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Integrated Crop Pollination: combining strategies to ensure stable and sustainable yields of pollination-dependent crops

Rufus Isaacs[a*], Neal Williams[b], James Ellis[c], Theresa L. Pitts-Singer[d], Riccardo Bommarco[e], and Mace Vaughan[f]

[a] Department of Entomology, Michigan State University, East Lansing, MI 48824, USA. isaacsr@msu.edu
[b] Department of Entomology, University of California, Davis CA, 95616, USA. nmwilliams@ucdavis.edu
[c] Department of Entomology and Nematology, University of Florida, Gainesville, FL, 32643, USA. jdellis@ufl.edu
[d] USDA-ARS Pollinating Insects Research Unit, Logan, Utah 84322, USA. Theresa.Pitts-Singer@ars.usda.gov
[e] Swedish University of Agricultural Sciences, Department of Ecology, SE-75007 Uppsala, Sweden. riccardo.bommarco@slu.se
[f] Xerces Society for Invertebrate Conservation, Portland, OR 97232, USA. mace@xerces.org

*Corresponding author: Tel: +517 355 6619; fax: +517 353 5598
E-mail address: isaacsr@msu.edu.

Abstract

Our growing human population will be increasingly dependent on bees and other pollinators that provide the essential delivery of pollen to crop flowers during bloom. Within the context of challenges to crop pollinators and crop production, farm managers require strategies that can reliably provide sufficient pollination to ensure maximum economic return from their pollinator-dependent crops. There are unexploited opportunities to increase yields by managing insect pollination, especially for crops that are dependent on insect pollination for fruit set. We introduce the concept of Integrated Crop Pollination as a unifying theme under which various strategies supporting crop pollination can be developed, coordinated, and delivered to growers and their advisors. We emphasize combining tactics that are appropriate for the crop's dependence on insect-mediated pollination, including the use of wild and managed bee species, and enhancing the farm environment for these insects through directed habitat management and pesticide stewardship. This should be done within the economic constraints of the specific farm situation, and so we highlight the need for flexible strategies that can help growers make economically-based ICP decisions using support tools that consider crop value, yield benefits from adoption of ICP components, and the cost of the practices. Finally, education and technology transfer programs will be essential for helping land managers decide on the most efficient way to apply ICP to their unique situations. Building on experiences in North America and beyond, we aim to provide a broad framework for how crop pollination can help secure future food production and support society's increasing need for nutritious diets.

Keywords: bee, food, sustainability, crop, biodiversity, management

Introduction

As production of crops requiring insect-mediated pollination increases globally, there is a greater demand for crop-pollinating bees (Aizen & Harder 2009). Bees pollinate most of the fruit, vegetable and nut crops that enrich the diets of a growing human population by providing essential nutrients that complement dietary staples (Eilers et al. 2011) and mitigate nutrient deficiencies (Chaplin-Kramer et al. 2014, Ellis et al. 2015). Given these trends, present and future demands compel the development of effective pollination strategies that employ appropriate bee species in efficient ways. To help address this challenge, we introduce the concept of Integrated Crop Pollination. We discuss how it might be implemented to help ensure the long-term stability of crop pollination, which is an essential component of sustainable and profitable production of many of our most nutritious crops.

The western honey bee (*Apis mellifera* L., Hymenoptera: Apidae) is an effective pollinator of many crops (Delaplane & Mayer 2000), but they are not always the most effective, and there is increasing recognition of the contributions of unmanaged populations of native bees (Winfree et al. 2011, Garibaldi et al. 2013) and other insects (Rader et al. 2016). A small number of bee species exhibit characteristics that lend them to management for use as crop pollinators (Torchio 1990, Mader et al. 2010), thereby offering alternatives for some crops or as complementary pollinators to honey bees. These different sources of insect-mediated pollination provide opportunities to integrate wild and managed pollinators to help ensure stable and sustainable crop pollination (Kevan et al. 1990; Williams et al. in press). However, growers and land managers have access to limited information for making practical decisions on the most effective and efficient strategies to support wild and managed pollinators for their crop pollination needs. Additionally, these decisions must be made within the context of the local or regional farm system, its existing pollination system, pest management intensity, economic resources, and the available bee species that are practicable to align with and integrate into the crop production system. Given the complexity of crop pollination, decision-support systems are needed for growers and other land managers to help ensure reliable pollination for stable and profitable crop production.

Integrated Crop Pollination

As an organizing concept to structure the development and evaluation of efficient and flexible pollination strategies, we introduce the concept of Integrated Crop Pollination (ICP). We define ICP as: *The use of managed pollinator species in combination with farm management practices that support, augment, and protect pollinator populations to provide reliable and economical pollination of crops* (Fig. 1). This concept includes the expectation that no single strategy will be the best option for all locations where a crop is grown, due to variation in the level of pollinator dependence, the managed and wild bee populations, crop variety, local economics of production, horticultural practices and personal preference. The approach builds on a strong foundation of research and implementation, ensuring the delivery of practical options aligned for diverse farming contexts.

Lack of comparisons between pollination strategies using a return-on-investment analysis approach inhibits growers ability to consider the relative benefits of honey bees and complementary of alternative strategies. By embracing the diversity of tactics that can be applied to specific farm situations, ICP provides a framework to guide the designing, development, and testing of multiple pollination strategies, including correlating their benefit to farm revenues. In many ways this approach echoes the development of Integrated Pest Management (IPM) 50 years ago, which brought a formal, quantitative approach to the interactions between pests, crops, and farm revenues (Kogan 1998). Here, we outline the key principles on which an ICP strategy can be developed, describe its primary components (Fig. 1), and discuss applied research needed to transition from concept to useful structure for decision-making by managers of specialty crops.

Integration of pollinators on farms

Managing crop pollination from an ICP perspective includes the integration and diversification of pollinators and will require balancing the pros and cons of using a single managed bee species such as the honey bee, mixtures of managed species, and/or wild bee pollinators. Although non-bee pollinators can be important in some contexts (Rader et al. 2015), for the purposes of this review they are not considered. The ICP framework (Fig. 1) recognizes the essential role of honey bees as specialty crop pollinators. In some situations, increasing stocking density can be the most effective and economical option for achieving the desired pollination goals with the greatest return on investment. In others, combining honey bees with other pollinating insects can improve pollination (Brittain et al. 2013a) and may reduce the risk of poor yields caused by annual variability in pollinator activity. We assume that the context under which alternative pollinators are likely to be most effective and economically practical is dictated by a combination of factors including the landscape surrounding the farm, how the farm is managed, the reproductive biology and phenology of the crops, and the relative efficacy and cost of different managed bee species. Each farmer will have a specific set of pollination options available that can be selected and integrated into their farming practices to provide for their pollination needs (Fig. 2), and so we recognize the challenge of developing specific recommendations when each farm setting is different. However, our broad view provides a structure for considering integration of pollinators into farm systems and exploring where this effort may be worthwhile. We begin by discussing alternative managed bees and wild bees, then consider management strategies for integrating them into crop production.

Managed honey bees

Honey bees are the dominant managed pollinator across the globe (De-Grandi Hoffman 2003). They are well suited for agricultural pollination because they forage on a wide range of flowering plant species, have large colonies with abundant workers, have a long history of management, and are relatively low cost for growers to rent them (Free 1993; Delaplane & Mayer 2000; Allsopp et al. 2008). From the small hobbyist to the professional commercial operator, beekeepers provide millions of colonies to support crop pollination (Potts et al. 2010, Calderone 2012), despite growing challenges to this industry. While they may be available in much greater abundance, honey bees are less efficient pollinators of some pollinator-dependent crops than other bee species (Thomson & Goodell 2001, Cane 2002, Artz & Nault 2011, Shipp et al. 1994, Stubbs & Drummond 2001, Desjardins et al. 2006, Dogterom et al. 2008, Garibaldi et al. 2013). Because other bees may be more efficient pollinators of crops, there has been long-standing interest in expanding the suite of managed bee species that can provide crop pollination (Bohart 1972, McGregor 1976, Free 1993, Strickler & Cane 2003, Peterson & Artz 2014). Alternative managed bees and wild bees may also address the pollination shortages suggested by the more rapid expansion of the area planted to pollinator-dependent crops than populations of managed honey bees (Aizen & Harder 2009). Despite their decades of use as crop pollinators, we know relatively little about the investment-response relationship for honey bee colonies in most crops. General guidelines are available and are based on older studies (Delaplane & Mayer 2000). However, there is an urgent need for research to explore optimal stocking rates and deployment patterns of honey bee colonies (e.g. Cunningham et al. 2015) as well as to understand yield responses in different farm settings (Gaines-Day & Gratton 2016) given the loss of feral honey bees in many regions and updated crop production practices that create higher bloom densities and introduce new cultivars.

Alternative managed bees

Of the approximately 4,900 bee species in North America (Michener et al. 1994), one bumble bee species and three solitary bee species have management protocols fully or nearly complete to support their use on a commercial scale (Kevan et al. 1990, Velthuis & van Doorn 2006, Pitts-Singer & James 2008, Peterson & Artz 2014), with similar low proportions of the bee fauna domesticated globally. The details of management approaches for these bees have been reviewed elsewhere (Mader et al. 2010, Delaplane & Mayer 2000), so here we consider specific points that pertain to integrated pollination. The value of bumble bee pollination in greenhouses is widely acknowledged (e.g., Shipp et al. 1994, Dogterom et al. 2008, Guerra-Sanz 2008), but in open field settings *Bombus impatiens* can also be an effective alternative to honey bees for lowbush blueberry (Desjardins & Oliviera 2006) and watermelon (Stanghellini & Ambrose 1998). Recent studies suggest their benefit is context dependent. In pumpkin fields stocked with either *A. mellifera* or *B. impatiens,* the landscapes surrounding fields moderated the benefit of supplemental pollination inputs (Petersen & Nault 2014), with the high background density of wild bumble bee colonies and other wild bees masking contributions by the purchased colonies. In other settings with a paucity of wild pollinators, the addition of commercial bumble bee colonies may be an effective strategy for pollination of pumpkin and other cucurbits.

Three species of solitary bees have been propagated and employed as pollinators of certain target crops. The cavity-nesting alfalfa leaf-cutting bee, *Megachile rotundata*, is widely adopted in North American alfalfa-seed producing regions as the primary pollinator for obtaining profitable seed yields. The ground-nesting alkali bee, *Nomia melanderi,* is managed for alfalfa pollination in Washington, where long sustained natural bee beds and some man-made ones can persist in well-suited soils under an amenable climate (Pitts-Singer & James 2008). *Osmia lignaria,* the blue orchard bee, is increasing being used for pollination of tree fruit and nut crops. Previously only considered for small-scale or organic orchards (Bosch et al. 2000, 2006), it recently has been combined with honey bees in large commercial orchards for pollination and propagation (Artz et al. 2014, Boyle and Pitts-Singer 2017). More information on the pollination potential, economics of management, and optimal use in various commercial field settings is needed to fully incorporate alternative managed bees into effective ICP systems. As an example, Table 1 highlights aspects to consider for the use of honey bees and blue orchard bees for crop pollination.

The value, benefits, and feasibility of using alternative managed bees as part of crop production strategies requires that their life cycles and nesting activities be considered along with their necessary management practices. For example, commercial bumble bee colonies can be purchased year-round and reared to have peak worker abundance to match the bloom timing of crops. These are also transportable and can be used on more than one crop per year, if colonies are kept healthy. With evidence of declines in some wild bumble bee species that are linked to increased pathogen loads (e.g. *Nosema bombi*) that may have been amplified or introduced from commercially reared colonies (Cameron et al. 2016), strategies for eliminating disease in commercial bumble bees will be a critical component of an effective ICP system that includes managed and wild bumble bees. In part to curtail the risk of disease spread or other negative ecological interspecific interactions (Graystock et al. 2016), some limitations are placed on moving bumble bee species beyond their native ranges for pollination outside of greenhouses, and producers are increasingly adopting pathogen screening (Huang et al. 2015).

Unlike honey bees and bumble bees, blue orchard bees have a solitary life history. They overwinter as cocooned adults and are ready to emerge ready to visit early spring flowers such as fruit trees, even when the weather is cool and damp. Nesting females live for about six weeks, and progeny remain in the nest for a full year before new adults emerge. Therefore, management protocols for bee storage using prescribed temperature regimes have been developed to ensure that adults emerge quickly and synchronously with crop bloom (Bosch et al. 2008). Because the blue orchard bee is a promising commercial pollinator (e.g., Bosch & Kemp 2002), systems for managing this species are being developed, including improvements in nesting materials and distribution of nest sites to maximize crop pollination and bee reproduction (Peterson & Artz 2014). The largest supply of bees comes from trapping in wild lands, which is not annually reliable, cost effective, or sustainable and differences in bee phenology by geographic source can cause management problems if trapped bees are sold for use to localities with mismatched climatic conditions (Pitts-Singer et al. 2014). Locally sourced bees and methods for their reproduction are major research priorities for the blue orchard bee industry.

Safeguarding all bees from pesticide impacts is paramount. For solitary bees, however, the incidental or accidental killing of foraging females terminates reproduction. Bee safety during crop bloom must be ensured through the limited or timely use of crop-protecting pesticides. Also, efforts are needed to protect bee population from arthropod natural enemies and vertebrate predators. The economic implications of using commercial bumble bee colonies or solitary bees as sole pollinators or in combination with honey bees have not yet been determined in most settings, yet this is a critical component for understanding how to integrate multiple bee species for pollination. Ultimately, the costs of each type of bee must be compared in the context of relative yield increases and per-acre revenues to understand the conditions under which combined strategies will be economically beneficial to growers.

Wild bees

Depending on the farm situation, wild bee populations can provide none, some, or all of the pollination needs of crop plants. The contribution of each species depends on its abundance, efficiency, fidelity, compatibility for pollinating the specific flower type, and flight range (Torchio 1990, Tepedino 1981, Thomson & Goodell 2001, Greenleaf et al. 2007). By taking these factors into account, programs to preserve, enhance or create farm landscapes to support bee populations will be more likely to deliver ecosystem services that secure or improve agricultural outputs (Kennedy et al. 2013, Garibaldi et al. 2014). Successful ICP must begin with assessing the role of different pollinators and how their contributions vary with farming context, crop type, and region. Having identified which species are effective at delivering conspecific pollen (Sampson and Cane 2000), the next step is to collect ecological and biological information about these species to identify factors that may boost their population growth and abundance, e.g., via enhanced availability and seasonal continuity of nest and flower resources (Schellhorn et al. 2015). Based on this information, the location and type of management intervention can be developed to improve pollination, with decisions rooted in economic analysis of the costs and returns of different strategies.

Diversity and pollination functioning

Promotion of bee diversity and multi-species integration at different spatial and temporal scales is expected to reduce the risk of pollination shortfalls (Kennedy et al. 2013), especially in years when weather conditions are less suitable for honey bee flight. A meta-analysis by Garibaldi et al. (2013) found that fruit set of many crops was positively correlated with wild bee visitation to flowers, but there are few long-term studies to determine how bee diversity buffers crop pollination against variable weather conditions.

Higher bee diversity is expected to increase the annual stability of crop pollination (Garibaldi et al. 2011). Given natural variability in wild bee populations from year to year (Williams et al. 2001), species diversity is expected to buffer pollination to the inter-annual fluctuations in abundance (Kremen et al. 2002). For example, mason bees will fly at cooler temperatures in spring orchards than will honey bees (Vicens & Bosch 2000), which should allow for pollination under conditions typically considered unsuitable for pollination by honey bees (Brittain et al 2013b). Whether this will lead to higher crop pollination remains unclear (Tuell & Isaacs 2010).

Bee species differ in their behavior on flowers (Chagnon et al. 1993), movement within crops (Heohn et al. 2008, Brittain et al. 2013b), and temporal pattern of visitation within single days and over the season (Tepedino 1981, Hoehn et al. 2008). The levels of pollination achieved through functional complementarity and facilitation among species can be enhanced by diversifying such functional groups of bees that pollinate crops (Gagic et al. 2015). Where there are multiple plantings of annual crops within a season, such as found in many diversified vegetable farms, seasonal crop diversity can support more diverse bee populations that can contribute to sustained pollination and thus higher annual yield. The importance of this complementarity will be augmented in polyculture systems where different bee species prefer different crops or are more effective pollinators of certain crops (e.g., Thomson & Goodell 2001, Javorek et al. 2002, Greenleaf et al. 2006). By implementing tactics to enhance bee diversity on farms, growers will increase the chance that high functioning species are present within the community of bees visiting their flowers during bloom (Kleijn et al. 2015).

Diversification of the bee community available to visit flowers during crop bloom also enables pollination synergies through facilitation among bee species. For example, the presence of wild bees in orchards and on row crops increases the pollination effectiveness of honey bees, such that each honey bee visit on average leads to better yield (DeGrandi-Hoffman & Watkins 2000, Greenleaf & Kremen 2006, Brittain et al. 2013a). The same effect can be achieved using combinations of managed species such as honey bees and *Osmia* species in almonds (Brittain et al. 2013a), and there is much yet to learn about how combinations of pollinators interact in different crops.

There is growing evidence for diversity of response among bee species to landscape change and other disturbances, including agriculture (Winfree & Kremen 2009, Carre et al. 2009, Cariveau et al. 2013). The ability to predict bee diversity in different farm landscapes can inform pollinator integration strategies, and we envision combining the model developed by Lonsdorf et al. (2009) and tested widely by Kennedy et al. (2013) into online mapping tools to support decisions on where to locate plantings to conserve bees on farms. Including an economic component will be critical for selecting locations providing positive revenue changes in nearby crops (Williams et al. in press).

Understanding the context of diversification and integration

Incorporating wild bees as part of an ICP strategy may lead to more sustainable agriculture region-wide. On the majority of small vegetable farms in the Mid-Atlantic region of the United States, wild bees alone provide sufficient pollination to some vegetable crops (Winfree et al. 2007). In this situation, maintaining habitat plantings for wild bees located near farms might be all that is needed to ensure pollination into the future. These are areas of vegetation that are rich in flowering plant resources, and they may be linear strips such as hedgerows or larger areas consisting of annual cover crops or diverse perennial plant communities. In farms with larger field sizes, managed bee integration may be needed because wild bees are too scarce to service the high density and abundance of flowers produced during crop bloom. Recognizing where different pollination strategies are most effective is critical to effective ICP.

The context under which pollination by alternative managed bees or wild bees is likely to be most effective and economical is dictated by regional land use, farm management, reproductive biology and bloom timing of the cultivated crop, and the relative cost of different bees (Fig. 2). Careful consideration of when integration of wild and managed bees is most likely to be functionally important can also reveal where and how changes to management practices (such as habitat enhancement to promote pollinator populations) can promote cost-effective ICP (Kleijn et al. 2011).

Intensively managed landscapes with large crop fields present greater challenges for the integration of wild bees for pollination (Fig. 2, right). Such landscapes offer fewer forage and nesting resources for wild bee populations outside of mass-flowering crops (Holzschuh et al. 2013, Jauker 2012) and, thus, support lower bee diversity overall. Where a mass-flowering crop is the desired target of pollination, large field sizes and locally intensive monoculture pose additional challenges (Isaacs & Kirk 2010), because of the high number of flowers and the low density of wild bees. Moreover, larger fields have interiors further from non-crop habitat that supports bees. Unless pollinator habitat can be interspersed throughout the fields and bees protected from exposure to bee-toxic pesticides, they will be more dependent on managed pollinators (Garibaldi et al. 2011).

Integration of practices on farms

Sustainable pollination using managed or wild bees requires that their populations persist over time on the farm or in surrounding landscapes (Kremen et al. 2007, Brosi et al. 2008). In general, the abundance of bees is governed by the availability and temporal continuity of resources required for the organism to complete its life cycle (e.g. nest site and material, food, mates, refuge) (Schellhorn et al. 2015), and by mortality or reduced fecundity caused by parasites, disease, predation and toxins (Cavigle et al. 2016, Cameron et al. 2015). These interactions are modified by the environment, where the main drivers are soil, climate, and nutrient availability. Bees need nesting and floral resources to persist, and these should be available throughout their flight seasons and also reliably present from year-to-year, whether as natural resources or constructed shelters.

Many farms are relatively devoid of floral resources for bees before and after crop bloom and beyond the growing season (Williams et al. 2012, but see Winfree et al. 2009), and intensive management also tends to remove key nesting substrates and overwintering sites for some bees (Forrest et al. 2015). However, there is still opportunity to apply the ICP approach in these settings. The extreme example of California almond orchards provides unique challenges for enhancing pollination services (Kremen et al. 2007), but also some lessons on what it will take to reduce dependence on honey bees. Many almond orchards are cultivated as large blocks of over 100 acres within simplified landscapes, and have very high blossom density in mid to late February when weather is unpredictable for insect flight. Wild bee populations by themselves are unlikely to yield high returns in this context because their already small population sizes are affected negatively by intensification and they cannot penetrate the large orchards. In contrast, smaller orchards or those in landscapes where native vegetation is near, receive substantial visitation by wild bees (Klein et al. 2012). In this setting, managed blue orchard bees, *Osmia lignaria*, can support honey bee-dominated pollination (Brittain et al. 2013a) such that the integrated strategy of combining managed species offers synergistic benefits for yield. Additionally, wildflower plantings near these orchards can improve the reproduction of *Osmia* bees without competing with the crop for pollinators (Lundin et al. 2017). Smaller almond orchards and those with later blooming varieties might benefit more from habitat that augments managed *O. lignaria* and wild bee populations.

Habitat enhancements

When landscape-scale management for wild bees is beyond the control of individual farmers, they can work collectively to maintain habitat that will support bees that is already present in the surrounding landscape. Coordinated regional programs should be considered for enhancing habitat across a scale that will support wild bee populations. However, local scale management can also affect their abundance and mitigate the negative effects of intensively managed landscapes (Rundlöf et al. 2008, Kennedy et al. 2013). Installing pollinator habitat to provide diverse flowering species on or adjacent to farms can attract and support wild bees (Carvell et al. 2007, Garibaldi et al. 2014, Williams et al. 2015) that may then enhance the delivery of pollination to adjacent crops (Carvaleiro et al. 2012, Blaauw & Isaacs 2014, Venturini et al. 2017). These same plants can attract many bee species that pollinate crops including honey bees (Williams et al. 2015), and provide them with a diversified pollen diet. When subjected to stressors such as pathogens, parasites, pesticides, unfavorable weather or any of their combinations, access to diverse pollen may provide nutritional benefits that influence the health of bees (e.g., Di Pasquale et al. 2013, Wheeler & Robinson 2014). If farmers can find the space for bee plantings or preserve existing resources, their efforts allow for great potential to increase sustainability of crop pollination into the future. Such habitat can occupy locations not suitable for crop production (marginal land) or along field margins, roadsides, irrigation canals, etc. However, if the benefit to crop yield is great enough, it may be possible to create bee habitat 'islands' or corridors within farms (Brosi et al. 2008, Carvalhiero et al. 2012) to ensure the presence of wild bee populations and nutritional diversity for all bees, including honey bees, during crop bloom.

Establishment of habitat for pollinators must balance multiple goals: enhance pollination and other services, minimize disservices such as supporting pest populations or attracting bees away from the target crops (but see Lundin et al. 2017), and maximize cost effectiveness. A key element of ICP is to develop a robust and flexible framework for guiding pollinator habitat from plant selection, to establishment, to streamlined assessment of function (Fig. 3). Careful selection of regionally-adapted plant species and a robust methodology for establishing plantings is critical to successful functioning. Plant mixes that bloom over the entire growing season will support a greater diversity of bee species and may benefit crops that bloom at different times of year, but targeted strategies that provide resources for particular bee species also can be designed to support specific pollinators while not supporting pests. Extended flowering promotes pollinator species whose flight periods extend beyond that of a single crop. For example, this is critical for support of bumble bee species whose queens and workers pollinate blueberry during May and June, but whose colonies grow through the summer (Blaauw & Isaacs 2014). These same habitats can also support large numbers of honey bees (Williams et al. 2015; Lundin et al. 2017) and could offset nutritional needs that currently are only partially met by feeding colonies with artificial nutritional supplements.

The addition of habitat for bees by growing areas of flowering plants within farmscapes represents only one option to diversify farming in order to support crop pollinators. The crop itself can provide vital resources to bees. In particular, adding mass-flowering crops to current, often short, crop rotations can enhance bee populations (Bennett et al. 2012). Bumble bees can build large colonies by summer, and their populations benefit from large coverage of mass-flowering crops in farm landscapes (Westphal et al. 2003). The timing and continuity of crop and non-crop bloom across the season is critical for colony performance, and studies in separate regions have shown that while early season resources led to increased production of workers, these did not consistently lead to higher queen production (Westphal et al. 2009, Williams et al. 2012, Persson & Smith 2013). Late-season flowering crops can release an apparent resource bottle neck and enhance production of reproductive bumble bees, but not workers (Rundlöf et al. 2014). These results suggest the importance of continuity of flower resources throughout the all phases of the colony cycle (Crone & Williams 2016). Other bee species that pollinate crops (such as megachilid and halictid bees) may be active during a shorter period of the growing season. To support them, adding flowers to the landscape has to be timed correctly (Russo et al. 2013). More research is needed to link the phenology of flowering crops in the landscape to communities of beneficial arthropods to identify which measures are likely to be efficient for specific bee species (Vasseur et al. 2013, Sardinas et al. 2016).

Horticultural practices

A comprehensive review by Klein et al. (2007) discovered a lack of information on the dependency of yield on insect pollination in many crops, especially those partially dependent on animal-mediated pollen transfer. This baseline information is critical for calculating the economics of ICP, both for the crop grower and for the manager of bees. Recently, the benefits of insect pollination for both yield and quality have been determined in major crops for which pollination, in many cases, has not been considered a key production factor (e.g., Cunningham & Le Feuvre 2013, Bartomeus et al. 2015, Lindström et al. 2016).

Many factors play a role in estimating the benefits of insect pollination, such as the interactions of nutrient, water and plant protection (Bos et al. 2007). For instance, water availability modifies the benefit of insect pollination for almond yield such that drought reduces yield more in fully than in poorly pollinated plants (Klein et al. 2015). Increased nitrogen reduces the benefit of pollination in oilseed rape, but pollination can recoup seed yields when little nitrogen is available, apparently increasing nutrient use efficiency (Marini et al. 2015). For seed production in red clover, pollination benefits increased synergistically with increased control of a pest insect (Lundin et al. 2013). Managing for enhanced soil organic matter can increase yield benefits from pollination in sunflower (Tamburini et al. 2016), and soil properties and pests interact with pollination in shaping yield in oilseed rape (Bartomeus et al. 2015, van Gils et al. 2016) and field beans (St-Martin & Bommarco, in final revision). These examples clearly show that pollination benefits often interact with, rather than simply add to, other resources in their relative contribution to crop yield (Seppelt et al. 2011).

A major knowledge gap is the lack of understanding of differences in pollination dependency among crop cultivars (Klein et al. 2007). Crop breeding programs rarely consider how pollination benefits vary among cultivars, or the level of pollen or nectar reward for bees. Oilseed rape has been well studied for this aspect, and screening demonstrates clear variation in benefits of cross-pollination (Hudewenz et al. 2013). Such large differences have been confirmed in field experiments where the most pollination dependent cultivars also gave the highest overall yields when pollinated (Lindström et al. 2016, Marini et al. 2015). New cultivars should be tested with self- and out-cross pollen as well as with locally-relevant bee communities during development in breeding programs. One option in response to declining bee availability from an agronomic perspective is to breed for less pollinator dependence. In almond for which pollen from a different variety (i.e., from a "pollinizer") is needed for cross-pollination of the target variety, there is keen interest in developing self-compatible cultivars that do not require such cross pollination (e.g. Holland et al. 2016). This would reduce the bee densities required to achieve complete pollination, and would result in single-variety harvest with the associated management efficiencies. Such benefits must be balanced against potential impacts on fruit/nut quality.

Pesticide stewardship

Growers apply pesticides (principally fungicides, herbicides, and insecticides) on/around crops to combat the many pests and diseases that threaten crop production and plant health. Such chemicals, particularly insecticides targeting crop pests, unsurprisingly can expose and harm the bees on which crop production depends (Johnson 2015). An effective ICP strategy will account for pesticide use and the potential for exposure to bees during crop bloom and at other times of the season. A framework for approaching such considerations is well-established already through Integrated Pest Management (Radcliffe et al. 2009). Indeed, the framework is designed to reduce unnecessary pesticide application, pesticide drift and environmental impact where decisions are explicitly based within an economic context. IPM can be adapted to include additional goals such as avoiding impacts to bees (Biddinger & Rajotte 2015).

Pesticide risk assessments for bees are derived largely from studies of honey bees, performed in few (mainly annual) crops, concentrated in North America and Europe (Lundin et al. 2015). Regulatory agencies require that plant protection products be tested for their effects on honey bees prior to registration under the presumption, albeit sometimes false, that other bee responses to pesticide exposure would be similar to those identified for honey bees (Thompson & Hunt 1999, Tasei 2002, Reidl et al. 2006, Biddinger et al. 2013). Regulatory agencies are reviewing their reliance on honey bee LD_{50} values as the primary basis of potential restrictions on pesticide use during crop bloom, and are developing protocols for greater inclusion of larval tests and sub-lethal effects within future regulatory frameworks (Fischer & Moriarty 2014, Environmental Protection Agency 2014, European Food Safety Authority 2014).

Pesticides can affect bees through multiple routes of exposure (Thompson 2012, Johnson 2015) and combinations can cause greater effects than individual exposures (Gill et al. 2012). Although growers avoid directly spraying pollinators, pesticides may contact bees when they are applied to blooming flowers. Pesticides also can drift to non-target sites if application parameters are not ideal, such as in windy conditions or when a blooming non-target crop is sprayed inadvertently because it is adjacent the target crop being treated. Bees may consume pesticides in pollen and nectar that exists either as surface residue or one that has moved systemically within the plant. Certain bees have additional routes of exposure that are less likely for other bee species. For example, honey bees may collect contaminated water to cool the nest and brood, and some solitary bees cut leaf pieces or gather moist soil for nest-building. Finally, foraging bees can bring sub-lethal doses of insecticides to their hive or nest, contaminating larval food and exposing other life-stages to pesticides.

Insecticides applied to crops that are not in bloom also have the potential to affect bees that contribute to crop pollination, but which remain active later in the growing season. Many pesticides have been detected on native bee species in agricultural landscapes (Hladik et al. 2016), although the effects of insect pest control programs on bees are variable among years and species (Tuell & Isaacs 2010; Rundlöf et al. 2015). There is mounting concern about the effects of systemic insecticides on bees and other non-target insects (Goulson 2013), and the development of ICP guidelines requires a broad view of how typical pest management programs can affect the economically-important pollinator within each region and crop. With this information, growers can make informed pest management decisions based on each pesticide's potential both to control the target pest and to affect bees and the pollination services they deliver. Recently, this approach has been termed Integrated Pest and Pollinator Management (Biddinger & Rajotte 2015).

International attention to Integrated Crop Pollination

The development of comprehensive ICP practices is a challenging task, but there are efforts underway across the globe in this direction. Examples include the International Pollinator Initiative (www.internationalpollinatorsinitiative.org) led by the Food and Agriculture Organization and recent efforts by the International Program on Biodiversity and Ecosystem Services to synthesize current understanding and to set international policy needs (www.ipbes.net/publication/thematic-assessment-pollinators-pollination-and-food-production). In Europe, members of the EU-funded Status and Trends of European Pollinators project (www.step-project.net/) have investigated pollinating insects and pollen limitation in numerous crop systems, while also exploring potential interventions to improve pollination and modeling implications of climate change on these interactions. More recently, the SuperB project (www.superb-project.eu/) has been developed to focus on conservation and sustainable management of ecosystem services mediated by pollinators, and the LIBERATION Project is looking broadly at ecosystem services to European agriculture (www.fp7liberation.eu). In North America, members of projects in Canada and the United States also are investigating crop pollination. The CANPOLIN project (www.uoguelph.ca/canpolin/) has been identifying key pollinators of major crop systems and in natural habitats. Members of project ICP based in the United

States (www.projecticp.org) are working to identify the most economically important pollinators in various fruit, nut, and vegetable crops, determine the factors driving their abundance on farms, and then evaluate habitat manipulation and alternative pollinators as potential mitigation strategies. Together these projects will advance our knowledge of crop pollination in modern agricultural systems and will contribute new insights that can support policies to safeguard pollination services (Dicks et al. 2016).

Delivery of ICP programs for farmers, extension educators, and farm advisors

Honey bee knowledge and extension information are currently integrated into most land grant university programs across the United States, and there is a wealth of experience and knowledge in the honey bee keeping community. Such compiled information is much less available and is less well developed for other managed bee species, and in many cases there are important parameters of their management that are not yet understood. Education on wild bee biology and management is starting to increase in university programs, which will help support long-term implementation of ICP and was one of the priority policy changes recommended by Dicks et al. (2016). If alternative managed bees become more cost effective and their return on investment can be better documented, perhaps a larger scale industry for rearing, managing, and deploying these bees can be developed to support ICP. Progress is being made towards this goal supported by major investments, including the development of western bumble bee species for commercial pollination and the propagation and management of blue orchard bees.

For growers making decisions about their relative levels of investment in different managed and wild bees versus the other potential components of their crop pollination system, the relationships between bees, costs, yield increases, and improved revenue are needed. Even the recommendations for appropriate stocking densities of honey bees are based on old studies with out-of-date cultivars in many crops (Free 1993, Delaplane & Mayer 2000), highlighting the need for more research before ICP guidelines can be fully developed. Similarly, there is limited information on the specific economic value and contribution of pollinator habitat and how to maximize that value. Planning tools for landowners on how to make decisions about the placement or protection of habitat or other features that support managed and wild bees have been developed (e.g. http://www.xerces.org/wp-content/uploads/2009/11/PollinatorHabitatAssessment.pdf). These tools are useful for educating landowners about ICP principles and farm planning, but they could be extended and refined from field testing and correlation with crop specific models.

As improved ICP methods are further developed for stocking and managing bees as well as to develop habitat for wild and managed bees, outreach to the farm community will be a critical component to ICP adoption. Strategies for engaging landowners include demonstration farms, workshops, field courses, case studies, written guidelines, and the use of peer-to-peer networks. Support for outreach on ICP practices should target cooperative extension, certified crop advisors, grower groups, NGOs, state and federal agricultural agencies, and other agricultural experts.

The USDA Natural Resources Conservation Service (NRCS) and Farm Service Agency (FSA) support extensive outreach on wild bee conservation efforts that support ICP practices (Vaughan & Skinner 2015). As mandated by the 2008 and 2014 Farm Bills, these agencies are incorporating pollinators into all of their conservation programs. While the level of support varies by region and over time, both agencies (in partnership with NGOs, such as the Xerces Society and Soil and Water Conservation Districts) are implementing programs through which growers can receive additional financial and technical support to adopt ICP practices nationwide. Engagement of the federal conservation agencies has the potential to significantly accelerate adoption of practices, and with the national U.S. goal of implementing 7 million acres of habitat to support wild bees and other pollinators by 2020 (Pollinator Health Task Force 2015) there is great potential to expand habitat to provide nectar, pollen, and nesting sites for wild bees.

An important consideration beyond of the core concepts of the ICP framework is that many of the pollinator habitat and farm management practices designed to support wild or managed bees can provide additional environmental benefits. ICP strategies for enhancing wild bees may also support natural enemies, especially if plantings are designed with this in mind (Wratten et al. 2012). Such a potential synergism provides added incentive for growers to consider adoption. Alternatively, the florally-rich habitat designed for pollinators could serve as a reservoir for pest insects, and more study of this risk is needed. However, recent studies using perennial wildflower or shrub plantings found greater biological control but no increase in pest insects within fields adjacent to pollinator habitat (Blaauw and Isaacs 2015, Morandin et al. 2016, Venturini et al. 2017). Broader benefits of pollinator habitats include buffers for erosion control, nutrient management, drift reduction, visual screens and barriers, and improved on-farm biodiversity (Hladik et al. 2017, Grudens-Shuck et al. 2017), which are increasingly important for certified U.S. organic farms.

Integrating an economic understanding of pollinators to agriculture

Economic assessments of pollination are tremendously useful for highlighting the value of wild bee abundance and diversity (e.g. Southwick and Southwick 1992, Losey & Vaughan 2006), but see Breeze et al. (2016) for limitations and future needs. Globally, the economic value of pollinators has been estimated to be roughly 10% of the value of agricultural production (Gallai et al. 2009). While these are important for understanding the contribution of pollinators to crop production, this is likely an underestimate because it only includes pollination leading directly to the human-consumed yield, omitting the value of seed production and livestock fodder. Additionally, values attributable to increases in quality may not be captured by mass-based production metrics (Garratt et al. 2014). For example, pollinator-dependent crops provide much of the vitamin A in regions of vitamin A deficiency (Chaplin-Kramer et al. 2014). Lastly, broad-scale valuations that are based on the crop plant's biology do not identify the contributions of different bee taxa to the value of pollination.

Methods exist to separate the economic contributions of various insect taxa, although detailed field data are required (Winfree et al. 2011). In the context of ICP, it is essential to know the relative economic value from managed and unmanaged taxa. A synthesis of data from >600 crop fields worldwide found that roughly 50% of crop flower visits came from wild insects rather than those managed for pollination (Garibaldi et al. 2013). A significant economic value of wild bee taxa also occurs even in crop systems where managed honey bees are abundant (Garibaldi et al. 2013, Kleijn et al. 2015). Because these syntheses are based on data sets collected by researchers interested in unmanaged bees, this finding may overestimate the global contribution of these taxa for some contexts. Therefore, more studies are needed that measure the economic contributions of managed and wild bee taxa using study locations that are stratified with respect to the geographical areas of main production for a given crop (see also Lautenbach et al. 2012).

Only a few studies have documented application of ICP economic assessment based on a cost-benefit analysis of alternative actions; for example, restoration of habitat for crop-pollinating bees to augment managed honey bees (Carvalheiro et al. 2012, Blaauw & Isaacs 2014). The costs of habitat restoration or augmentation also include the opportunity costs associated with not using that land area for production, if the habitat takes land out of production. These opportunity costs can be larger than the benefits in some circumstances (Olschewski et al. 2006, Brittain et al in prep), but not in others. For example, in a Canadian oilseed production region, the purely economic optimum is to leave 30% of the land area as pollinator habitat (Morandin & Winston 2006). Ever more intensive agricultural land use has not increased the yields per hectare of pollinator-dependent crops over the past two decades, even though it has increased the production of crops not dependent on pollination (Deguines et al. 2014).

With improved understanding of the economic value of managed and wild bees, we highlight the need to translate this into sampling tools that growers can use to make informed decisions on the need for adjusting managed or wild be populations during bloom. Growers or their crop scouts may conduct simple field samples of insect visitation to crop flowers, which can then be used to identify situations with insufficient pollination based on bee abundance. There is a strong link to IPM here too, and we highlight the need for the IPPM concept to be developed into practical decision tools that will support rapid research-based decisions about the need for adjusted stocking densities, investment in alternative managed bees, or implementation of conservation practices.

Summary and future directions

Development and implementation of ICP strategies for specialty crops will require attention to the following research and education priorities. First, it will be essential to know which insect species are economically valuable pollinators and what factors affect their abundance. Second, the relationships between bee abundance, pollen deposition, and crop yield must be studied to determine how much pollen deposition is needed for full yields. This is understood for some crops in some regions, but we do not have a complete picture of these most basic aspects of crop pollination for most specialty crops, limiting recommendations for optimal honey bee stocking densities. It will also be important to know how well habitat management practices can support bees and improve crop pollination, and also to gain an improved understanding of where this approach is, and is not, economical for growers. Greater understanding in the agricultural community of how to manage these alternative bees will require better access to information through transfer of knowledge to beekeepers and growers comparable to the depth and breadth of information delivered about honey bees.

Integrating training on wild and managed bees, and their application for crop pollination should be a priority for university biology entomology, and agricultural programs to help increase the ability of future research and extension educators to support implementation of sustainable pollination for specialty crops. In many agricultural regions, extension educators are in daily contact with beekeepers, growers, gardeners, and youth, developing and delivering education programs, and we would hope that the familiarity with ICP would rival that for IPM in the near future. The seeds of this change are being sown through increased attention to diversified crop pollination supported by funding agencies that are facilitating collaborative explorations between agricultural and ecological researchers studying pest management for crop potentiation and those focused on bees and crop pollination. Both issues are at the front of specialty crop growers' concerns, and development of ICP cannot proceed without an understanding of the implications for pest management. The converse is also true, as pest management for diseases during crop bloom and invasive species have the potential to limit wild and managed bee performance and survival.

On-farm demonstrations are also essential for facilitating stakeholder adoption. Therefore, we emphasize the value of working with leading growers to demonstrate ICP practices across the range of crop production situations for specialty crops. Social science analytical techniques also can be applied to identify and better understand the important motivations for stimulating the adoption of new pollination practices, which can help direct education efforts towards those with greatest chance of success. Finally, the spatial aspects of pollination services to crops must be considered for appropriate implementation across farm landscapes. This will be greatly facilitated by development of spatially-explicit decision tools that combine biological and economic aspects of crop pollination. Aerial images can be used to select crop areas of interest and then different bee species, placement strategies, densities, and habitat enhancements can be applied in various combinations to determine the expected relative profit of different strategies. Such systems will be needed to bring pollination decision-making to the level of sophistication used currently in many farms for other production inputs.

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Figures

Fig. 1. Schematic representation of Integrated Crop Pollination and the components that contribute to the development of an ICP strategy. ICP focuses on three general types of bees, supported by a combination of restoration and agronomic practices. It employs economic assessment to inform actions, combined with outreach support to deliver practical strategies to enhance sustainable pollination for crops.

Fig. 2. Conceptual representation of the relative importance of different types of bees in different farm settings. This depicts how habitat enhancements and alternative managed bees may be used to increase the diversity of bees providing pollination services to crop production in intensive settings, thereby mitigating potential pollination shortfalls if honey bees are unable to provide full pollination.

Fig. 3. Considerations for stepwise evaluation of plants for developing bee-enhancing pollinator plantings for use in farms to support bees, and subsequent implementation of these plantings. Habitat that is rewarding and well-established, and which has a benefit to yields of nearby crops can provide a positive feedback to further adoption in other farm settings.

1262 Fig. 1

1263

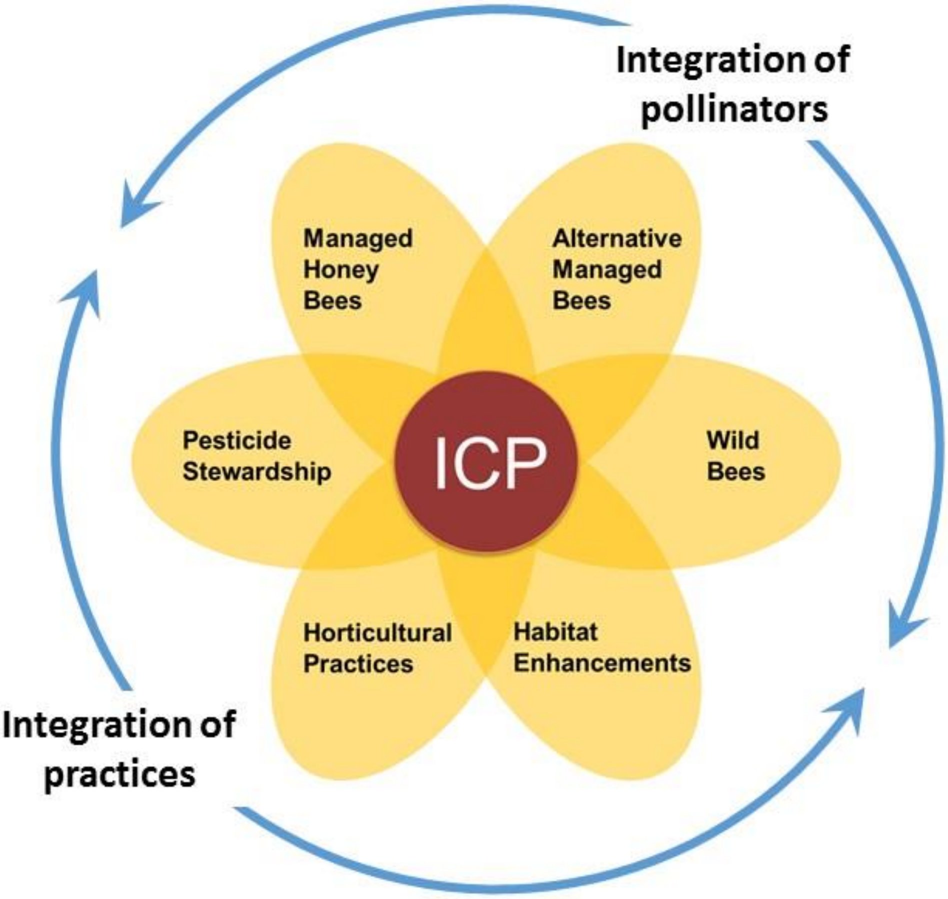


Fig. 2

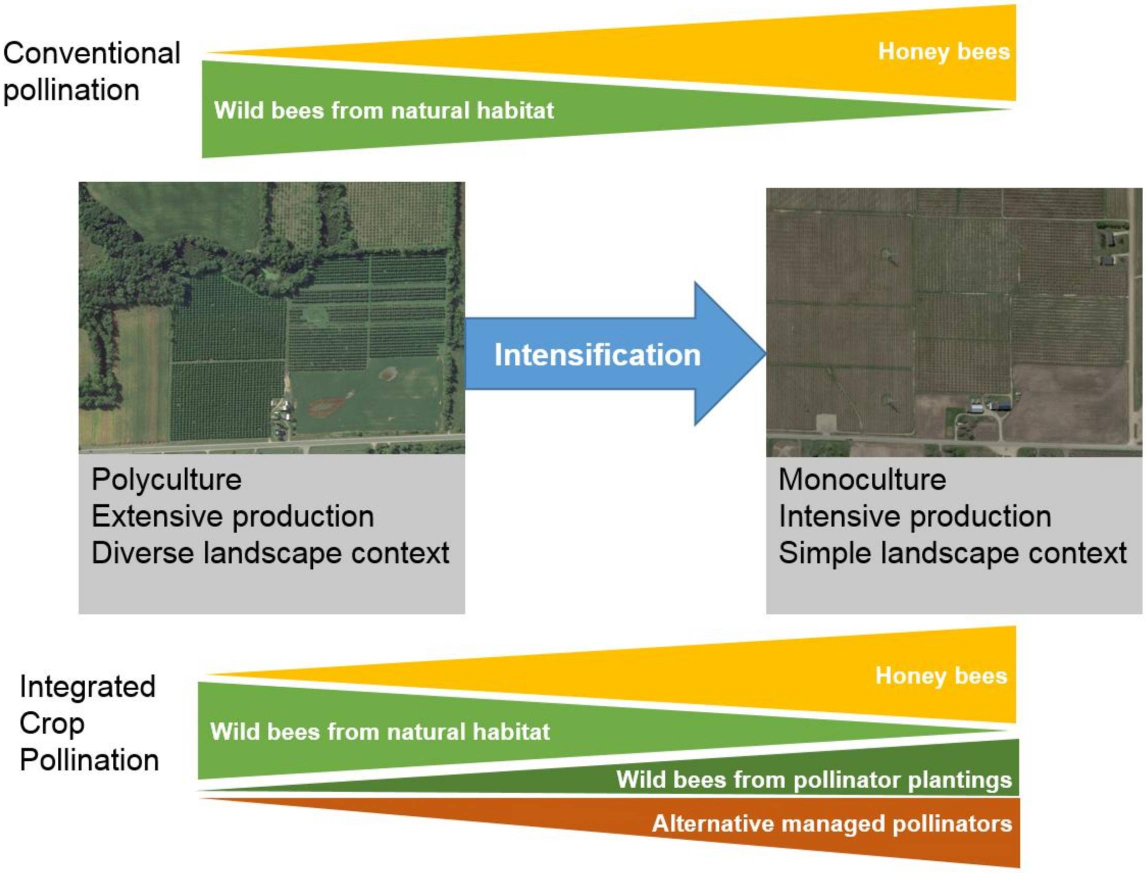
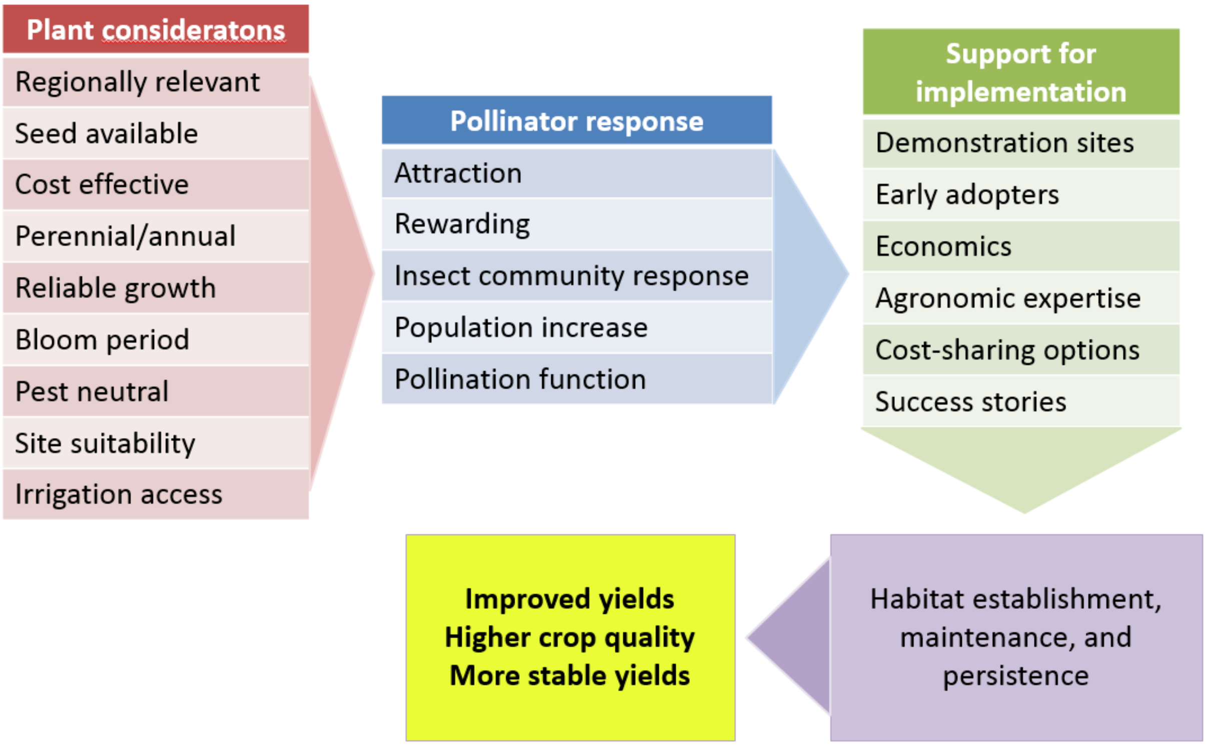

Conventional pollination
Honey bees
Wild bees from natural habitat
Intensification
Polyculture
Extensive production
Diverse landscape context
Monoculture
Intensive production
Simple landscape context
Integrated Crop Pollination
Honey bees
Wild bees from natural habitat
Wild bees from pollinator plantings
Alternative managed pollinators

Fig. 3


Plant consideratons
Regionally relevant
Seed available
Cost effective
Perennial/annual
Reliable growth
Bloom period
Pest neutral
Site suitability
Irrigation access
Pollinator response
Attraction
Rewarding
Insect community response
Population increase
Pollination function
Support for implementation
Demonstration sites
Early adopters
Economics
Agronomic expertise
Cost-sharing options
Success stories
Habitat establishment, maintenance, and persistence
Improved yields
Higher crop quality
More stable yields