.g. floral *and* nesting resources) is poorly understood (Sardiñas, Ponisio & Kremen 2016).

Consideration of functional trait diversity of plants and pollinators

A main challenge facing ecologists is a better understanding of how climate change is affecting ecological interactions among species so that we may maintain the essential services they provide, like pollination. To better understand mechanisms by which shifts in species interactions could occur, ecologists can quantify traits potentially involved in mediating these interactions and examine community-wide patterns of functional trait diversity (Diaz, Noy-Meir & Cabido 2001; Suding *et al.* 2005; Sandel *et al.* 2010; Mouillot *et al.* 2013). In particular, the originality and uniqueness of a species’ traits relative to others in the community define its functional role and contribution to functional diversity (Laliberté & Legendre 2010). Functional diversity often predicts ecosystem processes more accurately than species richness (Reiss *et al.* 2009; Gagic *et al.* 2015). Importantly for the conservation of biodiversity and ecosystem function, a functional trait approach allows the ability to quantify the degree to which interactions or ecosystem services may be maintained even if species composition changes (Díaz & Cabido 2001; Elmqvist *et al.* 2003; Laliberté *et al.* 2010). While functional trait approaches have had great success in community (Weiher *et al.* 2011; Spasojevic & Suding 2012) and restoration ecology (Funk *et al.* 2008; Wainwright, Wolkovich & Cleland 2012; Laughlin 2014), such approaches are just beginning to fully incorporate more than one trophic level (Sargent & Ackerly 2008; Coux *et al.* 2016) and will likely provide valuable insight to

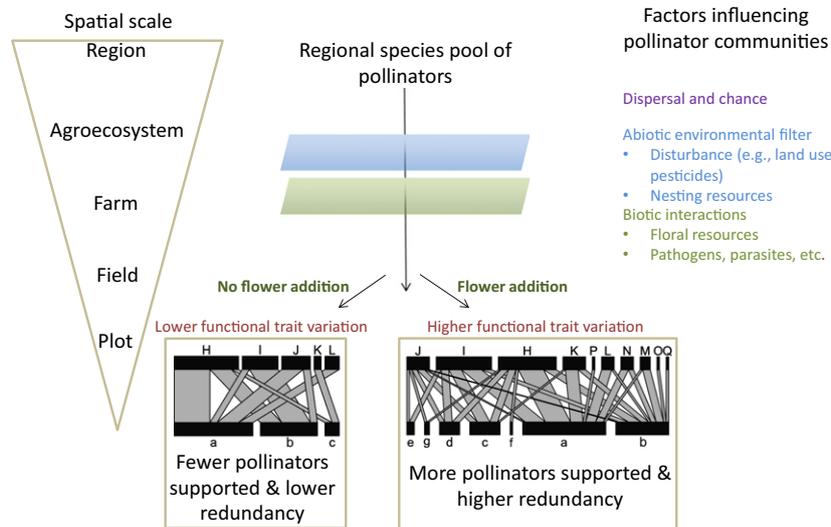


Fig. 1. The composition of pollinators in on-farm communities results from a series of abiotic and biotic filters, which may not be mutually exclusive (e.g. ‘nesting resources’ may involve biotic and abiotic components). The influence of these factors on pollinator communities varies with spatial scale. Past disturbances may have ‘disassembled’ these communities, and current communities may be a subset of this original community. Current communities may also reflect some re-assembly or novel assemblages. We can begin to assist this process of re-assembly of diverse and highly functional communities (i.e. potential for stability of pollination services) by manipulating, in particular, floral and nesting resources on farmlands. Because growers and managers have strong control over floral resources in agroecosystems, we illustrate examples of potential plant–pollinator interaction networks resulting from two scenarios: with and without the addition of wildflower plantings. By taking into account the functional trait variation of flowers being added, complementary suites of plants can be chosen to support diverse pollinator communities. Within the plant–pollinator networks, lowercase letters (a–g) and uppercase letters (H–Q) represent plant and pollinator species, respectively, and the width of the black bars indicates the relative number of interactions in which that species participates. [Colour figure can be viewed at wileyonlinelibrary.com]

how functional diversity contributes to patterns of species interactions across trophic levels – including plant–pollinator interactions – and after environmental changes.

Plant species often differ in their responses to environmental changes (e.g. Walther *et al.* 2002), and, taken individually, these studies can indicate an overwhelming array of species-specific effects with little predictive power. Perhaps even more discouraging for the synthesis of these idiosyncratic results is that the magnitude and direction of responses to environmental context can be variable among plant traits being investigated. Therefore, a functional trait approach may provide a useful perspective for a more immediate understanding of the effects of environmental change on plant–pollinator interactions, via shifts in plant traits (e.g. McGill *et al.* 2006).

Variation in the traits of individuals and species can influence plant–pollinator interactions (Junker, Blüthgen & Keller 2015) as well as pollinator fitness (Roulston & Cane 2002; O’Neill *et al.* 2011). Because farm management practices influence plant and pollinator diversity and composition, especially in intensely managed agroecosystems, these practices also influence trait distributions (Bengtsson, Ahnström & Weibull 2005; Grass *et al.* 2016). By investigating which traits of species and functional groups are most likely to be affected (positively or negatively) by environmental change and management practices in agroecosystems, we can provide a framework for understanding responses of biodiversity to these conditions. In addition, we can extend this perspective to proactively build and maintain agroecosystems that will be more robust to future

changes and to maintain pollination services and food security.

PLANTS

Growers typically have a high degree of control over on-farm plant communities, including crops themselves, weeds and non-crop plants grown to assist beneficial organisms, like pollinators. Plant species can be specifically added – or ‘assembled’ – to each system to complement the utility of existing suites of plants for pollinator forage. Selection of which non-crop species to grow for pollinator conservation typically considers plant traits that are important for pollinators (e.g. Tuell *et al.* 2008; Feltham *et al.* 2015; Williams *et al.* 2015), including flower phenology and abundance, nectar and pollen resources, floral morphology and petal colour, plant architecture and perenniality (or reseeding ability), as well as those important to farmers including ease and cost of plant propagation, plant or seed availability, and native status (i.e. zero to low risk of invasion and locally adapted to climate; Isaacs *et al.* 2009). Flowering plants with multifunctional roles, including harvestable commodities (e.g. sunflowers; Todd, Gardiner & Lindquist 2016), nesting substrates and materials for bees (Mader *et al.* 2011), services like windbreaks (Vaughn & Black 2006), and flowering cover crops that enhance soil nitrogen (e.g. Ellis & Barbercheck 2015) may also be used.

Selecting a suite of flower species that cover a range of complementary traits can provide diverse pollinator communities with ample floral resources throughout the growing

season (Russo *et al.* 2013). A diversity-minded selection approach can be used without advance knowledge of the composition of the resident pollinator community or the local pool of pollinator species that may be drawn in to the flower plantings. Given the asymmetric and nested structure of most plant-pollinator networks (Bascompte *et al.* 2003; Vazquez *et al.* 2009), it seems likely that a collection of well-selected plant species can together provide the bulk of floral resources necessary to support the survival and reproduction of a local pollinator community, though this has not been explicitly tested. To establish and maintain diverse pollination systems across the globe that are robust to environmental changes, efforts should be made to utilize suites of native plants that support both common, abundant pollinators (e.g. Carvell *et al.* 2006; Grass *et al.* 2016; Todd, Gardiner & Lindquist 2016), as well as those that are less common or more specialized (Russo *et al.* 2013). However, this approach has its limitations for pollinator conservation in that plant selection can only include those species able to thrive in agricultural settings, which include full sun and low water availability. For example, in the northeastern United States (U.S.), one of the most threatened genera is *Macropis*, oil-collecting bees which can only thrive where their host plant, *Lysimachia*, is available (Bartomeus *et al.* 2013a). Maintaining this pollinator and its plant association is not likely to be feasible specifically as part of an agroecosystem management scheme because *Lysimachia* require moist soil conditions (i.e. wetlands, swamps and lake margins) for growth. Thus, pollinators that need the most specialized conservation efforts may be less likely to be able to be supported by management compatible with agroecosystems (but see Carvell *et al.* 2006; M'Gonigle *et al.* 2015).

POLLINATORS

In addition to the floral resources provided by complementary suites of plant species, wild pollinator communities also require a diversity of species-specific nesting substrates and materials to survive and reproduce. For example, many solitary bee species nest above-ground in tunnels left by wood-boring beetles, in hollow plant stems, or in pithy twigs that the bees excavate. They also require specific nest-building materials, including leaves, pebbles, mud and tree resin, to construct their nests (Krombein 1967; Michener 2007). While there has been success creating artificial nesting habitat for commercial management of some native cavity-nesting bees in agricultural systems (e.g. *Osmia lignaria*; Bosch & Kemp 2002), as well as for research studies (e.g. Gathmann, Greiler & Tschamtkke 1994; Tschamtkke, Gathmann & Steffan-Dewenter 1998; Williams & Kremen 2007; Burkle & Irwin 2009a; O'Neill & O'Neill 2010; MacIvor 2016), little is known about the conditions required by ground-nesting bees and other wild pollinators (Roulston & Goodell 2011). The relatively short foraging and dispersal distances of many pollinator species require that, along with food resources, nesting resources be available within a localized area (Westrich 1996; Gathmann & Tschamtkke 2002; Zurbuchen *et al.* 2010). Because certain

nesting habitats may benefit some species, but not others, it is likely that a combination of nesting habitats is needed to sustain a diverse and abundant pollinator community.

Although bees are considered overall to be the most important pollinators (Free 1993; Michener 2007), we should also consider the contributions of non-bee floral visitors (e.g. flies, butterflies and beetles) to pollination services (Orford, Vaughan & Memmott 2015; Grass *et al.* 2016; Rader *et al.* 2016). Non-bee pollinators may be active at times of the day or under weather conditions when bees are not visiting flowers (e.g. McCall & Primack 1992; Cutler *et al.* 2012; Rader *et al.* 2013). For certain plant species, some non-bee pollinators can transfer pollen more efficiently and carry it further than bees (Rader *et al.* 2009, 2011). Non-Hymenoptera pollinator taxa are also unconstrained by the need for nesting substrate. All of these biological features are complementary to those exhibited by bees, and could influence the relative importance of non-bee taxa under the variable environmental conditions (Burkle & Irwin 2009b; Grass *et al.* 2016) that accompany climate change. Nevertheless, one would also have to consider other requirements of non-bee taxa, such as larval host-plant and prey availability (Holland *et al.* 2008), which could also be positively or negatively affected by climate change.

Overall, we expect intraspecific and interspecific variation in pollinator traits – including body size, mouthpart length, foraging distances, phenology, diet breadth (generalization), nesting and floral resource preferences, sociality, abundance, weather conditions preferred for flight, floral constancy and pollination efficiency, and susceptibility to pesticides and pathogens – to be important for sustained pollination services on farmlands over time. Syntheses of the effects of land-use change on pollinators may provide insight into what pollinator traits might be most affected by farm management practices. For example, nesting habitat (i.e. above-ground) and sociality are the traits most strongly associated with negative responses of bee species to land-use change (Williams *et al.* 2010). If different combinations of pollinator traits enable different functional roles (e.g. morphological, physiological or phenotypic traits that influence pollination services; Coux *et al.* 2016) in agroecosystems, then practices that support redundancy of pollinator species comprising trait combinations will be important for consistency of pollination, especially in the light of community dynamics and environmental change.

Best practices for integrating agriculture and pollinator conservation in a changing environment

Globally, agriculture is one of the leading types of land use (40% of Earth's land surface; Owen 2005). As such, the opportunity exists for farmlands to contribute significantly to the maintenance of biodiversity and habitat connectivity (McIntyre 1994; Kearns, Inouye & Waser 1998). Farmlands can have a dual role, not only providing food in the short-term but also enhancing long-term sustainability and biodiversity by acting as pollinator reserves.

CREATE GREATER LANDSCAPE CONNECTIVITY

In the U.S., some of our ‘best’ lands (e.g. most productive, topographically flat) are in agricultural cultivation, while our wilderness areas are often topographically complex with low primary productivity (Aycrigg *et al.* 2013; Belote & Aplet 2014). These differences bear significance in the light of climate change because environmentally dissimilar areas can be connected across fairly short distances in topographically complex landscapes, whereas much larger distances will require bridging to link climatic gradients in flat areas (Loarie *et al.* 2009). Thus, greater effort will likely be needed to create and maintain connectivity for pollinators in agroecosystems experiencing climate change. If floral and nesting resources are provided on farmlands in support of their role in pollinator conservation, this may automatically create greater connectivity for pollinators, especially those moving to track climate change in landscapes that need it most, though pollinator dispersal is poorly understood. These habitat enhancements could also aid wild pollinators deliberately translocated from elsewhere, in the same manner in which native biocontrol agents are moved about (see Unanswered Questions, and the dangers of assisted migration). It is important to note, however, that not only is pollinator dispersal poorly understood but also that increasing connectivity does not necessarily lead to positive ecological outcomes, as pathogens, invasive species, etc. may also use such corridors.

EMBRACE VARIABILITY IN POLLINATOR COMMUNITIES

To encourage healthy pollinator communities in agroecosystems, given uncertainty associated with environmental change, best practices will likely include strategies that embrace the certainty of inter-annual variability in pollinator composition and consider diverse groups of pollinators. Although a few, abundant wild pollinator species can provide sufficient pollination services (for target crops; Winfree *et al.* 2015), efforts to support diverse pollinator communities on farmlands are important in order to avoid relying on one or a few wild species for most of our pollination. Even when plants provide consistent floral resources, wild pollinator communities are dynamic in time and space (Burkle & Alarcón 2011), suggesting that variation in nest-site availability, pathogens, predators, weather and other factors interact in complex ways to affect populations. In particular, between-year fluctuations in the identity of the dominant pollinator taxa are the norm (Petanidou *et al.* 2008). In plant–pollinator networks from wildland systems, there is evidence that core, generalist pollinators are relatively stable in their central roles in the interaction network over several years (Fang & Huang 2012), but some studies suggest otherwise (Alarcón, Waser & Ollerton 2008; Petanidou *et al.* 2008; Crone 2013). The specific causes of these dynamics and the spatiotemporal scales of their occurrence are not known for most species (see Unanswered Questions). Regardless of the causes, these patterns emphasize the importance of species redundancy in pollination systems (Fig. 1), especially in agroecosystems where local communities of wild pollinators may be even less diverse than in less-disturbed areas. For example, when dominant bee species are strongly reduced in abundance or locally

extirpated, other diet generalists do not necessarily fill these roles (Burkle, Marlin & Knight 2013). Thus, instead of attempting to create conditions that stabilize pollinator populations and communities, a more sensible option accepts volatility and focuses on supporting redundancy and nested network structure (Tylianakis *et al.* 2010).

In the presence of pollinator population and community dynamics, there are a number of mechanisms by which pollination services might be stabilized across time or space. These stabilizing mechanisms include the portfolio effect (random and uncorrelated fluctuations in species abundances, leading to lower volatility of diverse systems), density compensation (negative co-variances in species abundances, reducing likelihood of system-wide declines in pollinator species), functional compensation (increase in the efficiencies of individuals as total abundance declines or community composition changes), response diversity (differential response to environmental variables among species) and cross-scale resilience (response to the same environmental variable at different scales by different species) (e.g. Kremen 2005). Thus far, most of these stabilizing mechanisms have not been explicitly tested for pollinator assemblages, especially in the context of farmlands (see Winfree & Kremen 2009; Cariveau *et al.* 2013; Bartomeus *et al.* 2013b for exceptions).

PROVIDE INCENTIVES AND OTHER MOTIVATIONS FOR GROWERS

Growers may consider this dual role radical and expensive, especially if added profits from on-farm pollination services do not directly outweigh costs of providing pollinator resources at the start of a conservation programme. However, the value of stable and diverse pollinator communities, along with other ecosystem service benefits of habitat enhancement (e.g. soil stability, pest control and nutrient cycling), could be high, especially in long-term environmental and economic analyses (Wratten *et al.* 2012). Costs and benefits in these analyses can be very difficult to measure, and while there are whole fields of study that deal with valuation from economic and ecological perspectives (e.g. Cardinale *et al.* 2012), it is beyond the scope of this review. Future valuation studies will aid the progress of this field.

Incentives (e.g. government subsidies) could be offered to support this dual role (Scheper *et al.* 2013), regardless of whether the focal crops require insect pollinators for seed or fruit set. First steps towards this goal that are flexible, affordable and feasible, relative to the cost of hedgerows, for example (M’Gonigle *et al.* 2015; Morandin, Long & Kremen 2016), include wildflower plantings (Blaauw & Isaacs 2014) and nesting habitat enhancement (e.g. MacIvor 2016). However, incentives – as the status quo – convey the idea that governments must pay growers for the inconvenience of pollinator conservation. When incentives are reduced or removed, previously supported practices are often abandoned (e.g. Helgin & Schrader 2003). Thus, other methods to encourage practices that support pollinators may be more efficient in the long term. For example, it may be more economically

profitable for growers to participate in pollinator conservation practices for reasons other than pollination services (e.g. aesthetic, moral and social capital from product branding; Kleijn *et al.* 2015). For example, to maximize their visibility to the public, while also minimizing interference with combines and other large machinery, wildflower plantings could be implemented along roadways (*sensu* Hopwood 2008; Garibaldi *et al.* 2014, 2017). Food product labelling may be leveraged by producers to gain social capital as ‘pollinator stewards’ (e.g. <http://www.cheerios.com/weneedthebees.aspx>) and potentially charge more for their product. For example, in the U.S., General Mills recently committed to plant 3300 acres of pollinator habitat on the farms from which it sources its oats, which is not a pollinator-dependent crop. In the United Kingdom, through Conservation Grade, food products that come from farms that have adopted a biodiversity-focused farming protocol, including planting wildflowers for pollinators, are branded ‘Fair to Nature’ (<http://www.conservationgrade.org>). The sale of these products generates funds for the continued support of increasing farmland biodiversity. While these alternative motivations are rarely considered and may not prove to be adequate for continued investment in pollinator conservation, we raise them here to highlight real problems that need to be overcome in order to effectively implement this envisioned dual role of farmlands.

Unanswered questions and top priorities for future studies

Despite many remaining uncertainties, there are particular unanswered questions that are primed for additional research on pollination services critical to sustainable food production. Interestingly, many of these research topics are applicable in both natural and managed systems, and stem from basic gaps in our understanding of pollinator biology and ecology. For example, *what factors limit pollinator populations* in different regions (reviewed in Roulston & Goodell 2011)? While floral resource requirements of pollinators are more deeply understood than other potential regulating factors like nesting resources or pathogens (Steffan-Dewenter & Schiele 2008; Dicks *et al.* 2015), there is still much to learn about the quality of different plant species as food resources (Fowler, Rotheray & Goulson 2016). Addressing these topics will require grounding in ecological theory, and we can draw on approaches used to address similar questions in plant ecology to guide our investigations.

WHAT ARE THE DRIVERS AND SCALES OF POLLINATOR DYNAMICS?

We lack a full understanding of the spatiotemporal scales at which fluctuations in pollinator populations and communities are most prominent. For example, when researchers in one area observe low numbers of bumblebees across a growing season, it would be useful to know whether all species of bumblebees are similarly affected, how long this pattern lasts, how widespread the decline is across landscapes, and whether other pollinator taxa are fluctuating synchronously.

Documenting these patterns will help provide a better understanding of the underlying causes, including for example, the degree to which region-wide climate conditions or local levels of parasites and pathogens are influencing pollinator dynamics. Regional and local drivers of floral abundance and community composition will undoubtedly directly or indirectly also influence pollinator dynamics, though the contribution of these drivers relative to others is unknown.

UNDER WHAT CONDITIONS ARE NESTING HABITATS MOST LIKELY TO BE LIMITING FOR DIFFERENT POLLINATOR GROUPS?

The most effective and economical ways to enhance nesting habitat for diverse pollinator assemblages is poorly understood. Ideally, increasing nest-habitat availability could be accomplished while minimizing the area of land removed from production by targeting areas such as field edges, roadways, powerline cuts and topographically non-cultivable patches within fields (e.g. Hopwood 2008; Noordijk *et al.* 2009; Wojcik & Buchmann 2012; Hopwood, Black & Fleury 2015). Clearly, we should not assume that practices promoting pollinator food resources also provide other potentially limiting resources or that all bees have the same nest-site requirements. For example, hedgerows aid species with above-ground nesting requirements (Ponisio, M’Gonigle & Kremen 2016), but do not enhance nesting for ground-nesting bees (Sardiñas, Ponisio & Kremen 2016).

IN WHAT CAPACITY DO FLORAL RESOURCES ACT AS POLLINATOR PATHOGEN TRANSMISSION HUBS?

The degree to which certain flower species, whether natural or cultivated, promote the harmful spread of bee pathogens in agroecosystems is unclear. It is possible that we may be able to use floral traits to predict which plant species and communities harbour the fewest pathogens and limit intra- and inter-specific disease transmission (reviewed in McArt *et al.* 2014). Although generalist plant species can provide floral resources for numerous pollinators, these plant species may also play key roles in pathogen transmission. Conversely, some plant species offer nectar or pollen resources that may have ‘medicinal’ or protective value for some pollinators (Manson, Otterstatter & Thomson 2010; Richardson *et al.* 2015; Spear *et al.* 2016). Understanding the roles of certain flower types in the transmission of pathogens, protection from parasites and self-medication will help avoid unintended management consequences, limit exposure to pathogens and assist pollinators in fighting pathogen infections.

WHAT IS THE UTILITY OF WILD POLLINATOR ‘TRANSPLANTS’?

If dispersal strongly limits pollinator recruitment to new patches across landscapes, especially those with few floral and nesting resources, perhaps using techniques like trap-nests to collect a diversity of regionally appropriate, locally adapted

bees from natural areas and translocating them to compatible agroecosystems could be used to overcome some dispersal limitation and speed pollinator restoration. Using trap-nests would, of course, aid only cavity-nesting solitary bees, but other techniques, similar to those developed to manage the native alkali bee, *Nomia melanderi* (Stephen 1960), could be tested for other ground-nesting bees. With any management of this kind, it is essential to ensure that pollinator populations have access to other required resources, so that sustainable communities are established. There are also potential drawbacks to such intervention, including spreading pathogens, predators and brood parasites (Xerces Society for Invertebrate Conservation, National Resources Defense Council & Defenders of Wildlife 2010; Graystock *et al.* 2016). Exploring these possibilities will tell us whether we can truly ‘assemble’ pollinator communities in ways similar to how we assemble plant communities, or whether resources are better spent supporting existing pollinator communities that remain after ‘disassembly’ associated with conversion of wildlands to agriculture.

Conclusions

To support pollination services and food security on farmlands, we need to provide food and nesting resources that are presently limiting to wild pollinators, while restricting conditions for their natural enemies. We can use plant traits to assemble appropriate communities of floral resources, but we may be more limited in our ability to control and assemble wild pollinator communities (Fig. 1). Coping with natural pollinator community dynamics necessitates supporting diversity and depending upon numerous key species. One of the best ways to do this is to restore and manage for healthy pollinator communities at the landscape scale, with well-connected metapopulations that support functional redundancy of interactions and resilience to environmental changes (Tylianakis *et al.* 2010). In areas dominated by large-scale commercial agriculture, wild pollinator populations are estimated to have experienced especially marked declines (Koh *et al.* 2016), and these areas may also be particularly poorly positioned to respond to climate change. Therefore, we advocate for wild pollinator conservation that targets as much agricultural land as possible for participation in this endeavour. Within this context, there are numerous avenues for future research into the potential dual role of farmlands in food production and wild pollinator conservation.

Authors' contributions

L.B. conceived the ideas and wrote the first draft; C.D. and K.O. contributed significantly to writing and revising subsequent drafts and gave final approval for publication.

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Data accessibility

This paper does not use data.

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