

2 Crop Pollination Services From Wild Bees

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Introduction

Historically, crop pollination needs were met by wild pollinators living within the farming landscape (Kevan & Phillips, 2001), and this is still true in less intensive agricultural systems (e.g., Ricketts et al., 2004; Morandin & Winston, 2005). For many modern crops requiring an animal pollinator, however, pollination is now managed as intensively as other aspects of agriculture by bringing large numbers of commercial pollinators directly to the field where pollination is needed.

Only a dozen species have been commercialized for use as pollinators (Parker et al., 1987; Batra, 2001), although thousands more species, primarily bees, participate in crop pollination (Nabhan & Buchmann, 1997). The most widely used pollinator, and the one with the longest history of domestication, is the honey bee, *Apis mellifera* (Crane, 1990), probably utilized for at least 90% of managed pollination services (Calderone, personal communication, 2005). The extent of our reliance on this single species for such an important service is risky. In the United States, managed stocks of the honey bee have declined by 50% over the past 50 years (National Research Council, 2007) due primarily to the mite, *Varroa destructor* (Morse & Goncalves, 1979; Beetsma, 1994), which both weakens individuals and transmits disease. Also, *Varroa* mites have developed resistance to the miticides (Elzen & Hardee, 2003), leading to high rates of over-winter colony mortality during some years (e.g., up to 50% across large areas of the United States), and thus high within- and between-year variability in the honey bee supply (National Research Council, 2007). *Varroa* has affected honey bee availability not only in the United States but also in Europe and the Middle East (Griffiths, 1986; Komeili, 1988).

There are two nonexclusive alternatives to our overreliance on the honey bee: domestication and commercialization of additional species (Parker et al., 1987; Kevan et al., 1990), and conservation and enhancement of populations of wild pollinators on or near farms (Batra, 2001). This chapter is concerned with the latter alternative.

Services Provided by Wild Bee Communities

We do not know how many unmanaged species contribute to crop pollination, nor what percentage of crop pollination results from visits by unmanaged species. Bees are the most important pollinators of many crops and are recorded visitors to 73% of the crop species that require pollinators worldwide (Nabhan & Buchmann, 1997). Thousands of bee species visit crop plants globally (Free, 1993), but few exhaustive surveys have been conducted. In northeastern North America alone, 190 species of bees are associated with lowbush blueberry (Kevan et al. 1990). In a single location in California, workers recorded 66 bee species visiting selected spring and summer crops (Kremen et al., 2002a). Other wild visitors to crops include flies, wasps, butterflies, moths, midges, thrips, beetles, birds, and bats (banana), thus representing 37 invertebrate and 7 vertebrate genera (Roubik, 1995; Nabhan & Buchmann, 1997).

Wild pollinators can contribute to crop pollination in four ways. First, they can substitute for the services provided by commercially managed pollinators, replacing them either fully or partially. Second, they can enhance the services provided by managed pollinators through behaviors that increase the effectiveness of the managed pollinator. Third, they can provide services to plants that are not efficiently pollinated by a managed pollinator. Fourth, they can enhance productivity in plants that self-pollinate and for which pollination is consequently rarely managed. In contrast, wild pollinators can also detract from crop pollination in several ways, either by nectar robbery, by competing for pollen with other, potentially superior pollinators, or by transferring heterospecific pollen that clogs stigmas.

When wild bees provide an equivalent (redundant) service to that of the managed pollinator, they can partially or fully substitute for that pollinator. In watermelon production in northern California, honey bees are often imported to fields to provide pollination services. Although their pollination efficiency is low relative to other bee visitors, honey bee contribution to overall pollination is high due to their high abundance under these circumstances. Thirty native bee species also visit watermelon flowers in this area and contribute to pollination. Although none of these species is abundant compared with the artificially high abundances of the honey bee, these species collectively provide on average 28–100% of pollination needs for watermelon (range = 6–100%), depending on the farm environment. Organic farms near natural habitats (low agricultural intensity) reliably receive a large proportion of their pollination requirements from the wild bee community; these farmers never import honey bees to their farms, and the honey bee contribution on its own is not sufficient to provide them with the services they need. Thus such farmers clearly are relying on wild pollinators to some extent. At the other

end of the agricultural intensification gradient, conventional farmers far from natural habitat never receive sufficient pollination from wild bees; such farmers always import honey bees to provide pollination services. Nevertheless, they do receive some benefits from wild bee visitors, although they may be unaware of these benefits (Kremen et al., 2002a, 2002b, 2004).

Wild bees can enhance the services provided by managed honey bees via behaviors that increase the rate of pollination. First, they can enhance per-visit pollination efficiency of the honey bee through behavioral interactions. There is a single documented example of this phenomenon (Greenleaf & Kremen, 2006b), but it is likely to be widespread in cropping systems that require movements between cultivars for successful fruit or seed production (e.g., both hybrid seed production systems and many orchard crops). In hybrid sunflower seed production, farmers plant 4 rows of male-sterile, nectar-producing (“female”) cultivars for every 6–10 rows of male-fertile, pollen- and nectar-producing (“male”) cultivars in a repeating pattern. Honey bees are stocked at 2–2.5 colonies per ha; nonetheless, lack of pollination is a major factor cited by farmers for underproduction. Individual honey bees tend to forage either for pollen or for nectar (Free, 1963). Honey bees had low pollination efficiency on hybrid sunflower relative to the most efficient wild bee visitors (mean of 3 seeds/visit compared with 19). There was a strong linear relationship, however, between per-visit honey bee pollination efficiency and the richness and abundance of wild bees present, increasing the number of seeds set per honey bee visit up to fivefold. Interactions between wild bees and honey bees caused honey bees to transfer more frequently from male to female rows, enhancing their per-visit efficiency. Thus on average, although wild bees contributed only a small proportion of total sunflower pollination directly, they doubled the effectiveness of honey bees and thus the value of the pollination services honey bees provide (Greenleaf & Kremen, 2006b).

Second, better seed and fruit set can result from the combined, complementary foraging activities of honey bees plus wild bees than from that of either group alone. In strawberry, the behavior and morphology of wild bees favors pollination of the basal stigmata, whereas that of honey bees promotes pollination of the apical stigmata. The result of visits by both groups was higher pollination rates (number of fertilized achenes/flower) and larger, more completely formed fruits (Chagnon et al., 1993).

Non-*Apis* bees are more effective pollinators than *Apis mellifera* for some crops that depend on animal pollinators for fruit set, including alfalfa, blueberry, and cranberry (Parker et al., 1987; Delaplane & Mayer, 2000). In these crops, honey bees cannot reliably work the floral mechanism that allows pollination (Proctor et al., 1996). Growers often import large numbers of honey bees, hoping that increasing the frequency of encounters will increase the number of successful pollination events. Alternative pollinators have been domesticated in some cases, including *Megachile rotundata* and *Nomia melanderi* for alfalfa, or *Osmia* species for blueberry, but the use of these pollinators is not widespread (see Crane, 1990, table 8.5). In some cases, growers rely almost entirely on wild bees. In the 1970s in Canada, blueberry growers became acutely aware of their reliance on native pollinators when applications of the insecticide fenitrothion to nearby forests for spruce budworm control greatly reduced many pollinator populations, a reduction that was then correlated with significant crop losses (Kevan & Plowright, 1989).

The majority of economically important fruit and vegetable crops that self-pollinate also benefit from pollination provided by insect vectors by enhanced fruit set and/or size (Klein et al., 2007). The mechanism may be due to increased deposition of self-pollen, cross-pollen, or both, reflecting the contribution of both genetic and physiological factors to fertilization, fruit set, and fruit growth (Proctor et al., 1996; Delaplane & Mayer, 2000). Growers of self-pollinating plants generally do not import pollinators (except in cultivation of greenhouse tomatoes, whose flowers need vibration, either by wind or an insect, to release their pollen); thus enhanced fruit production due to animal-mediated pollination in self-pollinating field crops is generally due to visitation by wild bees (Klein et al., 2003a; Ricketts et al., 2004; Greenleaf & Kremen, 2006a).

Visitation by some insects may actually be detrimental for crop pollination. Insects that cut holes at the base of the flower's corolla in order to obtain nectar resources may reduce a flower's attractiveness and deter other insects from visiting and pollinating the plant (Irwin et al., 2001). Insects that visit multiple flowering species may transfer heterospecific pollen during visits to crop flowers, which could then clog stigmas, reducing both the effectiveness of that visit and of subsequent visits by the same or other pollinators. In general, non-*Apis* individuals are thought to exhibit lower flower constancy than honey bees (Slaa & Biesmeijer, 2005); thus it is conceivable that non-*Apis* wild pollinators could reduce pollination services provided by honey bees through stigma clogging, although I know of no examples in crops.

Insects (usually bees, but also pollen-eating beetles) that remove large amounts of pollen while depositing only tiny amounts can be negative, rather than positive, for pollination function in crops. The extent to which a given species (whether wild or managed) is detrimental versus beneficial for crop pollination services depends on three things: (1) its species-specific behavior, leading to its mean ratio of pollen removal to deposition; (2) the composition of the pollinator community; and (3) whether the amount of available pollen is a limiting factor. Under limiting conditions (i.e., all pollen produced is removed), if one visiting species has a high ratio of pollen removal to deposition relative to other community members, its contribution to pollination will be negative, because it removes pollen from the system that other pollinators could otherwise deposit. If it has a low removal to deposition ratio relative to other species, or if there are no other pollinating species, then it increases pollination (Thomson & Thomson, 1992; Thomson & Goodell, 2001). If the amount of pollen is not limiting, however, then more visits from any visitor that deposits any amount of pollen add to the total pollen deposited on the crop. Pollen supply will depend greatly on the cultivar, crop breeding system, and other details of cultivation (e.g., proportion of plants supplying pollen in the crop field).

Although wild bee pollinators may augment or in some cases substitute for the services provided by commercially managed pollinators, it is important to recognize some inherent limitations to services provided by wild, unmanaged bees. Wild pollinator populations are notably variable in space and time (Roubik, 2001; Williams et al., 2001); thus services they provide may not be consistent enough to meet the needs of large-scale intensive agriculture. Unlike the honey bee, which forms permanent colonies of 30,000 to 50,000 individuals, non-*Apis* bees often have relatively small population

sizes, particularly at the beginning of the flight season for multivoltine or social species with multiple generations of workers within a season.

Commercially managed pollinators are clearly critical to the success of modern agriculture, but wild, unmanaged pollinators, despite the caveats noted previously, could reduce the risk of depending overly on just one or a few commercial species. Risks from relying on only a few species come from: (1) the challenges of maintaining a stable supply of commercial pollinators, given problems of managing the genetics, pathogens, and parasites of honey bees and other commercial pollinators (National Research Council, 2007); and (2) limitations in pollination services provided by only a few pollinator species (see the upcoming section on the role of diversity). For example, honey bee workers communicate with each other about the spatial location and quality of foraging resources. This social behavior can lead to massive recruitment of workers to a crop that is rewarding in pollen and nectar, but it may also result in workers concentrating in selected areas of the field, which can bring about uneven crop pollination across the field. In the worst case, honey bee workers leave the crop altogether to forage on more attractive noncrop resources (Free, 1968). Although less numerous and certainly more patchy in their distributions, wild bees may complement the services provided by honey bees (Chagnon et al., 1993) and spread pollinators over a larger area of the crop (Proctor et al., 1996). Given their small, patchy populations, however, the goal of managing for wild pollinators should be to augment the services provided by commercial pollinators by maintaining diverse communities that collectively provide more stable services than any individual wild pollinator species could (Tilman et al., 1998; Klein et al., 2003b; Kremen et al., 2002b, 2004).

Economic Value of Services From Wild Pollinators

Estimating the economic value of services provided by wild pollinators is complicated for three reasons. First, different approaches to estimating the value of pollination services yield widely differing results (Kremen et al., 2007). The lowest value would be the cost to replace wild bee pollination services with commercial pollinators (Muth & Thurman, 1995). The highest value comes from establishing the proportional dependence of a crop on animal pollination and then multiplying this proportional dependence by the gross value of the crop produced (Robinson et al., 1989a, 1989b). Second, in situations in which both managed and wild bees contribute to pollination services, determining the contribution of each requires intensive field documentation (Greenleaf & Kremen, 2006b; Olschewski et al., 2006; Prieset al., 2007). Such information is rarely available. Nabhan and Buchmann (1997) have suggested that contributions from wild bees would be similar to those from managed bees, but using the same basic approach of Robinson et al. (1989a, 1989b), Losey and Vaughan (2006) estimated the contribution to U.S. fruit and vegetable production of wild bees at \$3.07 billion, less than 20% of the contribution of honey bees (\$17.01 billion). Third, interactions between wild bees and honey bees that augment pollination services require yet another level of field documentation

(e.g., Chagnon et al., 1993; Greenleaf & Kremen, 2006b) and may dramatically increase the value attributed to wild bees. For example, in the hybrid sunflower seed production described earlier, Greenleaf and Kremen (2006b) attributed only 7.3% of the gross value of the U.S. hybrid sunflower seed crop (\$26.1 million) to wild bees through direct pollination but an additional 39.8% to their enhancement of the pollination services provided by honey bees. The direct contribution provided by honey bees without the beneficial effects of wild bees was 52.9%.

Effects of Agricultural Land Use on Wild Bee Communities and Pollination Services to Crops

Agricultural land use may have either positive or negative effects on pollinator communities and the services they provide, depending on the intensity of agricultural land use, the spatial scale (Tscharntke et al., 2005), and the biome, although too few studies have been conducted to predict these effects with certainty. Both site and landscape-scale factors may be important (see figure 2.1). In a Mediterranean biome in California, agricultural intensification, which included both the reduction of nearby natural habitat and the predominance of large-scale industrialized agriculture (for a definition, see Tscharntke et al., 2005), led to reductions in the species richness and abundance of wild bee pollinators on watermelon (Kremen et al., 2002b, 2004), tomato (Greenleaf & Kremen, 2006a), and sunflower (Greenleaf & Kremen, 2006b), with concomitant estimated reductions in the services wild bees provide to these crops. In these studies, a common factor influencing wild bee distributions appeared to be the area of nearby natural habitats (chaparral and oak woodlands) within several kilometers of the farm site. The proportional area or proximity of natural habitat was positively correlated with bee species richness, abundance, the number of nesting bees found on farms, and the magnitude and stability of pollination services provided by wild bees (Kremen et al., 2004; Greenleaf & Kremen 2006a, 2006b; Kim et al., 2006). Local farm management type (organic vs. conventional) only weakly affected these community response variables once the landscape level effects were factored out, although for sunflower, the interannual continuity of sunflower availability within foraging range of bees was equally important (Greenleaf & Kremen, 2006b). Individual bee species were differentially sensitive to the gradient of agricultural intensification, but none increased in response to it (Kremen, 2004). The species that were the more effective pollinators in watermelon were also the more sensitive to agricultural intensification; thus their loss exacerbated the effects on pollination services (Larsen et al., 2005).

Similarly, in the neotropics, distance to wild forest patches significantly influenced the richness and abundance of wild bees visiting and pollinating coffee in Costa Rica (Ricketts, 2004) and grapefruit in Argentina (Chacoff & Aizen, 2006). These wild bees included indigenous solitary and social bees and feral colonies of introduced *Apis mellifera scutellata*. Over a span of 100 meters from the forest edge, visitation dropped precipitously by 75% (Ricketts et al., 2004), although a decline in pollination services was

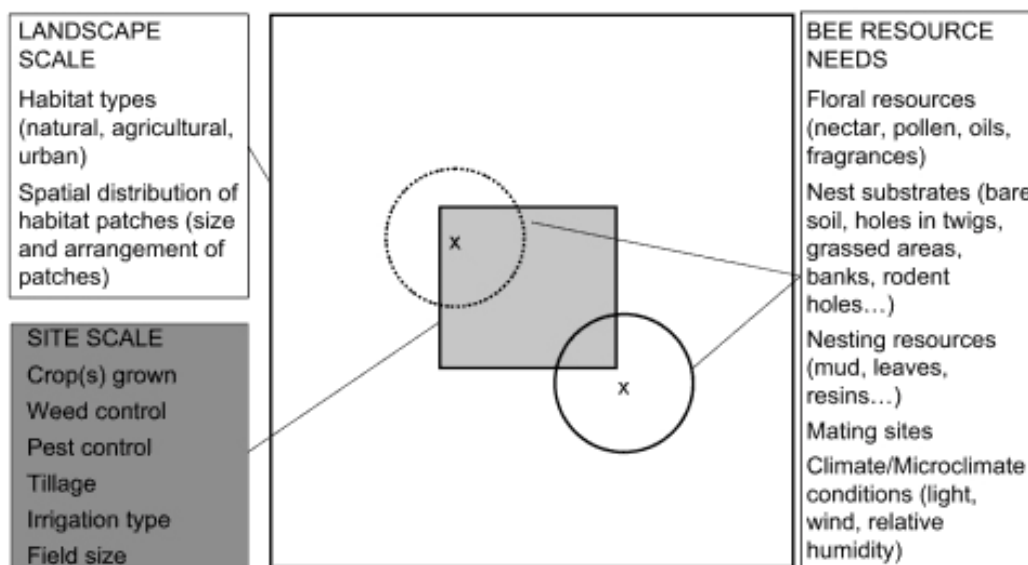


Figure 2.1 Schematic depicting the influence of site and landscape-level factors on bees in an agricultural landscape. The small gray box denotes a farm field embedded in a larger landscape, which generally includes multiple habitat types. Each x denotes the nesting site of one female bee, and the circle around each x denotes the foraging range of the bee. One female nests off the farm (solid circle) and the other nests on the farm (dashed circle), but in both cases, their foraging ranges encompass both farm and off-farm areas. Bees require floral and nesting resources that are available within their foraging range and throughout their adult flight period, as well as suitable climatic/microclimatic conditions for flying, foraging, and mating. At the farm scale, management practices influence both the availability of floral and nesting resources and microclimate conditions through the choice of crops and cultural practices, including weed control, irrigation, and tillage. Use of pesticides influences mortality rates of bees and bee predators and parasitoids. At the landscape scale, the heterogeneity of the habitat influences the diversity and abundance of available floral resources and of nesting sites/substrates within the bees' foraging range (circle), which tends to be larger in species of larger size.

not observed until 1600 meters (Ricketts, 2004). Similarly, richness and visit frequency of native wild bees visiting grapefruit (*Citrus paradisi*) declined precipitously with distance from the forest edge in Argentina (by eightfold within 1,000 meters), and the visit frequency of feral *Apis mellifera scutellata*, which accounted for 95% of visits, dropped by twofold over the same distance (Chacoff & Aizen, 2006). In coffee fields in Indonesia, distance to wild habitat affected the richness of native social but not solitary bees, whereas light levels within the fields were strongly, positively correlated with solitary bee richness and with the abundance of both solitary and social bees. Fruit set was significantly correlated with both factors (Klein et al., 2003b). In macadamia (*Macadamia integrifolia*) orchards in southern Queensland and New South Wales, Australia, the abundance of its most common native pollinator, *Trigona carbonaria*, but not of managed *Apis mellifera*, correlated with the proportional area of *Eucalyptus* forests within 1 kilometer of orchards

(Heard & Exley, 1994). In contrast, on the Atherton Tablelands in northern Queensland, where honey bees were not managed for pollination, distance from rainforest corresponded with a decline in both feral *Apis mellifera* visits and in fruit set of macadamia, although there was no correlation between fruit set per raceme and *A. mellifera* abundance per site (Blanche et al., 2006). In the same area, beetle visitors to custard apple (*Annona squamosa* × *A. cherimola*) declined in diversity and abundance with distance from rainforest habitat, with a corresponding decline in fruit production (Blanche & Cunningham, 2005; Pritchard, 2005). Similarly, wild stingless bees (*Trigona* spp.), but not feral *A. mellifera*, declined in abundance with increasing distance from rainforest in longan orchards (*Dimocarpus longan*), with a corresponding decrease in fruit set (Blanche et al., 2006). In these mosaic environments of tropical forest and agriculture, forest patches again appear to play an important role in providing habitat for native and non-native bee pollinators of crops and thus for pollination services.

In temperate agricultural landscapes in Europe with patches of seminatural habitats (calcareous grasslands, woods, meadows, and other habitats), distance to these patches influenced diversity, abundance and pollination services provided by social and solitary bees. In both of two self-incompatible plants, mustard (*Sinapsis arvensis*) and radish (*Raphanus sativus*), reproductive output was halved first at a 250-meter distance from patches and then again at 1,000 meters (Steffan-Dewenter & Tschardtke, 1999). In contrast, the abundance of common *Bombus* species in this same landscape type did not correlate with the proportional area of seminatural habitat but did positively correlate with the proportional area of such mass-flowering crops as oilseed rape, clover, and sunflower. This finding suggests that the enormous flush of pollen and nectar resources provided by large fields of monoculture crops can promote abundance of selected bee species (Westphal et al., 2003), particularly if pollen and nectar resources provided by these crops are staggered across the bumble bee flight season.

Although wild bees on crops generally show a decline of diversity, abundance, and services with agricultural intensification (*sensu* Tschardtke et al., 2005), not all studies of bee communities (including bees visiting noncrop resources) show the same diversity and abundance trends. For example, in the Atlantic Coastal Pine Barren's ecoregion of the northeastern United States, the richness and abundance of bee species in fragments of this habitat increased significantly when surrounded by a predominantly agricultural matrix compared with a predominantly forested matrix (Winfree et al., 2007). Agricultural habitats also had significantly greater richness and abundance than naturally forested habitats, and more species were found to be unique to the agricultural areas as compared with the forested areas. Forests in the Pine Barrens are composed of a pine overstory with a low-diversity, ericaceous understory. Both floral richness and abundance were higher in agricultural areas than within Pine Barren forests. In this system, agriculture apparently enhances rather than detracts from bee richness and abundance, although it must be noted that the intensity of agricultural land use is relatively low (approximately 30% of land uses within 1.6 km of sample sites) compared with other study systems. In this case, agriculture may mimic various early successional habitats in which bee species often thrive (e.g., Carvell, 2002; Potts et al., 2003; Grixti & Packer, 2006). Positive effects of agriculture on pollinator communities may be more likely to

occur in regions in which the presence of agriculture increases rather than decreases habitat heterogeneity within the foraging range of bees (e.g., <2 km), such as farming landscapes that include relatively small field sizes, mixed crop types within or between fields, and patches of noncrop vegetation, such as hedgerows, fallow fields, meadows, and seminatural wood or shrublands (Eltz et al., 2002; Tschardt et al., 2005).

In summary, based on reported studies, pollination services provided by wild bees are most likely being reduced in many of the areas in which they could be contributing to crop pollination. At the same time, numbers of commercially managed honey bee colonies have also declined, and challenges for honey bee management are increasing (National Research Council, 2007). Yet there are comparatively few documented instances of shortages in pollination services. This suggests that we are not yet in crisis; but, to be cautious, we should take preventive measures now. In particular, our heavy reliance on honey bees makes production of some crops (especially almond and other orchard crops) vulnerable to sudden, unforeseen changes in its abundance, such as appear to be occurring with increasing frequency in the United States following winter season declines (National Research Council, 2007).

Role of Diversity

A more diverse community of wild pollinators can provide a greater amount of pollination services to a greater number of crops with greater stability. More diverse communities of pollinators in agricultural systems also have greater total abundances and rates of visitation to crop flowers (Steffan-Dewenter & Tschardt, 1999; Klein et al., 2003b; Ricketts, 2004; Larsen et al., 2005; Pritchard, 2005; Chacoff & Aizen, 2006). The strikingly consistent positive relationship between abundance and richness across these studies suggests that the loss of richness will generally reduce the number of visits and hence the level of pollination services provided to crops by the wild bee community, given a strong correlation between visit number and pollination services across systems (Vázquez et al., 2005).

Although many pollinator species that visit crops are generalists, different crop species nonetheless attract different, albeit partially overlapping, sets of pollinator species from the local species pool. Therefore, maintaining diverse pollinator communities locally is important for providing pollination services to a more diverse set of crops. Within a crop, a diverse group of pollinator species can provide better pollination services than a single species can, due to different foraging behaviors (e.g., strawberry; Chagnon et al., 1993) or to interactions that influence foraging movements (e.g., sunflower; Greenleaf & Kremen, 2006b). Within a crop, diversity of the pollinator community is also important for ensuring the stability of pollination services across time and space. Several lines of reasoning support this assertion. From theoretical principles, we know that more diverse communities whose populations fluctuate in a random, uncorrelated fashion will provide more consistent services than will less diverse communities (the portfolio effect; Tilman et al., 1998). Empirical work supports the claims of theory, although few

studies have yet been conducted. Richer communities provided more stable pollination services to watermelon crops from day to day within a season (Kremen, unpublished data) and from bush to bush within a coffee field (Klein et al., 2003b; Steffan-Dewenter et al., 2006). High-diversity communities may include an array of species with broader physiological and behavioral ranges that are able to fly and to pollinate flowers under a wider array of environmental circumstances and thus to provide greater consistency than lower-diversity communities (Herrera, 1995; Bishop & Armbruster, 1999; Klein et al., 2003b).

Insect populations, especially bees, fluctuate greatly in the wild from year to year, as well as within seasons and across space (Herrera, 1988; Wolda, 1988; Roubik, 2001; Williams et al., 2001). Such transient losses are unlikely to affect pollination services to a given plant species as long as the system is relatively diverse (Williams et al., 2001; Memmott et al., 2004; Morris, 2003). In the watermelon system, entirely different bee species predominated in their visit frequencies (abundances) in 2 successive years, and hence their species-specific contributions to watermelon pollination. In both years, however, the community collectively provided sufficient services on high-diversity farms (Kremen et al., 2002b). In Costa Rica, decline in 1 year in the abundance of feral non-native *A. mellifera scutellata* was partially balanced by increases in abundances of native species (Ricketts, 2004). In these systems, managing for wild bee richness, rather than for the abundance of a particular species, is an important factor in maintaining a consistent level of service.

Managing for Wild Bee Populations and Services in the Agroecosystem

Wild pollinators are mobile organisms that often utilize a multiplicity of resources; often, different resources are localized in different, noncontiguous habitats (Westrich, 1996; see figure 2.1). Maintaining wild pollinator populations, therefore, requires understanding resource requirements and then managing habitats and landscapes to provide food resources, nesting habitats, overwintering habitats, and breeding areas. Resources must be available within foraging/dispersal distances, or organisms will die or have low reproductive rates. Managing for pollinator populations requires thinking not only at the site scale but also at the landscape and even the regional scale.

For example, in California, many of the bee species visiting crop plants are generalists with long flight periods (e.g., *Bombus* and *Halictus* species; Kremen et al., 2002a). They require a suite of floral resources stretching from early spring to mid-fall (January to October for some species) and may, therefore, depend not only on the weed and crop resources that are available on farm lands but also on wild, native plants that occur in neighboring riparian, chaparral, and oak woodland areas (Kremen et al., 2002a; Williams & Kremen, 2007). Decreasing the area of natural habitat within a given radius of a farm site (or, conversely, increasing the distance to patches of natural habitat; Harrison & Fahrig, 1995) could increase the energetic requirements to obtain floral

resources and thus to produce offspring (Orians & Pearson, 1979). Species that depend on native plants for all or part of their life cycle may either drop out completely or diminish in abundance on farms with little natural habitat within foraging range of the bee species (e.g., Larsen et al., 2005). Conversely, alternative resources provided in the agroecosystem may mitigate the loss of resources in natural habitat. Williams and Kremen (2007) monitored offspring production in experimental cavity nests of *Osmia lignaria*, the blue orchard bee, and found that resources available on organic farms partially substituted for preferred resources from wild plants, reducing the dependence of *O. lignaria* productivity on the proximity of natural habitat on organic farms. In contrast, on conventional farms that did not have such onsite resources, *Osmia* productivity rates declined significantly with increasing distance to natural habitat, and offspring survival was below replacement in the most isolated sites.

Bee species will differ in their capacity to nest on farms. Some bee species require rodent nests or cavities in wood in which to nest, and these may not be available on farm sites. Bees that excavate nests in the ground may suffer mortality from flood irrigation and plowing if they nest in agricultural fields (Shuler et al., 2005). In California, less than half of the ground-nesting bee species found visiting sunflower were also found nesting on or in sunflower fields (Kim et al., 2006). If nests are located offsite, it provides a constraint to the distance they will be able to forage; thus only farms within foraging range will receive pollination services. Foraging ranges differ widely among species and are strongly related to body size; in the California system foraging ranges are below 2 kilometers (Greenleaf et al., 2007).

It therefore seems clear that managing at the landscape scale, as well as at the site level, will be important for restoring, preserving, or maintaining pollinator communities and services. How much land is enough to provide sustainable pollinator communities and services? Only a few studies have addressed this issue, and far more work remains to be done. Kremen et al. (2004) observed a log-linear relationship between the amount of pollination services provided to watermelon and the proportional area of natural habitat within several kilometers of the farm site. Full pollination services could be provided by wild bee communities at approximately 30% natural habitat cover or above. We know even less about how patches of habitat should be optimally configured to deliver pollination services to crops in the surrounding agricultural matrix. Indeed, because many pollinator populations are not limited to natural or seminatural habitat patches but, rather, utilize different elements in both natural and agricultural areas, a better question may be, How complex should the landscape be to ensure population persistence of pollinators (Tscharntke et al. 2005)? In addition, we know little about the factors that limit bee populations. Is it floral resources, nesting sites, or both? What role do predators, parasitoids, parasites, and disease play in limiting bee populations, and how do these factors respond to landscape structure?

Although our knowledge is incomplete, a great deal could currently be done to improve the situation for wild pollinators in agricultural landscapes, acting both at the site (field) and landscape scale. Site-level management actions could include introducing multi-cropping, allowing cover crops to flower or permitting weedy borders, restoring native plant hedgerows that consist of phenological suites of plants that support pollinators,

creating small patches of bare ground for nesting, installing bumble bee boxes and trap nests, and leaving small patches of woods for cavity-nesting bees (Vaughan et al., 2004). In areas of Eastern Europe, alfalfa growers successfully managed for a wild pollinator, the alfalfa gray-haired bee (*Rhopitoides canus*), by carefully timing and spacing cutting of alfalfa bloom so as to provide alfalfa bloom throughout the life cycle and bare soil for nesting during the peak nesting period (Bosch, 2005). In the United Kingdom, growers plant flower-rich field margins to enhance pollinator abundance on farms (Dover, 1997; Carvell et al., 2004). The specific composition of plantings may be important in determining pollinator abundance and diversity (Gurr et al., 2004; Pywell et al., 2005), but it is not known whether such field strips enhance population size and persistence of pollinators or simply redistribute them within the landscape.

Such small-scale restorations or changes in field management practices could promote floral and nesting resources for bees at little or no cost to farmers. To the extent that these practices enhance populations rather than redistribute individuals, small-scale changes that initially incur small annual costs could have cumulative effects that ultimately pay for themselves, allowing farmers to reduce rental payments for honey bees or to weather periods of scarcity of commercially managed pollinators (Kremen et al., 2002b). Such management practices could ultimately transform farm sites from sinks to sources of native bees by increasing reproductive rates above replacement (*sensu* Pulliam, 1988). In California, organic farms acted like source habitats for experimental *O. lignaria* populations compared with conventional farms, which acted like sinks, with reproductive rates above replacement on organic farms but below replacement on conventional ones (Williams & Kremen, 2007). Landscape-level management actions could include coordinating small-scale efforts among growers to build larger “patches” of bee-friendly farms and enhance connectivity between them through restoration of riparian or other corridors and through conservation of existing seminatural and natural habitats. Such actions are evidently much more difficult and expensive to implement and will generally be more likely to happen if they simultaneously promote multiple ecosystem service benefits (Balvanera et al., 2001). It may rarely be the case that the economic benefits from enhanced pollination services alone are sufficient to bear the costs of managing sites and landscapes for wild pollinators (Olschewski et al., 2006).

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