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Review Article: Beneficial Interactions of Weeds and Pollinators to Improve Crop Production

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ABSTRACT

Weeds are widely seen in a negative light, as being unsightly and possibly pulling resources away from crop plants. Traditional farming practices use selected beneficial "weeds", however, to provide floral resources to beneficial insects and support them through added biodiversity within farms. The global annual economic value of insect pollination is enormous, with more than a third of all crops dependent on pollinators worldwide. This free ecosystem service is steadily declining as we face a global pollinator decline crisis in areas of intensive agriculture. The loss of natural resources through land conversion has decimated insect populations; therefore, there has been interest in enhancing pollinator populations by providing alternative non-crop resources to increase food production. Weeds may be useful in this goal, as they provide resources that attract and may maintain populations of pollinators. In this review, the possibility of using weeds in agriculture to increase floral resources for pollinators and crop yield will be examined. Weeds can provide extensive, free resources to insects, and understanding their interactions in agriculture needs more focus now than ever in changing environments. Fallow lands have always been used by insects and are an important part of their diets in fragmented ecosystems. Understanding their utility could help shape agricultural practices and ameliorate global pollinator decline.

Introduction

Cultivated crops often require pollinators to ensure high yields, a major focus of agricultural entomological research over the last century. There has been growing interest in enhancing pollinator populations by providing alternative resources to increase food production (Blaauw and Isaacs, 2014). The presence of non-crop plants may be very useful in this approach, and weeds may provide resources that attract and maintain populations of pollinators. The role of weeds in agriculture as a tool for insect pollinator enhancement is an emerging topic of inquiry in agroecology, with various debates and results (Altieri and Nicholls, 2004). In this review, the possibility of having weeds defined as wild, unwanted plants, in agricultural fields to increase floral resources for pollination and ultimately crop yield will be examined. Just as insects disappear with the disappearance of their flowering weeds, they can also reappear when their weeds return (Pickett and Robert, 1998). We consider here the possibility of weeds being used in agriculture to increase floral resources for pollinating insects to increase pollination and crop yield.

Pollinators

Almost 35% of crops depend on pollinators globally (Klein et al. 2007). Pollination of at least 63 crops is vulnerable to agricultural intensification, which may reduce the diversity and abundance of pollinators (Klein et al. 2007).

There is a widespread pattern of loss in pollinator richness and abundance resulting from agricultural intensification and habitat loss. With less pollination, more land will be needed for agriculture to produce these crops, resulting in demand for natural habitat destruction, especially in the developing world (Aizen et al. 2009). The global annual economic value of insect pollination was estimated to be 9.5% of the value of global agricultural production, or upwards of $173 billion worldwide (Potts et al. 2010).

Pollination by bees and other animals increases the size, quality, and stability of harvests for 70% of leading global crops (Ricketts et al. 2008), including blueberries (Nicholson and Ricketts 2019), coffee (Klein et al. 2003), oilseed rape (Bommarco et al. 2012), strawberries (Klatt et al. 2014), tomatoes (Greenleaf and Kremen 2006), and mango (Carvalheiro et al. 2012), to name just a few. Because native species pollinate many of these crops effectively, conserving habitats for wild pollinators within agricultural landscapes can help promote pollination services (Garibaldi et al. 2013). Relationships between pollination services and distance from natural or semi-natural habitats have strong exponential declines in both pollinator richness and native visitation rate (Ricketts et al. 2008). Nesting pollinators travel relatively short distances from the nest to forage: most species of bee are known to travel less than two kilometers away (Rands and Whitney 2011). Small scale practices can have major effects on pollination services, then, especially for insects with short flight ranges (Garibaldi et al. 2014)

For 17 crops in agricultural landscapes around the globe, a significant negative effect of distance from natural habitat- due to habitat loss and conversion- was found on the richness and abundance of wild bees (Ricketts et al. 2008). Visitation rates by pollinators on crops decline as distance from natural areas increases, reaching half of its maximum at just 0.6km away from natural habitats (Ricketts et al. 2008). Pollination services decline exponentially with distance from plantings, and perennial and older flower strips with higher flowering plant diversity are found to enhance pollination most effectively (Albrecht et al. 2020). Most wild plant species (80%) are directly dependent on insect pollination for fruit and seed set, and many (62–73%) plant populations show pollination limitations (Ricketts et al. 2008). Tropical crops pollinated primarily by social bees may be most susceptible to pollination failure from habitat loss (Ricketts et al. 2008). Exposures to pesticides and pathogens, coupled with food stressors, can impair immune responses, rendering bees more vulnerable to parasites (Goulson et al. 2015). Removing stressors by increasing floral availability in farmlands through retaining or restoring areas of semi-natural habitat can improve nest site availability and reduce dietary stress.

Climate change also poses a threat to both pollinators and crops. Heat stress results in lower yields of crops, such as with faba bean (*Vicia faba*). However, insect pollination partially recovered faba bean yield loss following heat stress, with significantly lower yield losses in plants pollinated by the buff-tailed bumblebee *Bombus terrestris* with increased transfer of pollen to damaged flowers (Bishop et al. 2016). Insect pollination may increase production stability in changing environments, becoming more important in crop production as the probability of heat waves increases. Therefore, maintaining pollination services requires the conservation and management of sufficient resources for wild pollinators within agricultural landscapes, such as suitable nesting habitats and sufficient floral resources.

Proximity of nesting habitats to agricultural fields is critical for insect pollinated crops. On average, fields 1.5km away from natural habitat patches can be expected to contain 50% of the pollinator diversity of fields closest to these patches (Ricketts et al. 2008). As distances from natural habitats increase, fewer pollinator species forage to that distance or nest in fields so isolated from their natural resources. Field margin manipulation can enhance the proportion of land available to longer-distance nesting foragers such as honey bees, and short-distance foragers such as solitary bees for foraging, regardless of the distance over which they normally travel to find food (Rands and Whitney 2011). Many solitary bees prefer to nest in exposed soil; therefore, the disturbance created in many agricultural fields may actually create preferred nesting substrate for some of these ground-nesting species (Ricketts et al. 2008). Limited flight ranges of insects can cause a loss of connectivity between habitat types; however, this loss is partially mitigated by the abilities of some bee species to nest and reproduce within agricultural landscapes (Kremen et al. 2002). Several species found in isolated farms readily nest in the ground within agricultural fields or fallow farm borders (Kim et al. 2006). These small species have relatively low resource demands per individual, and therefore may be able to survive and reproduce on the resources provided by flowering weeds when crops are not blooming (Crooks and Sanjayan, 2006). Bees usually nest in one habitat type, most frequently in the ground or dead plant stems, including tree cavities, but require other types of habitats for forage, like natural prairies, forests, and wildflower meadows (Ricketts et al. 2006). In California watermelon fields, for example, the species most often absent from isolated fields also tend to be the most efficient pollinators, exacerbating the effect of declining richness on pollination services (Larsen et al. 2005). Connectivity among different habitats in a landscape can affect these important ecosystem services, many of which provide economic benefits to human populations (Ricketts et al. 2006).

High aculeate or stinging hymenopteran diversity, including species of conservation concern, can persist in agricultural environments containing 21–22% semi-natural habitat (Wood et al. 2015). Adding floral resources significantly increases aculeate diversity more so in simpler, intensively farmed landscapes, with around 5–10% semi-natural habitat (Wood et al. 2015). One way to provide for more habitat in which to conserve native bees and other species biodiversity, as well as nonrenewable resources, would be to improve the yields on existing crop lands. This can be accomplished, in part, by introducing the most efficient pollinators for these crops (Batra, 1995).

Adding plant and insect diversity to the barest agricultural landscapes ensures efficient pollination and productivity, which in turn reduces the need for converting natural areas into agriculture to feed growing populations. Pollinator supporting plants are more successful when background floral resources are scarce. In South Africa, for example, the importance of weed species richness for enhancing crop sunflower seed set increased with larger distances from natural areas, underscoring their importance in isolated homogenous landscapes (Garibaldi et al. 2014).

There is a pollinator decline crisis in areas of intensive human land use and landscape simplification, including farmlands (Dainese et al. 2019). Pollinators are sensitive to the presence or absence of floral resources, with their populations fluctuating in turn. A number of insect groups and farmland birds have shown marked population declines over the past 30 years, with the average decline of terrestrial insect abundance about 9% per decade (van Klink et al. 2020). Correlational studies indicate that many of these declines are associated with changes in agricultural practices (Marshall et al. 2003). However, local-scale diversification can change overall population trends, providing hope for directed conservation tactics.

Decline in pollinators is interlinked with weed and habitat decline, through increased applications of pesticides (van der Valk et al. 2013), fertilizers (Nicholls and Altieri, 2013), and the expansion of monocultures. Herbicidal eradication of weeds removes nectar that weeds can provide for pollinators (Nicholls and Altieri, 2018). With large synchronous blooms of a single crop and vegetational simplification, mutualisms between insects and flowering plants are greatly diminished. The lack of floral resources within or around a farm before and after the crop blooms can cause a decline in pollinators between seasons (Carol and William, 1997). Pollinators can use weeds as alternative or additional resources in a farm (Batra, 1979) before a crop blooms, during, and after. This increases pollinator health and proximity to crops, and in turn increases crop yields (Carol and William, 1997).

Native bees and other insects are important contributors to global crop pollination (Batra, 1967, 1995). The contribution of wild, free-living bee species in California alone is between $937 million to $2.4 billion per year in economic value of crop pollination, with no cost to farmers for this ecosystem service (Chaplin-Kramer et al. 2011). These native bees can provide full pollination services for free, without the use of managed honey bees, in farms near natural areas (Kremen et al. 2002). However, pollinators require 15 or more flowering species providing a season-long food supply to be healthy and remain in a farm (Willmer, 2011). Weedy refuges with wildflowers, then, provide this floral diversity and palliate the pollinator decline crisis, especially in monocultures (Pickett and Bugg, 1998). Patches of flowering habitats work as refuges; however, if the farm is too large (>5 ha) native pollinators cannot spill-over and spread into farms (Nicholls and Altieri, 2013).

On-farm diversification may be an important refuge for both specialist bees and other pollinator species that are vulnerable to floral resource simplification resulting from land development (Guzman et al. 2019). Increasing diversity of native bees can assuage low populations of agricultural European honey bees (Kremen et al. 2002), and recent studies have highlighted the importance of overall biodiversity on pollination success and crop yield (Kremen et al. 2007, Garibaldi et al. 2016). There is evidence that artificially bringing in hives of agricultural honey bees can increase crop pollination temporarily (Rader et al. 2013), but that during fluctuating crop and pollinator needs, native pollinators can provide significant crop pollination when near natural areas. Honey bees negatively affect the mutualistic interactions between native bees and plants, and there is evidence that when they dominate the landscape pollinator-dependent crops will be less productive than with a more diverse pollinator array (Aizen et al. 2020).

Native bee communities, for example, can provide full pollination services for watermelon, a crop with heavy pollination requirements (Kremen et al. 2002, Njoroge et al. 2010, Rader et al. 2013). Native bees also can buffer against the negative impact of climate warming on honey bee pollination of watermelon crops, exemplifying how biodiversity can stabilize ecosystem services against environmental change. Similarly, diversified organic farming increases insect functional diversity (Goded et al. 2019), enhancing pollinator diversity, abundance, crop pollination, and yield. Ecosystem services arguments and conserving biodiversity concerns both concur, therefore, on the potential benefits of increasing diversity with weedy species. Such connectivity may be provided by deliberately planted strips of native plants, wildflowers, or simply uncleared ground that has been colonized by weeds.

Weeds are by definition tenacious, hardy plant species: they grow without being cultivated, and often where they are not wanted. Weeds are classically defined as plants that spontaneously grow on land modified by humans, while arable weeds are those that occur in regularly cultivated fields, yet there is still no definite answer to “what makes a weed a weed?” (Bourgeois et al. 2019). Agricultural weeds have specific functional traits that make them tolerant to arable fields, such as soil disturbances and fertilization, making a large overlap in the weedy potential of non-weed species. Most weeds are therophytes with earlier and longer flowering, larger leaf area, and affinity for nutrient rich sunny dry environments compared to non-weeds (Bourgeois et al. 2019). Many weeds can be non-native, but some native plants also have weedy propensities. With decreasing landscape diversity, weedy floral resources are often all that remains. Weeds may be insect- or wind- pollinated, aiding genetic variation and adaptation to disturbances. They are often self-compatible and may automatically produce seed without pollinators (Baker 1974), ensuring their continued presence in the seed bank. This environmental plasticity allows successful persistence of “weeds” in disturbed habitats (Baker 1991). Weeds are an essential reservoir of pollen because of their continuous flowering phenology (especially during the late spring period) and their high species richness, which contributes directly to the pollen diversity dietary needs of insects (Requier et al. 2015).

A number of studies have examined the benefits of planting strips of wildflowers near crops to enhance pollination (Ouvrard et al. 2018; Tschumi et al. 2016; Feltham et al. 2015). Similarly, when comparing wildflower plantings with weeds to support wild bees, in one site the numbers of honey bees did not differ significantly between wildflowers and weedy control plots, showing the economic significance of both kinds of floral resources to pollinators.

Floral rewards

Nectar

Bees, wasps, flies, butterflies, and some moths utilize nectar, a common floral reward. While all flowers have pollen, not all flowers have nectar, but many of those visited by insects do (Baker and Hurd, 1968; Goulson, 1999; Faegri and Van Der

Pijl, 2013). Nectar is used for their daily energy intake. It is the metabolic precursor for beeswax and is processed into honey, the food reserve for overwintering bees that do not forage in winter (Bretagnolle and Gaba, 2015).

Honey bees collect nectar from flowering plants, and the different types of honey are named for the dominant flowering plant resource present in certain locations and seasons. High honey bee densities may have an impact on other pollinators via competition for floral resources (Torné-Noguera et al. 2016). A well-developed suction pump in the head represents an important adaptation for nectar-feeding insects, such as Hymenoptera, Lepidoptera, and Diptera. This pumping organ creates a pressure gradient along the proboscis, responsible for nectar uptake (Karolyi et al. 2013). Large-body flies such as *Syrphidae* have pollen collecting hairs, long, spirally grooved bristles, and elongate mouthparts to ingest nectar and pollen from flowers.

Butterflies use amino acids in nectar to enhance their fitness and fecundity, acting as agents of natural selection on nectar composition in plants, supporting the existence of a relationship between nectar preferences and fitness benefits (Jervis and Boggs, 2005). Interestingly, Map butterflies (*Araschnia levana*) can use nectar as adults to override impacts of poor larval food (Mevi-Schütz and Erhardt, 2005). Similarly, the provision of adequate nectar resources and larval host plants within intensively managed arable landscapes is likely to be essential to the successful conservation of butterfly species. Weedy patches in the crop have a direct benefit to butterfly richness, with mobile species taking advantage of these spatially and temporally unpredictable nectar resources (Pywell et al. 2004). Adequate shelter, floristically diverse field margins, and availability of nectar resources can increase the abundance of immobile butterfly species in arable landscapes, as well as presence of larval host plants and the abundance of mobile species (Pywell et al. 2004).

Pollen

In addition to nectar, pollinators need pollen from a variety of plants, and rely on a wide diversity of plants for their pollen needs throughout the season, even during crop flowering (Requier et al. 2015). Pollen is used for brood development, as it contains proteins, fats, mineral salts, amino acids and vitamins, and is stored in small quantities as it deteriorates rapidly (Bretagnolle and Gaba, 2015). Pollen collected and stored in hives can provide a record of what species the honey bees have collected (Anderson et al. 2014).

Weeds represent a substantial part of the honey bee annual diet. To overcome the need to feed colonies artificially during a period of food supply depletion, it is necessary to increase either the diversity of crops or the abundance and diversity of floral resources in association with crops: weeds, grasslands, hedgerows, or field margins (Requier et al. 2015). This provides free resources to agricultural bee colonies, as well as native insect species. Pollen resource diversity and quality also enhances resistance to fungal diseases, tolerance to pesticides, and immunity in honey bees to parasites, diseases, and pathogens (Di Pasquale et al. 2013; Requier et al. 2015).

Agricultural honey bees have a high botanical richness in their pollen diet, mostly from trees and weeds, and are influenced by local landscape composition. Weed species constitute the bulk of honey bee diets between mass flowering crop periods (up to 40%) and are therefore suspected to play a vital role at this time period (Requier et al. 2015). This is especially critical during late spring, where there is a food supply depletion period of both pollen and nectar and a peak in honey bee populations. Early in the season, similarly, crop species were less used for pollen (11%) than other floral resources. In contrast, honey bees relied heavily on woody and herbaceous plants like weeds from semi-natural habitats to meet their pollen requirements, totaling more than 60% of their annual pollen diet (Requier et al. 2015). At the first pollen peak, for example, honey bees massively foraged on floral species from adjacent habitats rather than the crop rapeseed for pollen, possibly due to better nutrition of the weed pollen for their needs at that time (Requier et al. 2015).

Honey bees use a wide variety of resources for their pollen diets, then, in order to ensure the health of the entire colony. This may explain why bees foraged on more plant species than expected during rapeseed blooming, because larvae are more numerous during this period, with high quality pollen requirements (Keller et al. 2005).

For 85% of 41 different bee species examined, the whole pollen content of more than 30 flowers is required to rear just a single larva (Müller et al. 2006). As only about 40% of the pollen contained in a flower is available to a single female bee, however, these estimates have to be multiplied by a factor of about 2.5 to correct for pollen that has already been removed and for pollen that will later be removed by other flower visitors (Müller et al. 2006). With the exception of honey-bees, *Apis spp*., most of the Apidae appear to forage at a maximum of 2km from their nests, and a majority under 1km (Rands and Whitney, 2011). The survival and development of honey bee colonies is influenced by the regularity, quality, and quantity of nectar and pollen after overwintering for the replacement of workers, during spring and summer when the population has peaked, and in autumn for the storage of winter food (Wratten et al. 2012).

Pollen foraging plays an important role in pollination and in the life of all bee colonies that adjust their foraging to natural variation in pollen protein quality and temporal availability (Jha et al. 2013). *Bombus vosnesenskii*, the yellow-faced bumblebee, collects pollen from a wide range of plant families and does not exhibit a significant preference for native versus non-native species (Jha et al. 2013). Similarly, it was found that bumblebees forage further in pursuit of species-rich floral patches and in landscapes where patch-to-patch variation in floral resources is less, regardless of habitat composition. This demonstrates extreme foraging plasticity in wild pollinators, and that floral diversity, not density, drives bee foraging distance (Jha and Kremen, 2013). Non-native wild plant species flowering in late summer, then, can fill a forage gap for the diet of both honey bees and generalist wild bees during this time (Wood et al. 2018).

Additionally, native bees such as *Hylaeus spp.* are more likely to carry less pollen and exhibit higher floral fidelity compared with the non-native honey bee *Apis mellifera* (Miller et al. 2015). By contrast, honey bees are more likely to carry mixed pollen and forage on invasive plant species (Miller et al. 2015). Honey bees tend to be found more frequently and in greater abundance in mass-flowering crops whereas wild, solitary bees are more abundant in semi-natural areas, grasslands and weedy strips (Bretagnolle and Gaba, 2015).

For both wild and honey bees, weeds are a limiting resource: quantitatively for honey bees, especially between mass-flowering periods, and qualitatively for the more selective wild bee foragers (Bretagnolle and Gaba, 2015). The decline in wild bee diversity is, therefore, strongly correlated with the decline in weeds and wildflowers.

Wild flowers are strongly dependent on pollinating insects for their reproduction: 78–94 % of flowering species rely on pollination (Ollerton et al. 2011; Winfree et al. 2011). Native and rare weed species and wildflowers are pollinated by wild bees, with honey bees actively collecting pollen from wildflowers, helping to ensure the conservation of floral biodiversity. The presence of wild bees on flowers also can cause behavioral changes in honey bees, which, when disturbed, forage on other flowers, helping to pollinate crop plants and increase the success of pollination (Riedinger et al. 2014). For instance, when weeds are present in sufficient numbers or close to crops, the wild bee community is more abundant, pushing honey bees away to pollinate crop flowers which in turn increase crop production (Carvalheiro et al. 2011).

Pollen abundance is also important for wild bees (Müller et al. 2006). Oligolectic, or specialized pollinator species demand a great abundance of their preferred plant resources, and populations of some species with a narrow diet have declined more so than generalists, in line with declines of their preferred plants (Kleijn and Raemakers, 2008). Therefore, over-representation of a single source of resource in the bees' diet could have detrimental effects upon development of the colony for certain species, and the lack of dietary diversity may lead to a lack of micronutrients essential to larval development (Rands and Whitney, 2011). Wild and honey bee networks are interconnected through the weeds, on which they both depend as a limiting resource, either in space (wild bees) or time (honey bees) (Bretagnolle and Gaba, 2015).

Pollinators are often associated with field margins and their associated hedgerows as remnants of semi-natural habitat to provide food, overwintering and/or nesting resources. When examining spill-over between oilseed rape and unmanaged margins, wild plant species all overlapped in flower-visitor niche (Stanley and Stout, 2014). Oilseed rape overlaps in terms of species of flower-visitor (pollinator niche), and in terms of individual flower visitors, with co-flowering wild species that grow in the field margins and hedgerows (Stanley and Stout, 2014). Enhancing these areas, then, can lead to an increase in the availability of forage to pollinators that nest within the landscape (Rands and Whitney 2011).

The pollinator niche of wild plant species shared with oilseed rape was 26 % (Stanley and Stout 2014). In general, insects did not specialize on a single flower type, and carried pollen from a range of different wild plant species. Very little oilseed rape pollen was found on the stigmas of wild plants, indicating that the deposition of crop pollen may not be a mechanism for interference to pollination services. Insects foraged on both the crop and wild plants in the margins, the majority of which carried pollen from both the crop and wild species (Stanley and Stout, 2014). Seven wild plant species growing in field margins and hedgerows around mass-flowering oilseed rape in Ireland, for example, overlap with the crop in terms of the individual insects that visit their flowers (Stanley and Stout, 2014). As floral richness increases, then, so does variety in bloom periods and thus the overall temporal availability of pollen and nectar resources in field margins (Morrison et al. 2017).

Pollinator Networks

Ecologists have described pollinator networks as maps of all the documented associations between and among pollinator and flowering plant species in a given area or habitat (Lewinsohn et al. 2006; Fortuna et al. 2010). In agroecosystems, there is de-specialization of plant-pollinator networks, lowering the risk of pollinator absence due to environmental disturbance (Rollin et al. 2016). These mutualistic pollination networks are essential ecological processes, and their stability depends on many species interactions (Parra-Tabla et al. 2017; Jauker et al. 2019). Habitat loss affects the diversity of wild bee communities, with social bees and small generalist bees substantially affected (Bommarco et al. 2010). Habitat fragmentation has profound effects on pollinator networks, creating the extinction of ecological interactions and networks (Janzen, 1971).

Rare weeds in farmlands, then, can act as an indicator as to the stability of a community, since their presence is in part due to pollinators, the slowest to recover after high levels of agricultural intensity (Rollin et al. 2016). Community level studies have shown that maintaining the structure of the entire food web is important, because a greater diversity of pollinators, and of pollination guilds, can improve yield and stability (Hoehn et al. 2008), and because rare plants may be linked to common plants through shared pollinators (Wratten et al. 2012).

Mass flowering plants can act as ‘pollinator hogs’, which can reduce the pollination success of adjacent co-flowering neighbors by drawing pollinators from these plants (Ghazoul 2006; Koptur and Barrios 2020). However, very attractive mass-flowering plants can also act as magnets, producing pollination ‘spillover-effects’ through increased pollinator movements to adjacent co-flowering taxa, potentially either increasing pollination (Thomson, 1978) or impacting it through the transfer of mixed-species pollen (Gilpin et al. 2019). In 10 of 18 comparisons, co-flowering species supported a slightly higher diversity of pollinators than magnets, with honey bees comprising a significantly lower proportion of flower visitors in 14 comparisons, with no evidence of pollinator spillover effects (Gilpin et al. 2019).

Additionally, florally enhanced field edges harbor more taxonomically and functionally abundant, diverse, and compositionally different bee communities compared to bare edges (Nicholson et al. 2020). However, enhancements did not increase the abundance or diversity of bees visiting crops, indicating that the supply of pollination services was unchanged following enhancement. Promoting resource diversity, therefore, improves multiple dimensions of biodiversity, underscoring its conservation value, but these benefits may not be spilling over to crops. Floral plantings have great potential to benefit ecosystem service provision, but to do so will need to be carefully tailored for functioning at specific spatial scales. Increasing flower diversity and the age of these plantings are important drivers through which this can be achieved (Albrecht et al. 2020)

Temporal availability of mass flowering crops can change pollinator preferences, as well as the stability of wild pollinator networks. Pollinator abundance increases with flower abundance, vegetation height, and floral diversity (Morrison et al. 2017). The conservation of plant diversity safeguards native pollinator diversity and the specialized links between pollinators and specific weed species, as well as enhance overall biodiversity and ecosystem services (Requier et al. 2015). This safeguarding also buffers against possible lapses in pollination by agricultural European honey-bees, whose populations are declining at a rapid rate (Paudel et al. 2015), by ensuring native bee health and range in farmlands. The connections between plants and insects, and the presence of weed species, can serve as indicators of the biodiversity in arable lands.

Debate

An area of debate that needs further evaluation is the concept that weeds providing nectar to beneficial insects may also provide resources to crop damaging pests, and even attract beneficial insects away from the crop (Capinera 2005). In addition, because pathogens can infect a wide variety of plants over many plant families, weeds can act as vectors of pathogens for crops (Wisler and Norris, 2005). Similarly, there is the question of “superweeds”, resulting from genetic drift of genes from genetically engineered crops into surrounding weed populations (Bain et al. 2017). Additionally, as insects are mobile, tracking their movements and activities between weeds and crops is difficult to quantify (Norris and Kogan, 2000). There is also the issue of the benefits of leaving weeds as a source of nectar for beneficial insects when increased fecundity of pests may arise due to nectar obtained by the adults (Shields et al. 2019). Alternatively, monitoring of insect pests hosted by weeds can allow managers to anticipate problems and selectively support beneficial species. This approach to understand insect behavior may prove a useful management technique in agriculture.

Similarly, the economic value of field margins as refuge for pollinators to increase agricultural productivity is difficult to quantify, and therefore few farmers manage these areas to enhance beneficial insects. Native pollinators, predominantly bees, may be responsible for almost $3.07 billion of fruits and vegetables produced in the United States; however, the specific added value of field margin resources to their success has not been calculated (Losey and Vaughan, 2006). The total contribution of wild pollinators was valued between $49.1 million and $310.9 million, for which there is no direct payment from producers (Allsopp et al. 2008). These values illustrate the importance of maintaining natural and other forage areas for the conservation of insect pollinators.

It is difficult to successfully link the enhancement of pollinator habitat adjacent to crop fields with increased yield, a factor that may affect widespread adoption of such practices by farmers (Wratten et al. 2012). Despite positive effects of adjacent natural habitats and records of increased pollinator abundance and flower visitation, there is a lack of research documenting pollination spill-over in the other direction- into crops from flower rich margins or from ‘pollinator-enhancement’ areas (Wratten et al. 2012). Therefore, managing flowering weeds at tolerable levels to provide alternative resources for pollinators within farms is a relatively neglected habitat management tactic.

Additionally, the number of observed pollinators may increase initially with total open flower richness, but then has been seen to decrease for more than nine open flower species (Morrison et al. 2017). This decrease in observed pollinator abundance may be due to the fact that as species richness increases, density of each individual species decreases. Native pollinators can provide full and free pollination services, but further studies as to their behaviors and requisites for success can help provide solutions to the pollinator decline crisis.

Furthermore, since wild pollinators and honey bees forage on similar resources between the mass-flowering periods of crops, pollinators may compete for resources. This raises the question as to how focusing on honey bees for crop or honey production may be detrimental to wild bees. This is an important issue because reducing wild bee communities may reduce the abundance of weeds that are not pollinated by honey bees, and consequently reduce the abundance of honey bees.

Understanding the dynamics of these complex networks and how the spatiotemporal composition of landscapes affects relationships within the networks remains a challenge for agro-ecosystem management (Bretagnolle and Gaba, 2015).

Further quantification must be addressed before farmers can readily use weeds to manipulate insects. For example, how does increasing the numbers of beneficial insects affect certain pest species, and what is the overall economic impact of insect manipulation? It is difficult to model any potential increase in agricultural production in relation to broader adoption of habitat enhancements. Assessing such economic impacts requires distinct valuations of component parts, and there is uncertainty about the interconnected nature of ecosystem services (Diaz et al. 2007, Wratten et al. 2012). Pollinators and other organisms do not distinguish between field boundaries, making counting units difficult to discern, and some species typically perform more than one function, such as hoverflies whose larvae consume insect pests while adults are pollinators (Wratten et al. 2012).

The critical period of interference between specific weeds and crops, also, is likely to vary, and is still not well quantified (Altieri, 2018). Determining when the benefits of added pollination of crops outweigh crop interference of weeds for certain species is essential. Judging when there are enough weeds to support pollinators and beneficial insects, but to not pull nutrients and interfere with the crop's production, is crucial to successfully employing weeds as insectary plants.

Conclusion

Overall, the use of weeds in increasing beneficial insects has shown promise (Araj et al. 2019; Provost and Pedneault, 2016; Kremen et al. 2002; Pickett and Bugg, 1998). While increasing plant diversity and resources to increase pollination may not always prove a success, studies on specific crops, regions, and weed species, can allow us to learn how these variables affect plant-insect ecological dynamics. Furthermore, with increased pollination and crop yield, economic valuation can allow us to gain insight on the feasibility of implementing this practice in agriculture. This review has shown that studies are needed to understand not only the behavior of insects in floristically diverse vs. depauperate landscapes, but also how anthropogenic manipulation can affect ecological interactions among crops and pollinators. In attempting to increase pollinators by promoting the presence of weeds, it is inevitable that interactions among weeds and other species can occur, and should be investigated in various crops, as well as monitored in adjacent natural systems. The best management practices moving forward are to quantify the economic ramifications accompanying the increased habitat complexity provided by weeds and in cases where there are benefits to this approach, to take advantage of the free services they may provide.

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Conflicts of Interest

The authors have declared no conflicts of interest.

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