Ann. N.Y. Acad. Sci. ISSN 0077-8923

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Issue: *The Year in Ecology and Conservation Biology*

The conservation and restoration of wild bees

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Bees pollinate most of the world's wild plant species and provide economically valuable pollination services to crops; yet knowledge of bee conservation biology lags far behind other taxa such as vertebrates and plants. There are few long-term data on bee populations, which makes their conservation status difficult to assess. The best-studied groups are the genus *Bombus* (the bumble bees), and bees in the EU generally; both of these are clearly declining. However, it is not known to what extent these groups represent the approximately 20,000 species of bees globally. As is the case for insects in general, bees are underrepresented in conservation planning and protection efforts. For example, only two bee species are on the global IUCN Red List, and no bee is listed under the U.S. Endangered Species Act, even though many bee species are known to be in steep decline or possibly extinct. At present, bee restoration occurs mainly in agricultural contexts, funded by government programs such as agri-environment schemes (EU) and the Farm Bill (USA). This is a promising approach given that many bee species can use human-disturbed habitats, and bees provide valuable pollination services to crops. However, agricultural restorations only benefit species that persist in agricultural landscapes, and they are more expensive than preserving natural habitat elsewhere. Furthermore, such restorations benefit bees in only about half of studied cases. More research is greatly needed in many areas of bee conservation, including basic population biology, bee restoration in nonagricultural contexts, and the identification of disturbance-sensitive bee species.

Keywords: agri-environment scheme; ecosystem service; Farm Bill; global change; land use change; pollination; pollinator; pollinator conservation; pollinator restoration; restoration ecology

Introduction

The importance of bees

As the world's primary pollinators, bees are a critically important functional group. Roughly 90% of world's plant species are pollinated by animals,[1,2] and the main animal pollinators in most ecosystems are bees.[3] Although other taxa including butterflies, flies, beetles, wasps, bats, birds, lizards, and mammals can be important pollinators in certain habitats and for particular plants (*e.g.*, Refs. 4 and 5), none achieves the numerical dominance as flower visitors worldwide as bees.[3] The likely reason for this is that unlike other taxa, bees are obligate florivores throughout their life cycle, with both adults and larvae dependent on floral products, primarily pollen and nectar.[6]

In addition to their crucial role for wild plants, bees are the main pollinators of agricultural crops, 75% of which benefit from animal pollination.[7,8] Honey bees, primarily *Apis mellifera* and to a lesser extent *Apis cerana*, are widely managed in hives for crop pollination and are presumably the most important agricultural pollinators worldwide (as domesticated species, these are not covered in this review, except for regions where they are native or feral). Declines in the number of managed honey bee hives in the United States over the past 50 years,[9] in conjunction with recent losses due to Colony Collapse Disorder,[10] have raised concern about the extent to which global agriculture relies on a single-managed bee species. Although at a global scale neither managed honey bees nor the yield of the crops they pollinate has declined over the past few decades, dependence on bee-pollinated crops is increasing faster than the supply of honey bees, which suggests that problems may occur in the future.[11–13]

The role of native, wild bees as crop pollinators may be substantial, but is more debated than is

doi: 10.1111/j.1749-6632.2010.05449.x

their importance in natural ecosystems. Non-*Apis* species are equally effective or better pollinators than are honey bees for many crops.[14–20] The challenge in using these species for crop pollination is not quality but rather quantity, and management techniques exist only for a small number of non-*Apis* taxa.[16–18,21–23] Wild, unmanaged native bees also provide crop pollination as an ecosystem service. Unmanaged bees alone can fully pollinate crops in some agricultural contexts[19,20,24,25] and are frequent flower visitors in others,[26] thereby contributing to meeting the crop's pollination needs. In addition, when present with honey bees, native bees can enhance honey bee effectiveness.[27,28] The role of native bees as crop pollinators helps to generate support for bees' conservation.

Bee diversity and biogeography

Bees as a monophyletic group constitute the Apiformes.[6] Roughly 18,000 bee species have been described, with the true total number of species likely near 20,000.[6] In contrast to most other taxa, bee biodiversity peaks not in the tropics but in arid temperate areas.[6,29–31] Global hotspots in recorded bee diversity include the southwestern USA and the Mediterranean. In contrast, warm temperate areas such as eastern North America, Europe, and southern South America are intermediate in diversity, and the moist tropics are relatively depauperate[31] —although recent collecting work in the neotropics suggests that bee diversity may be higher there than previously assumed,[6] and at present only a third of neotropical bee species have been described.[32] None of these biogeographic conclusions is based on sampling that is standardized for either effort or area sampled; all are therefore subject to sampling biases. However, the general patterns have held up for almost three decades, which suggests they have some validity. If tropical bee diversity is indeed low, then bees may provide an exception to the general rule that the best conservation values, in terms of protecting the most biodiversity for the least cost, are to be found in the tropics.[33]

Several hypotheses have been proposed to explain the low diversity of tropical bees. First, ground-nesting bees constitute the majority of species in many communities, and they may be largely excluded from the wet tropics because their nests would flood and/or their larval food supplies would be subject to fungal attack.[6,34,35] Second, tropical bee communities tend to be strongly dominated by a small number of eusocial species, primarily from the groups Apidae and Meliponini.[36] These super-abundant, perennially active and floral generalist bees may use a large fraction of the available floral resources, thereby excluding other species.[6,35] This hypothesis raises the question of why social bees dominate tropical bee communities, and whether their dominance is a cause or an effect of the low species richness there.

Sociality may help explain the exceptionally high bee diversity observed in deserts as well. One hypothesis is that social species, which have long flight periods and require continuous bloom, are excluded from deserts, where bloom in temporally patchy. This makes floral resources available for a greater variety of less abundant, solitary species.[37] A second hypothesis centers on the role of oligolectic (dietary specialist) species, which constitute a high proportion of the desert fauna.[30,38] Oligolectic species may be able to time their emergence to the temporally erratic bloom of their host plant species better than polylectic species, thus creating selection for dietary specialization on the part of desert bees, and subsequently high diversity.[39,40] Third, variable rainfall at relatively small geographic scales, as found in deserts, provides a possible mechanism for speciation: if conspecific populations in neighboring localities emerge at different times, the populations would not interbreed and may diverge genetically.[40] All of these hypotheses about the causes of bee biodiversity patterns remain to be rigorously tested.

Several phylogenetically important bee lineages comprise small numbers of species and are geographically restricted, making them prime candidates for conservation efforts. The family Stenotritidae includes just 21 species and is primarily restricted to western Australia. The megachilid tribe Fideliini represents an ancient lineage of host-plant specialist bees that are restricted to arid regions of Chile (2 species), Morocco (1 extremely rare species), and southern Africa (11 species). Finally, the melittid tribe Macropidini represents a highly specialized lineage of mostly oil-collecting, host-plant specialist bees. *Afrodasypoda plumipes*, for example, is known from just a handful of specimens collected in the Richtersveld National Park in northern South Africa. Such lineages highlight the need to consider conservation efforts directed at geographically restricted and phylogenetically important bee lineages (entire paragraph, Bryan Danforth, pers. com.).

The extent and causes of bee decline

Conservation status of bees

The question of whether we are in the midst of a global pollinator decline has received much attention in the media as well as the academic literature,[9,41–47] but is difficult to answer empirically due to a lack of pollinator monitoring programs and long-term data series. The need for establishing pollinator monitoring programs was recognized internationally in 1993 when pollinators were incorporated into the Convention on Biological Diversity, which has been signed by 168 countries (http://www.cbd.int/agro/pollinator.shtml). Pollinator monitoring is an important goal of the EU's ALARM program (http://www.alarmproject.net/alarm/objectives.php), which is now collecting monitoring data in several countries.[48] Other regional pollinator protection initiatives are in place,[45] but have not yet collected large-scale data.

The best data for entire bee communities come from the EU and provide strong evidence of declines. Citizen science data from the United Kingdom and the Netherlands show significant declines in bee species richness when comparing data from before and after 1980.[49] In Belgium, 25% of bee species have declined during the second half of the 20th century whereas only 11% have increased.[50] Across European countries, 37–65% of bee species are on lists of conservation concern,[51–53] although none is yet Red Listed with IUCN, due to lack of the required documentation about conservation status. However, northwest Europe, where bee communities have been best studied, is one of the most intensively human-used regions of the world and has been for many centuries.[49,54,55] Relative to the rest of the world, results from this region could therefore overestimate declines, because bees are responding to more intensive human land use than elsewhere; or underestimate them, if the remaining fauna on which studies are based are already the subset of species that persist well in agricultural environments.

The bumble bees (the genus *Bombus*) are the best-studied bee taxon and the only taxon that has been globally assessed for its endangerment status. Eleven percent of *Bombus* species should probably be listed as "near threatened" or above by IUCN.[56] However, only one species is currently listed, because the others lack the documentation required by IUCN. Most studies of Bombus have taken place in Europe, where many species are declining.[57,58] Half of the *Bombus* species historically known from Britain are either extinct, or in danger of extinction.[57] Of the 60 *Bombus* species known from west and central Europe, 30% are now threatened throughout their range according to IUCN criteria, and 7% went extinct in this region between 1951 and 2000.[59] The main cause of *Bombus* decline in the UK and western Europe is widely agreed to be the agricultural intensification that took place in the 20th century.[57] Several components of agricultural intensification are likely important including the decline of preferred bumble bee forage plants in the landscape,[60,61] the loss of relatively unmanaged grasslands and other uncropped habitats such as hedgerows, and the development of synthetic fertilizers that replaced bee-friendly leguminous cover crops such as clover as a means for restoring nitrogen to agricultural soils.[57,58] Although many *Bombus* species have declined, others are doing well despite these changes in land use. Life history factors associated with species decline vary somewhat across studies but include floral specialization, later emergence times, range extent, and climatic niche.[57,61–67]

Bombus species are less well studied in North America but some species are clearly declining there, for somewhat different reasons than in Europe. Three formerly common North American species in the subgenus *Bombus sensu strictu*, *B. affinis*, *B. terricola*, and *B. occidentialis*, have all declined dramatically, while a fourth which was always rare, *B. franklini*, is now close to extinction.[68,69] For example, *B. affinis*, which was once common across much of eastern North America, disappeared from 42 of 43 sites between the early 1970s and mid 2000s.[68] The working hypothesis proposed to explain these declines is parasite infection from commercially reared congeners. In particular, the fungal pathogen *Nosema bombi* may have spread to wild North American bees from commercial *B. occidentalis* and *B. impatiens* raised for greenhouse pollination in Europe, and then imported into the United States.[70] In support of this hypothesis, commercial *Bombus* are known to have higher pathogen burdens than wild bees, and to forage outside the greenhouses.[71]

Furthermore parasite loads on individual *Bombus* (whether wild or commercial) increase with proximity to greenhouses, and a spatially explicit model of pathogen spillover from commercial to wild individuals predicts observed parasite loads well.[71,72]

In North America other causes of *Bombus* decline, and other *Bombus* species, are less well studied. In contrast to the case in Europe, neither floral specialization nor habitat and range size effects explain North American declines across 14 *Bombus* species.[68] Consistent with the British case, however, *Bombus* declines in Illinois cooccurred with large-scale agricultural intensification.[69] As in Britain, roughly half of the *Bombus* species in Illinois are now either extirpated or in broad-scale decline.[69]

Given that *Bombus* is the best studied bee genus, what do *Bombus* declines tell us about the status of the other 442 bee genera?[6] *Bombus* might be particularly vulnerable because they are social (see below), whereas most bee species are solitary. *Bombus* are also larger than most other bee species, although this might bias their extinction risk in either direction (see below). In Belgium, *Bombus* have declined more than have most other genera.[50] However, the published literature as a whole shows no significant difference between *Bombus* and all other non-*Apis*, non-*Bombus* species in terms of their sensitivity to human disturbance.[73] If *Bombus* are not notably different from other genera, then their decline does not bode well for the other 99% of the world's bee species whose conservation status is even more poorly known.

Long-term data for non-*Bombus* bee communities outside of northwest Europe are sparse. Roughly half of the 60 *Hylaues* species endemic to Hawaii are either extinct or in danger of extinction.[74] However, islands in general and Hawaii in particular are well-known hotspots of extinction,[75] so these results cannot be generalized to continental faunas. A 21-year time series exists for Euglossines (orchid bees) in a tropical forest, during which populations showed high variability but few consistent trends in abundance, but data were collected in a relatively undisturbed area and therefore do not reflect the effects of anthropogenic changes.[76]

Threats to the conservation of bees

Habitat loss, invasive species, and (potentially) climate change are considered the main causes of species loss for taxa other than bees.[77–80] Most workers consider these to be the most important causes for bees as well[81]

Habitat loss and fragmentation

Habitat loss is currently the leading cause of species endangerment[77,78] and is predicted to be in the future.[79] A recent meta-analysis shows that habitat loss and fragmentation negatively affects the abundance and species richness of wild bees.[73] However, this effect is only significant in studies for which analyses included at least one site that was extremely isolated, variously defined (depending on the criteria used in the study) as a habitat fragment of less than 1 ha, a site more than 1 km from the nearest natural habitat, or a site with less than 5% natural habitat remaining in the surrounding landscape. Studies that did not include such extreme sites showed a negative trend, but it was not significant.[73] Most (61%) of the studies contributing to the meta-analysis included an extreme site. This raises the possibility that there is a research bias in the existing literature, in that habitat loss has been studied where it is more extreme than would be found in a random sample of global ecosystems. To assess whether research bias exists, we would need to compare the land cover surrounding the sites included in the meta-analysis, to land cover surrounding a random sample of sites globally. This has not been done.

The high variability in bees' response to land use change[73] may result, in part, from the fact that some bee species appear to do well in human-disturbed habitats. In fact, some studies of bees and habitat loss define "bee habitat" to include anthropogenic habitats such as suburban gardens and agricultural grasslands, and to exclude the native vegetation type (e.g.,[82,83]). Some types of temperate forests, in particular, appear to support relatively few bees,[6,82,84–87] although the needs of forest-obligate bee species have not been sufficiently researched. Agricultural lands, when not too intensively managed, can provide good habitat for many bee species,[19,88–91] as can urban/suburban areas.[85,92–94]

Bees' use of human-disturbed habitats, in combination with the ecosystem services they provide, may make them especially well suited to conservation planning that combines ecological and economic criteria, and includes both preserved and human-used habitats. These planning methods can be more effective biologically and also less expensive than traditional conservation using nature reserves.[95] Furthermore, in contrast to better-studied vertebrate taxa, small habitat patches may be sufficient to support insects, including bees, in otherwise disturbed landscapes.[96–98]

Climate change

Climate change could cause widespread extinctions of bees, as it could for other organisms, if bees are unable to migrate fast enough to keep up with the regions within their thermal tolerances.[80] As yet there are almost no published data on this question for bees.[99,100] An as yet unpublished, comprehensive analysis of 527 European bee species suggests depending on the climate change scenario, Europe could lose 14–27% of its bee species by 2050 due to climate change.[101] Climate change could negatively affect oligolectic bees in particular if the phenology of bees and their host plants do not change in concert. This appears to be the case, as bees advance their emergence times faster than plants as temperature increases.[101] The effects of climate change may be exacerbated by habitat loss. For example, Warren *et al*.[102] found that among British butterflies, habitat specialists and less mobile species were less able to track climate changes. Bees with similar characteristics will likely be at greater risk due to climate change.

Nonnative species

Species invasions, along with habitat loss and climate change, rank among the top causes of species endangerment globally.[77,79,103] Bees could be negatively affected by nonnative plants, and/or by nonnative bees including the pathogens and parasites they carry. As yet, it is not possible to generalize about how nonnative plants affect bees. Many studies of nonnative plant–pollinator interactions have focused on single plant species known *a priori* to be particularly attractive to pollinators,[104] which may introduce a research bias. Studies that have examined entire plant–pollinator webs should not suffer from a research bias, and have found that the nonnative plants have either fewer,[105] similar,[106] or more[107] insect species visiting them, as compared to native plants. The net effect of nonnative plants on bee populations will depend not only on the bee species that the nonnatives currently support, but also on what native plants the nonnatives displaced. I am not aware of any studies that accounted for this aspect with experimental or historical data. Last, nonnative plants may benefit generalist bees more than they benefit specialists,[108] thereby adding to the list of risk factors for specialists.

The role of nonnative bees in native bee declines has generated much interest, especially given the human-subsidized spread of the honey bee to all continents except Antarctica. Competition, however, is notoriously difficult to demonstrate in an ecological context. Most studies of competition between native and nonnative bees have been observational and based on forager densities at flowers, and have found generally negative effects,[109] but forager densities may be unrelated to native bee reproduction.[109,110] The sole fully experimental study to monitor native bee reproduction in the presence and absence of honey bees found a significant negative effect of honey bee density.[111] However, the study took place in a system with strong bottlenecks in floral resource availability, which may have increased the chances of finding competition.[111] On European grasslands, wild bee reproduction is not negatively correlated with the observed density of honey bee foragers.[112] There are few studies of native bee competition with nonnative taxa other than honey bees, but the limited evidence suggests that competition can occur, for example, between native and exotic *Bombus* species.[109,113] The spread of pathogens from nonnative or commercially reared bees, to native wild bees, is emerging as a significant cause of native *Bombus* decline in North America (see above).

Pesticides

Apis mellifera is widely used as a model organism in studies of pesticide toxicity and is highly sensitive to many insecticides.[114,115] Honey bees, and likely other bees as well, have relatively few detoxication genes, which increases their susceptibility to pesticides.[116] Relative to honey bees, wild bees might experience less pesticide exposure since they do not forage as exclusively on agricultural crops. On the other hand, native bees nesting near crops might experience more exposure since they forage at times of day and times of year when honey bees are not present. While growers often reduce or avoid spraying pesticides during periods of honey bee activity there is less consideration for wild, native bees.[117] Pesticide labeling, if it mentions bees at all, generally states that bees should be closed into their hive before spraying, which is obviously not relevant to native species.

Few studies have compared pesticide toxicity in non-*Apis* species to *Apis*, and the results have been variable.[118] Laboratory colonies of *Bombus impatiens* fed spinosad-contaminated pollen at concentrations they are likely to encounter in the wild experienced few lethal effects, but showed impaired foraging behavior.[119] There are only a few field- or landscape-scale studies of pesticide effects on native bee abundance, and in meta-analysis they do not show a significant negative effect (Ref. 73; but see also Ref. 120, which shows significant negative effects of phosmet on the reproduction of a nonnative, non-*Apis* bee). Clearly more studies of this topic are needed.

Genetically modified crops

The effects of genetically modified (GM) crops on bees were reviewed by Morandin.[121] Crops modified for increased herbicide resistance account for 72% of global GM acreage, and this trait is unlikely to negatively affect bees directly, although it could affect them indirectly if higher herbicide use in GM fields results in fewer floral resources for bees.[121] In contrast crops modified for insect resistance could harm bees if the relevant proteins are both toxic to bees and expressed in pollen. To date, 99% of the commercialized insect-resistant GM crops have contained genes for the insecticidal *Bacillus thurigiensis*, which is not toxic to bees.[121] Other types of genetic sequences conferring insect resistance are being developed, however, and should be tested on both honey bees (which is generally done) and non-*Apis* bees (which is rarely done) prior to commercial release.[121].

Features of bees that affect their extinction risk

Genetic effects

The genetic effective population size (N_e), which determines a population's rate of loss of genetic diversity over time, is on average an order of magnitude smaller than the census population size (N).[122] Bees probably have an even smaller N_e/N ratio than most taxa because they are haplodiploid,[123] and because their population sizes are highly variable over time.[124,125] At present there are too few studies of N_e in bees to rigorously assess their N_e/N ratio. However, published values of N_e even for nonthreatened bees in mainland habitats are low, relative to the N_e of 50–500 thought to be necessary to avoid inbreeding effects and loss of evolutionary potential, respectively:[122] 40–102,[126] and 20.[127] This suggests that from a genetic perspective, bee populations are even smaller than they appear.

In principle, haplodiploids might be able to purge deleterious recessives through exposure in haploid males, and thereby avoid the negative fitness consequences that generally accompany reduced genetic diversity.[128,129] While haplodiploids suffer less from inbreeding depression than diploids, inbreeding depression is still substantial for them.[130] The few studies of inbreeding effects in bees show mixed results.[131]

Another reason why bees as a group may be vulnerable to genetic decline is their complementary sex determination system. Individual bees that carry two different alleles at the sex-determining locus develop as females whereas individuals with only one allele, or two copies of the same allele, develop as males. All unfertilized haploid eggs develop into males. However if heterozygosity is low and a fertilized egg is homozygous at the sex-determining locus, it will develop as a diploid male. Diploid males are generally inviable or at least infertile. They therefore reduce population growth, making already genetically impoverished populations even more vulnerable to the vortex of extinction associated with negative genetic, demographic, and stochastic effects. Monte Carlo simulations suggest that bee populations with diploid male production are an order of magnitude more vulnerable to extinction than are diploid populations, or even haplodiploid populations without diploid male production.[132] Some studies have found high diploid male production in wild bee populations,[127,133] but others have not, even in highly inbred populations.[134]

Bee species that are oligolectic or rare appear to be more vulnerable to genetic effects. Oligolectic bees have more genetically isolated populations and lower genetic diversity,[135–137] likely because their distributions are limited by the distributions of their host plants. Rare bee species also have more genetic differentiation and/or smaller N_e as compared to common species.[58,131,138] For example, populations of the rare *Bombus sylvarum* persisting in fragmented British habitats has N_e values of only 21–72, suggesting that they fall near or below the limit of genetic viability (insofar as a N_e of 50 is thought to be necessary to avoid inbreeding effects;[122]). Similarly, the rare *B. muscuorum* shows significant genetic differentiation between populations only 3 km apart, and in all populations at least 10 km apart, whereas studies of widespread, common *Bombus* species do not detect genetic differentiation even in populations separated by hundreds of kilometers.[138]

Social bee species may be particularly vulnerable to genetic effects because for them N_e is more closely related to the number of nests than to the number of individuals.[139] This means that census estimates, which are largely based on worker densities, are likely to greatly overestimate N_e and may not even be correlated with it.[140] Several recent synthetic analyses have found that in bees, sociality is associated with sensitivity to human disturbance. In a meta-analysis of 54 published studies, the abundance and species richness of social bee species is significantly, negatively affected by human disturbance, whereas effects on solitary species are non-significant.[73] In a species-level analysis of 19 data sets, social species are more sensitive to disturbance and in particular to pesticide use.[141] Across 23 studies of crop flower visitation by wild bees, visitation rate declines more steeply with increasing distance from noncrop habitat for social as compared with solitary species.[26] The cause of social bees' increased sensitivity is not known, although multiple mechanisms can be postulated.[26,73,141] Low N_e and genetic effects should be added to the list of possibilities.

Reliance on mutualist partners

Because bees are dependent on plants and vice versa, it would seem logical that both are more vulnerable to extinction, since the loss of one taxon leads to the loss of the other.[142–144] There is some evidence for this. In intensively human-used regions, declines in bees and the plants they pollinate are positively correlated.[49,61] Among animal-pollinated plants, species that require outcrossing are more sensitive to habitat fragmentation, suggesting a role for mutualist loss in local extinctions.[145] Models and data for specialist herbivores and pollinators, and for obligate body parasites for whom the host is also the habitat, suggest that widespread extinction of these groups could occur should hosts become extinct.[146,147]

On the other hand, in terms of comparing the vulnerability of bees to other organisms, it is not clear what the appropriate null is, given that most organisms are dependent upon others in complex ways. Most bee species are floral generalists,[38,148] making bees as a group less reliant on single mutualist partners than are specialist herbivores or obligate body parasites. Furthermore, plant–pollinator networks have two features that might make them relatively robust to species loss. First, the distribution of the number of partners per species is highly skewed, such that a minority of "core" species have many partners and interact largely among themselves, while most species have few partners.[149] This makes the network more robust to species loss in general, although it is sensitive to the loss of the highly interacting core species.[149] Furthermore, core species may be the most abundant species,[150,151] in which case they are less likely to go extinct. Second, plant–pollinator networks are generally asymmetrical with regard to specialization, meaning that specialist pollinators interact with generalist plants, and specialist plants with generalist pollinators.[152,153] Therefore, the loss of a specialist from the system is unlikely to result in the loss of its mutualist partner.

Last, many published studies may overestimate the dependence of particular pollinators on particular plants due to undersampling. First, in many sampling designs, rarity is confounded with specialization in that pollinators for which few specimens were collected will of necessity be collected from a small number of plant species. This bias can be corrected with rarefaction or by using an appropriate null model in analyses,[150,151] but until recently most investigators did not make this correction. Second, most published studies are based on only 1–2 years of data, but examination of long-term data shows that pollinators visit different plants over time.[154] For both of these reasons, many bee species may be less dependent on particular plants, and therefore more robust to plant species extinction, than has been assumed.

Use of partial habitats

Bees require multiple resources to complete their life cycle, including pollen,[155] nectar, and nest substrates and nest-building materials.[156] These resources are often gathered from different locations, making bees reliant on multiple, "partial habitats."[157] This might make bees vulnerable to disturbance insofar as they would be negatively affected by the loss of any of these habitats. On the other hand, if resources are provided by the disturbed habitats themselves and bees are facultative in their use of such habitats, bees might be less vulnerable to disturbance than are other, more habitat specialist, taxa. For example, bees use floral resources from both agricultural and natural habitats in mosaic landscapes,[158,159] and models that incorporate this complementarity between habitat types have high explanatory value in predicting bee abundance and species richness.[160]

Floral specialization

Dietary specialization is associated with a higher extinction rate and/or with sensitivity to disturbance for a variety of nonbee taxa.[161–166] Oligolectic bee species gather pollen from a small number of related flower species, whereas polylectic bees are pollen generalists (even oligolects are dietary generalists for nectar;[167]). Oligolectic species probably account for a large fraction of global bee diversity, since they constitute about 30% of species in temperate communities and up to 60% of species in the more species-rich deserts.[148] Oligolecty is a significant predictor of bee species' decline over time in northwestern Europe,[49] and of sensitivity to fragmentation in a desert ecosystem.[94] Even among European *Bombus*, all of which are polylectic, species with more specialized diets show greater population declines over time.[61] Presumably the risk of decline is heightened by being more reliant on a smaller number of food sources. In addition, oligolectic bees have more genetically isolated populations and lower genetic diversity (see above), which further increases their susceptibility to decline.

Other life history traits

Species that nest above ground, and species that use previously established nest cavities, are more sensitive to disturbance than are species that nest in the ground or excavate their own nests.[141] These species may be more sensitive because they are more likely to be nest-site limited. In contrast to other taxa, body mass does not predict sensitivity to disturbance across bee species.[141] Perhaps the lack of relationship is not surprising given contrasting predictions about body size and extinction risk for bees. For vertebrates, large body size is associated with greater extinction risk.[168,169] However for butterflies, the most mobile species have lower extinction risk.[170] In bees, body mass is positively correlated with mobility.[171]

Strategies for bee conservation

Formal protection of threatened species

Insect conservation generally lags far behind insects' functional and numerical importance, and bees largely share the fate of other insects in this regard. Insects account for an estimated 73% of the animal species on earth,[172] yet only 5–20% of insect species have even been named, much less had their natural history described.[173] Only 70 insect species have been recorded as going extinct to date, but several lines of evidence suggest that this number reflects our inadequate knowledge more than it reflects reality.[174] First, extinctions can only be recorded for described species, and these are likely to be the more common and widespread species, which have lower probabilities of extinction as compared to undescribed species.[175] Second, most recent recorded insect extinctions are from Lepidoptera, the best-studied insect order,[174] which constitutes only 15% of described insect species.[172] Third, 78% of the recorded insect extinctions are from the United States,[174] which is high in taxonomic expertise but low in biodiversity, relative to other nations. Even within the conservation research community, there is a bias against insects: despite accounting for 63% of all described species, insects account for only 7% of the published papers in leading conservation journals.[176]

Insects are underrepresented in species protection programs as well. Countries that have carefully inventoried their insects find that at least 10% are vulnerable or endangered,[177] which would correspond to at least 95,000 insect species being vulnerable or endangered globally (based on the 950,000 scientifically described insect species globally;[178] the true number of threatened species might be an order of magnitude greater). Yet only 771 insect species have been evaluated for candidacy on the global IUCN Red List—73% of which were subsequently determined to be threatened.[179] Even for invertebrates that achieve listing under the US Endangered Species Act, the allotted funding per species is more than an order of magnitude less than that received by mammals and birds.[180]

Recent evidence from the few insect taxa that have been monitored suggests that insects may be declining even more rapidly than better-studied taxa such as plants and birds.[181] Over the past 2–4 decades, 71% of British butterfly species declined, compared to 54% of birds and 28% of plants.[181] Over the past 35 years, 54% of British moth species have declined significantly.[182] Based on their rates of decline, 21% of the moths in this study would be considered threatened nationally according to IUCN criteria, yet none is currently listed by the British Red Data Book.[182]

Bees share the fate of insects generally in being poorly known and poorly protected, although the estimated proportion of bee species that are scientifically described is thought to be higher than for most insect taxa (17,500 out of >20,000, or up to 88%;[6]). Currently, no bee species is listed as threatened or endangered under the US Endangered Species Act, even though many species are known to be very rare and/or steeply declining, or likely extinct.[68,70,74] Similarly, two bee species are listed on the global IUCN Red List.[183]

Economic reasons for conserving bees

Because bees provide valuable ecosystem services the question arises to what extent economic arguments alone can motivate bee conservation. The use of economic, ecosystem-service-based arguments to justify conservation is controversial. Some believe that such arguments undermine the moral legitimacy of the conservation movement, which has historically been based on ethical arguments kept distinct from questions of economic gain.[184] From a practical standpoint, if conservationists adopt economic arguments they could then find that in many cases, the most profitable course of action is to convert natural areas to human use. In addition, the cost-benefit analysis of a given situation is likely to fluctuate over time, with changing commodity prices, property values, and alternative methods of providing the ecosystem service in question,[184] whereas biodiversity conservation is a long-term commitment. On the other hand, even though global estimates of the value of ecosystem services have been criticized for their economic methodology,[185,186] by any accounting natural areas and the species they harbor provide extensive and often underappreciated services to humanity. It seems wise to include these services when considering the relative merits of conservation versus alternative land uses. Crop pollination services from native pollinators have featured prominently in this debate.[184,187]

From an ecological point of view, two issues have emerged as important challenges to valuing crop pollination. (The economic aspects of valuing pollination services are outside the scope of this review but are covered elsewhere.[188]) First, in order to estimate the economic benefit of a given level of pollination, one must know how pollen deposition translates into fruit production. This requires knowing not only pollen deposition per flower in the field, and the dose-response curve for pollen deposition versus fruit set per flower, but also the dose-response curve for the number of flowers fully pollinated versus fruit set per plant or per unit area.[19,189] Asymptotic fruit set at the plant or field scale may be reached at lower levels of pollination than would be estimated at the flower scale because many plants produce more flowers than they can set into fruit, even when resources are not limiting.[189] Another reason why changes in pollen deposition may not translate into changes in crop production is that production can be limited by other factors, such as fertilization, pest or weed control, and available water. Pollination will only have direct economic value when it is the factor limiting production. Pollination limitation can be measured experimentally in the field.[190,191] Or if the pollination requirement of the plant is known, pollination services can be valued relative to this threshold, on the assumption that pollination will be limiting at some point(s) across space or time. In nature, 62–73% of plant populations show pollination limitation,[190] and crops are even more likely to be pollination-limited because other potentially limiting factors such as sunlight, soil fertility, pest and weed control, and water are provided in abundance in most commercial agricultural settings (although this point is debated;[192,193]). Pollination can also not be limiting because it is already being provided by honey bees. Many studies value native bee pollination independently of the pollination provided by managed pollinators, but methods for valuing the two simultaneously exist.[188]

A second critical issue for pollination service valuation is calculating not only the economic benefit of conservation, but also its opportunity cost—which in agricultural contexts generally means the profits foregone by not converting native bee habitat to crop production. One of the first empirical studies of crop pollination service value found that wild bees from forest fragments contributed $62,000 per year, or 7% of the farms' annual income, to one Costa Rican coffee plantation.[194] Since the study was conducted, however, the price of coffee fell and the plantation was converted to pineapple, which does not require insect pollination, indicating the critical role of commodity price fluctuations and opportunity costs involving alternative land uses.[184] When tropical forest in Indonesia is valued for the pollination services its resident bees provide to coffee plantations, the result (€46 per ha) is lower than that found in the Ricketts *et al.* study by a factor of six.[195] The authors attribute this difference to forest fragmentation, in that Indonesian plantations are surrounded by large blocks of forest, which reduces the per ha value, whereas two forest fragments provided all the pollination services in Costa Rica.[195]

The economic optimum for pollinator habitat conservation could be found by modeling the trade-offs between ecosystem service provision to existing crop fields, and the opportunity costs of foregoing alternative land uses, that is, converting natural habitat to crops. Two published models exist for such situations. In Canada, canola seed set increases with increasing wild bee abundance, which is in turn a function of the amount of seminatural habitat surrounding crop fields. The model predicts that the economic optimum is reached when 32% of the land area is left uncultivated;[196] when changes in land use were implemented experimentally, the landowner found that the optimum was closer to 15%.[121] In the most thorough evaluation to date of the economic trade-offs between crop pollination services and land use, Olschewski *et al.*[197] calculated the marginal loss curve for pollination services as a function of forest loss for coffee plantations in Ecuador and Indonesia. The authors included other potential crops in addition to coffee as alternative land uses, as well as subtracting the variable costs of crop production from scenarios where production was reduced. In all modeled scenarios, the economic optimum involved deforestation, that is, the value of pollination services was not sufficient to preserve existing forests on economic grounds alone. The value of forest conversion only equaled the value of preservation when forests were almost gone.[197]

In sum, based on the limited research to date we can't conclude that the economic value of pollination services alone will provide sufficient incentive for farmers to preserve native bee habitat in the long term. This is even more likely to be the case when a substitute for native bee crop pollination services, namely pollination by managed honey bees, is added to the equation. There will always be an element of risk involved in relying on a single managed species to pollinate all agricultural crops, and having native bees available provides a valuable backup against this risk. But farmers may not consider this insurance value to be a sufficient reason to alter their land use practices, when honey bee rental costs can be more economical route to meeting current pollination needs.

This does not obviate the need to evaluate the pollination services provided by wild bees, and to include their value in policy decisions. In order to optimize land use decisions, it is essential to sum all of the types of ecosystem services provided by the same land area,[198] and the economic value of wild bee pollination remains an important component of this summation. Even when data on other ecosystem services are lacking, the value of crop pollination can contribute significantly to decisions when the multiple benefits of conserving pollinators (not just the economic benefits) are weighed against alternative land uses.

Restoring bee communities

The context of bee restoration so far has been predominantly agricultural, likely because significant governmental funding exists for pollinator restoration on agricultural lands. Although the limited research on pollinator restoration in natural areas is regrettable from an ecological point of view, the agricultural emphasis is potentially a powerful approach given that agriculture currently accounts for 33% of global terrestrial land area,[199] and another billion ha will likely be converted to agriculture by 2050 as crop production expands to feed a growing human population.[200] In addition, the pollination services that bees can provide to crops increases their suitability for agricultural restoration programs and the appeal of such programs to farmers.

What factors limit bee population size?

In order to design effective restorations, it would be useful to know what factor(s) most often limit bee population size, so that these factor(s) could be restored. The resources bees require to complete their life cycle can be roughly divided into those related to nesting (the appropriate substrate, such as bare soil, stems, or cavities, and for some species the materials necessary to create the nest interior, such as leaves or resin), and those related to foraging on flowers (pollen and nectar).[157] As yet no experimental restoration has evaluated the relative effectiveness of restoring floral and nesting resources. However, a number of studies have suggested that either floral or nest site availability can limit bee reproduction or population size. Population size of a floral specialist, *Andrena hattorfiana*, closely tracks the availability of pollen resources provided by its host plant.[201] The likelihood of this species being limited by floral resources is probably higher than average, however, because it is a ground-nesting floral specialist. Another floral specialist, *Dieunomia triangulifera*, shows evidence of population limitation by both floral resources and other factors.[202] Within a natural system of isolated mountain meadows, *Bombus* colony reproduction is higher in meadows with more floral resources.[203]

Two studies have provided nest sites experimentally, and then examined the role of floral resource availability in bee reproduction. The reproduction of *Osmia lignaria* in agricultural landscapes exceeded replacement at sites where floral resources were more available within the species' flight distance, and was likely below replacement at sites with fewer floral resources.[158] Similarly, it took *Osmia caerulescens* and *Megachile versicolor* twice as long to provision their nests in fields with fewer floral resources.[204] This difference probably translates into lifetime fecundity because solitary bees are thought to continue provisioning nests until the end of their lifetime.[205] These studies provide weaker evidence for the generality of floral resource limitation, however, since nest site limitation was at least partially removed as a factor.

The one experimental study of nest site limitation found that *Osmia rufa* populations increased by a factor of 35 when nest sites were augmented.[206] Observational data from a similar system also suggest nest site limitation, in that old meadows similar in floral resource availability have more wood-nesting bees when old trees are present.[207] In an applied context, the provision of nest sites for *Nomia melanderi* and *Megachile rotundata*, which are used for alfalfa pollination in the western USA, allows for much larger population sizes than would otherwise be present;[21] however, floral resources are unlikely to be limiting in this agricultural context. All but one of the species reported above are cavity-nesting, and their populations might be more often limited by nest site availability than is the case for ground nesters.

Bee populations could be limited by other factors such as predation or parasitism,[57,208] or, at the egg and larval stages of the life cycle, by fungal pathogens in nests.[35] For example, *Bombus vagans* workers have a 14% chance per day of being attacked by a crab spider (Thomisidae), and 13–20% of *Bombus* workers are lethally parasitized by Conopid fly parasitoids (reviewed in[208]). However, there is little research on the overall importance of these factors to population growth for wild bee species. The one experimental study to measure parasitism as a function of bee nest density found little evidence of top-down regulation; in fact, parasitism was inverse-density dependent in most years.[206] In any event, it is not clear how to control parasites and predators within a restoration context.

Floral restorations

Pollinator restoration to date has focused on restoring floral resources within an agricultural context. The precedence given floral restorations is supported by evidence that large-scale declines in forage plants are associated with large-scale declines in pollinators, particularly for *Bombus* species,[49,60,61] and by the studies of bee reproduction and floral resources, although nest site restoration may also be critical and merits further study.

A critical element of restoration plantings for pollinators is the choice of plant species to include in the mixes. Mixes ought to include plant species that in combination provide a long period of bloom, and are preferred by a diverse pollinator community. Relatively few studies have used quantitative information to determine the best species; however, efforts are progressing in that direction. In the United Kingdom, bee preference has been studied primarily by comparing bee visitation to the different restoration protocols available to farmers through government-subsidized restoration programs. Not surprisingly, bees prefer planting mixes that are specifically designed to produce flowers, as compared to grass-based restoration protocols, or less intensively managed crop areas.[209–212] The relative attractiveness of floral planting mixes and natural regeneration varies across studies; however, natural regeneration often involves agricultural weeds that can be more acceptable to pollinators than to farmers.[209–211,213] In the United States, far less research on restoration protocols has been done. Bee preference for different flowering plant species suitable for agricultural restorations has been experimentally and/or statistically tested, and then incorporated into restoration protocols, only in California,[214] Michigan[215] and New Jersey.[216]

An important finding to emerge from studies of floral restorations is that often only a few plant species are responsible for the great majority of bee visits.[64,209,210,212] This suggests that restorations can be made more efficient and cost-effective by focusing on a subset of highly attractive species, rather than simply increasing floral diversity. Unfortunately for North American restoration ecologists, most of the key bee plants so identified in EU studies are exotic weeds in North America, highlighting the need for analogous research on this continent. In addition, studies of the entire bee community are needed, as most research to date has considered only *Bombus*.

A limitation of many studies assessing which flowers are attractive to bees is that they are based on use rather than preference. When a field researcher surveys bees visiting different flowering plant species, the plant receiving the greatest number of bee visits could achieve this through being preferred by bees (the variable that researchers seek to assess) and/or because its flowers are more abundant than those of other plant species (a statistical outcome not relevant to bee preference). Preference, as opposed to use, can be calculated from observational data on both bee visitation rates and floral abundance,[62,217,218] or in experiments in which the different plant species are offered simultaneously at standard densities.[215]

Nest site restoration

Although nesting resources may be critical in determining bee densities, this aspect of bee restoration has received less attention than have floral resources. There is limited information on the microhabitats preferred by nesting bees. British *Bombus* queens nest-searching in agricultural habitats prefer sites with banks or tussocky vegetation,[219] and Swedish *Bombus* queens prefer tussocks or withered grass.[220] Guidelines for creating nest sites for different types of bees are available from the Xerces Society.[214] Studies of the relative efficacy of restoring different types of bee nests sites, analogous to the comparisons done for floral resources, and studies of the population-level consequences of nest site restoration, are greatly needed.

The farm bill and agri-environment schemes

Bee restoration on agricultural lands has taken place largely within the United States and the EU, both of which have significant funding in place for such programs. In the United States, federal funding for habitat restoration on agricultural lands is channeled largely through the Farm Bill (formally the Food, Conservation, and Energy Act) and administered at the state level by the Natural Resource Conservation Service and the Farm Service Agency. Government spending for Farm Bill conservation programs averaged \$3.5 billion per year from 2002–2007.[221,222] Although "conservation" is broadly defined within the Farm Bill to include many goals in addition to biodiversity conservation, Farm Bill funding still dwarfs many forms of government funding for conservation on nonagricultural lands. For example, in 2003 only \$0.8 billion was spent on the conservation and restoration of all 1335 threatened and endangered species listed under the Endangered Species Act—none of which was a bee (http://www.fws.gov/endangered/pubs/index.html). The Farm Bill offers around a dozen programs in which landowners can voluntarily enroll to receive financial benefits for restoring habitat, primarily on formerly agricultural lands. Many of these programs are suitable for bees; furthermore, the 2008 version of the Farm Bill explicitly prioritized pollinators as a target for restorations.[223]

In the EU, government-sponsored agricultural land conservation falls largely under the aegis of agri-environment schemes (AES), for which annual funding in 2003 was €3.7 billion.[55] Participation in AES programs is mandatory for EU counties under the Common Agricultural Policy.[212] As of 2005, AES cover roughly 25% of the farmland in the 15 older EU countries.[55] AES offer farmers many options for which they are compensated financially, including restoring habitat on buffer areas or set-aside fields, and/or farming in-production fields less intensively.

Given the large amount of taxpayer money being spent on agricultural habitat restoration, and the increasing role of pollinators in such programs, a critical question is whether these programs are effective in restoring pollinators. In the United States little research has been done on this issue. Of the

Farm Bill programs, the Conservation Reserve Program (CRP) is the largest, with roughly 4% of national cropland area being enrolled.[224] Historically, the goals of the CRP program have been controlling erosion and agrochemical runoff, as well as regulating crop production volume. More recently, the goals of carbon storage and habitat creation for birds has been emphasized.[225] In 2008 pollinators became a high priority wildlife taxon for CRP projects.[223] Butterflies benefit from CRP restorations, but there have not yet been any studies of CRP effects on bees.[226] The practice of sowing CRP restorations with nonnative grasses is widespread[225] and likely diminishes the value of these habitats for bees.

The two Farm Bill programs most suited to pollinator restoration are the Environmental Quality Incentives Program (EQIP) and the Wildlife Habitat Incentives Program (WHIP). EQIP is the second-most funded program, after the CRP, and its goals include both improving the environmental quality of lands associated with livestock production, and habitat restoration for wildlife on agricultural lands.[224] WHIP receives less funding, but unlike other Farm Bill programs it is focused exclusively on wildlife habitat.[224] Both EQIP and WHIP can reimburse private landowners for up to 75% of the costs of restoring wildlife habitat. As of 2008, pollinators are a priority taxon for EQIP restorations,[223] and pollinators are prioritized in some states (e.g., New Jersey) for the WHIP program as well. There are currently no published studies of the effectiveness of EQIP or WHIP protocols in restoring bees or other pollinators, although a study of EQIP pollinator restorations is in progress (C. Kremen, Unpublished data).

In the United Kingdom and Europe there is a larger base of research on the effectiveness of government-sponsored agricultural programs AES in restoring biodiversity in general, as well as pollinators in particular. Biodiversity is one of several stated goals of AES, with the others including the historical and esthetic value of landscape preservation, and improving soil and water quality.[227] The first quantitative assessment of the broad-spectrum biodiversity benefits of AES found no significant effect on target taxa, although there were weak positive effects on nontarget taxa including bees.[228] A meta-analysis 2 years later concluded that only 54% of 62 studies comparing AES and non-AES fields found significant biodiversity effects of AES.[229] A common experimental design flaw was noted that could artificially inflate the perceived benefits of AES: the locations chosen for AES enrollment may have higher biodiversity prior to AES implementation, as growers often choose fields that are less suitable for intensive agriculture to begin with.[55,229] Furthermore, AES predominantly benefitted common species that may be in less need of protection than rare species[55]—although it is important to note that AES were not designed to benefit rare species, which may be absent from agricultural habitats in the first place.[230] The findings on inconsistent biodiversity benefits have had a significant political impact given the large amount of government funding spent on AES programs.[227]

AES management significantly benefits bee communities as compared with conventionally managed controls in about half of the studies done to date, consistent with the mixed biodiversity benefits reported for other taxa. The increase in *Bombus terrestris* colony weight, a proxy for reproduction, is not significantly different between colonies placed on conventional farms and those placed on farms with AES-types restorations.[231] AES management in intensively farmed Dutch landscapes significantly increases bee species richness, although the bee fauna was poor throughout the study with only three species recorded.[228] Swiss hay meadows enrolled in AES have significantly greater bee abundance and/or species richness than do conventionally managed hay fields.[55,232,233] In England, bee abundance is significantly higher in fields with 6-m wide grass margins, as compared to fields without margins.[234] Various other forms of AES management in three other studies done in Spain, the Netherlands and the United Kingdom, however, show no significant benefit to bees.[55] In terms of the benefits they receive from AES restorations, bees appear about average relative to other taxa that have been studied (Table 1).

Organic farming as a method for restoring bees

Although the exact requirements for organic farming certification differ by country, all are based on guidelines issued by the International Federation of Organic Agriculture Movements, and involve foregoing synthetic fertilizers, pesticides, and herbicides.[235] In the United States, biodiversity standards

Table 1. **Rank of bees relative to other taxa examined in the same study in terms of response to agri-environment scheme field-scale habitat restoration protocols. 1 = most positive response, 5 = least positive response**

Study design	Rank of bees	Other taxa studied	Reference
Paired comparison of AES versus control fields; outcome = species richness	1.5 (tied with hoverflies) of 4	Plants, hoverflies, birds	(Kleijn *et al.*[228])
Paired comparison of AES versus control fields; outcome = species richness	4 of 5	Plants, orthoptera, spiders, birds	(Kleijn *et al.*[55]), Spain
Paired comparison of AES versus control fields; outcome = species richness	2 of 5	Plants, orthoptera, spiders, birds	(Kleijn *et al.*[55]), Switzerland
Paired comparison of AES versus control fields; outcome = species richness	4 of 5	Plants, orthoptera, spiders, birds	(Kleijn *et al.*[55]), UK
Paired comparison of AES versus control fields; outcome = species richness	4 of 5	Plants, orthoptera, spiders, birds	(Kleijn *et al.*[55]), the Netherlands
Paired comparison of AES versus control fields; outcome = species richness	3 of 4	Plants, grasshoppers, spiders	(Knop *et al.*[232])
Paired comparison of fields with and without 6-m grass margin strips; outcome = abundance and/or species richness	In top 3 of 6	Plants, grasshoppers, spiders, carabid beetles, birds	(Marshall *et al.*[234])

were added to the organic certification program administered by the USDA in 2009 (Eric Mader, Xerces Society, pers.com.). There is also a suite of farm characteristics associated with organic farming but not required for organic certification. When compared with conventional farms, organic farms often have smaller field sizes, greater crop diversity, greater area of seminatural or fallow habitat, and higher abundance and diversity of weedy flowers, and these features may be important in supporting bees.[236–238] Recent reviews have found that organic as compared to conventional farming generally supports greater biodiversity across a range of nonbee taxa, with plants being the most strongly benefitted.[236,239] At the time these reviews were done, there were too few studies of bees to assess bees' response as a taxon.

Organic farming might be expected to benefit bees, first due to reduced insecticide use, and second because reduced herbicide use can lead to a greater abundance and diversity of floral resources. On the other hand, some pesticides used by organic farmers are highly toxic to bees, and the increased tillage that organic farmers often use as a replacement for herbicides can destroy nests of ground-nesting species. Studies investigating

Table 2. **Studies comparing the abundance, species richness, and/or reproduction of wild bees as a function of farm management (organic vs. conventional)[a]**

Study design	Result	Significance Significance level	Reference
Wild bee species richness in winter wheat fields	Higher species richness in organic fields	***	(Clough *et al.*[235])
Wild bee pollination services to watermelon	No difference	NS	(Kremen *et al.*[243])
Wild bee visitation rate to four crops	No difference	NS	(Winfree *et al.*[91])
Wild bee abundance in canola fields	Greater abundance in organic fields	***	(Morandin and Winston[242])
Wild bee abundance and species richness in fallow strips near organic versus conventional winter wheat fields	Greater abundance and species richness near organic fields	*	(Holzschuh *et al.*[241])
Wild bee species richness in winter wheat fields	Higher species richness in organic fields	***	(Holzschuh *et al.*[240])
Reproduction of a solitary bee, *Osmia lignaria*	Higher reproduction on organic farms, but only in landscapes lacking natural habitat	*	(Williams and Kremen[158])

[a]Several studies finding positive effects are not independent because they were done at the same sites (Clough *et al.*[235]; Holzschuh *et al.*[240]; Holzschuh *et al.*[241]). NS $P > 0.10$, $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$

changes in wild bee communities and/or pollination services as a function of farm management have obtained mixed results. Bees are significantly more abundant in and near organic as compared with conventional winter wheat fields in Germany,[235,240,241] and also in organic as compared with conventional canola fields in Canada.[242] A solitary bee, *Osmia lignaria*, provisions significantly more nest cells on organic as compared to conventional farms when farms are set within agriculturally intensive landscapes.[158] However, the difference is not significant when farms are surrounded by more natural and seminatural habitat cover, because in that case the bees can forage outside of the farm and are not so dependent on local farm management.[158] Organic farming has no effect on native bee pollination services to watermelon in California,[243] or on wild bee abundance on several crop plants in New Jersey and Pennsylvania[91] (Table 2).

Several studies have partially separated the components of organic farming to better isolate the variables that affect bee communities. In one of the studies finding no significant benefit of organic farming, conventional and organic farms were distinguished only by the criteria for organic certification (use of synthetic fertilizers, herbicides, and pesticides); the two classes of farms did not differ in other variables often associated with organic farming, including field size, crop diversity, or weedy flower abundance or species richness.91 The lack of significance in this study suggests that the habitat heterogeneity often associated with organic farming may be more important to bee communities than organic certification *per se*, as is the case for some nonbee taxa.[244–246] Wild bees may be particularly benefitted by weedy flowers and a variety of crops that provide forage for a longer period, since few bee species have flight seasons short enough to be supported by a single monoculture crop.[241] In contrast, insecticide use has had surprisingly weak effects on wild bee communities in the small number of studies that have explicitly quantified this factor.[241,243] This

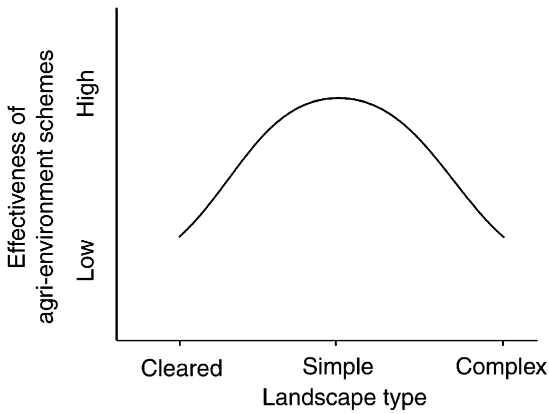

Figure 1. **A hypothesized interaction between landscape context and the effectiveness of AES restorations. Cleared landscapes are defined as <1% noncrop cover, simple as 1–20%, and complex as >20%. Note the shape of the curve would be strongly asymmetrical if the X-axis values were evenly spaced. The hypothesis suggests that the benefits of a given restoration effort will be greatest in landscapes that are already highly agricultural. From Tscharntke *et al.*[247]; used with permission.**

similarly suggests that organic farming requirements *per se* may be less important than other land use practices associated with organic farming. A final consideration is that the effectiveness of organic farming may be contingent on the larger landscape surrounding the farm (see below).

Where should restorations be done?

Restoration of bee habitat within agricultural landscapes is generally done at small scales, ranging from 2–6 m buffer strips to fields of a few ha. Where should such restorations be done, in order to maximize their effectiveness? Tscharntke *et al.*[247] hypothesized an asymmetrical, hump-shaped relationship between landscape heterogeneity and restoration effectiveness (Fig. 1), such that restorations are less effective when done in heterogeneous landscapes (defined as <80% cropland) where pollinators are present without restorations, most effective in intermediate landscapes (defined as 80–99% cropland), and less effective in homogeneous landscapes (defined as >99% cropland) where pollinators are largely extirpated and few sources of colonists for restorations exist.

Several studies have since tested the relationship between local- and landscape-scale factors and have confirmed that the two interact, and that the effectiveness of local bee restorations increases consistently with increasing cover of cropland (which most authors have interpreted as arable, i.e., row crops) in the surrounding landscape. As yet no study has tested the hypothesis that effectiveness declines in the most intensively managed landscapes (>99% cropland). In a system where all sites are set within highly heterogeneous landscapes (<40% arable cropland), neither local- nor landscape-scale factors explains crop visitation by native bees; rather, native bees are abundant throughout the entire system.[19,91] This is consistent with the hypothesis that in highly heterogeneous landscapes, bees are supported by the landscapes themselves and restoration is not required. In a system where the proportion of arable cropland in the landscape varies from 20–95%, bumble bee density in restored patches increases more than linearly with increasing arable crop cover.[248] Similarly, there is an interaction between bee species richness in organic versus conventional wheat fields and surrounding land cover, such that the organic/conventional difference increases with the proportion of arable croplands over a range of roughly 20–85%.[240] Last, the reproduction of a solitary bee species is similar on organic and conventional farms when both are near patches of seminatural habitat, but diverges on farms set within intensively agricultural landscapes.[158] Studies of nonbee taxa have also found that the benefit of organic farming is greatest in the most intensively agricultural landscapes.[249,250] These studies are broadly consistent with the work finding that the economic value of pollination services provided by natural habitat outweighs the value of land conversion only in the most degraded landscapes (see above).

Restorations can also be accomplished by reducing the intensity of a single land use variable, in which case the biodiversity gains can be plotted against land use intensity as a bivariate relationship. The steepness of the resulting slope indicates where biodiversity gains are greatest for a given incremental change in land use intensity (Fig. 2). A study of plant species richness and nitrogen inputs (a proxy for land use intensity) shows that the benefits of reducing nitrogen inputs are greatest in the least intensive systems[54]—the opposite of the conclusion reached by the studies of organic farming and arable crop cover reviewed above. In reality,

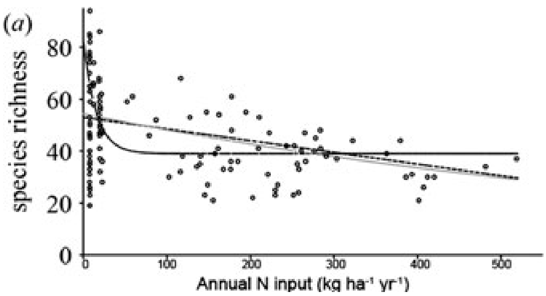

Figure 2. **The relationship between plant species richness (per 100 m^2) and annual nitrogen input (a proxy for land use intensity) on agricultural grasslands in Europe. *Curved lines* indicate the best fit that was found with a curvilinear function; *straight lines* resulted from a less explanatory linear function. The biodiversity benefits of reducing N inputs by a given amount will be greatest where the curve is steepest, in the least intensively farmed landscapes. From Kleijn *et al.*[54]; used with permission.**

the optimal location for a restoration is determined not only by relative benefits, as in Figure 2 or the studies of organic farming above, but also by relative costs. This full cost-benefit approach has not yet been applied to the question of what landscape context offers the best restoration value.

The cost-benefit approach has been used for a larger-scale question: whether biodiversity conservation and restoration should be focused on agricultural lands at all. In an influential paper, Green *et al.*[251] contrasted two approaches to biodiversity conservation: wildlife-friendly farming, which involves integrating conservation into agricultural landscapes through, for example, AES and Farm Bill restorations; and sparing land for nature, which entails concentrating agricultural production in high-intensity, low-biodiversity areas while protecting more natural areas elsewhere for biodiversity. Green *et al.* propose that the relative efficacy of these two approaches can be evaluated by considering how rapidly agricultural yield declines when wildlife-friendly farming is implemented—specifically, by plotting the density of a given species of conservation concern against agricultural yield. If this curve is concave, then wildlife-friendly farming is predicted to be the best conservation approach, because species declines are slower than yield increases as agricultural intensification increases (Fig. 3A). Conversely, if the curve is convex, then intensive agriculture combined with land sparing is predicted to be the best approach because species declines are rapid even when yields are low (Fig. 3B). Note that Green *et al.*[251] compare the shape of the biodiversity–yield relationship across entire study systems to identify the optimal system for conservation projects (Fig. 3), whereas Kleijn *et al.*[54] seek the optimal location for restoration within a given system by finding the area with the steepest slope (Fig. 2).

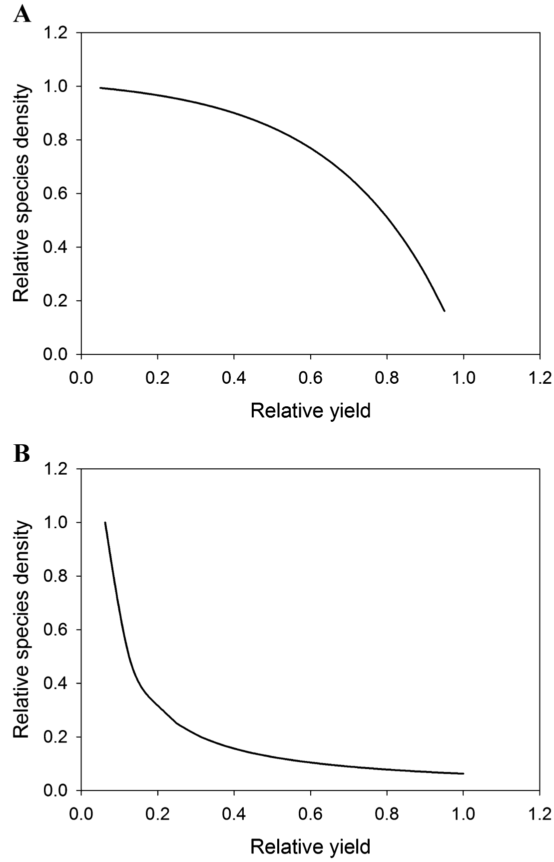

Figure 3. **Two species density versus agricultural yield relationships that lead to different conservation strategies. (A) When species density decreases slowly with initial increases in yield, wildlife-friendly farming can be an effective conservation approach. (B) Conversely, when species density decreases rapidly at low levels of yield increase, land sparing is predicted to be the best conservation approach. After Green *et al.*[251]**

If one assumes a fixed global need for food, as assumed by the model of Green *et al.*,[251] then greater yields will tautologically lead to less land area being used for agriculture because yield is defined as food production per unit area. However, on a *per capita* caloric basis enough food is already produced globally, which suggests that factors other than the need for food, such as distribution inequities, are driving agricultural land conversion.[252–254] Two additional factors make it difficult to evaluate the relative effectiveness of the wildlife-friendly farming and land sparing approaches. First, empirical density-yield relationships of the type shown hypothetically in Fig. 3 are not yet known for any species.[251,255] Although relationships are generally negative for the few taxa that have been investigated,[256,257] the shape of the relationship is not clear. In addition, the extent to which biodiversity-friendly agriculture reduces crop yields is controversial. Restorations that take land out of production presumably reduce yields, but the transition to organic farming can either reduce or increase yield.[254] Organic farming is, however, more expensive, which suggests that another variable—the cost of production—should be considered in the cost-benefit analysis.

Second, there is as yet little evidence that using land for intensive agriculture leads to sparing land for nature elsewhere.[258] Yield and deforestation rates can be negatively correlated,[255] but this is not necessarily a causal relationship. At a local scale, both agricultural yields and the extent of land under production can be limited by the same factors—capitalization and technology—such that when limits on yield are removed, it becomes profitable for farmers to farm more land, not less.[259]

Differences between developed temperate and developing tropical systems need to be kept in mind when comparing among approaches to conservation and restoration Agricultural expansion over the next few decades is predicted to occur largely in the developing world.[255] Yet what we know about bee restoration through AES-type approaches is based largely on northwest Europe, which is one of the most agriculturally developed areas of the world.[54] Tropical bees that have only recently encountered agriculture may be less robust to it and in greater need of land-sparing approaches, as compared to the bee fauna that persists in areas with a long history of agricultural land use. Last, in terms of global conservation planning it is important to keep in mind that the per area costs of conservation in USA and UK, including AES-type restorations, are among the highest in the world.[33]

For pollinators specifically, several factors weigh in favor of focusing restoration on agricultural lands. First, significant funding for such restorations already exists, at least in the EU and USA, whereas less funding is currently available for nonagricultural restorations. Second, ecosystem services arguments for pollinator conservation are most relevant in agricultural areas. And third, agricultural systems have the potential to provide suitable habitat for at least some bee species. One study has quantitatively evaluated how AES restorations might affect both bee biodiversity and crop yield. Based on a study of bees in winter wheat fields, an increase in organic farmland from 5% to 20% is predicted to increase the species richness of bees in fallow strips by 50%, and the abundance of solitary bees by 60% and of bumble bees by 150%.[241] These benefits can be compared to the 40% decrease in yield (kg/ha of wheat) incurred by changing from conventional to organic agriculture.[240] In this study, 100% of the bee species were polylectic, indicating that the dietary specialists, which may be in the greatest need of conservation, have likely been lost from the system already.[241] This serves as an important reminder that only a subset of bees, namely those found in agricultural settings, are benefitted by agricultural restorations.

Do bee restorations restore ecosystem services to crops?

This is an important question about which we know surprisingly little. Restoration protocols that restore pollinator biodiversity may not restore ecosystem services, and vice versa, because a small subset of species commonly provide the majority of the ecosystem services (*e.g.*, Ref. 260). For example, single, common bumble bee species provided 49% of the pollination services to watermelon, out of 46 native bee species found pollinating the crop (Fig. 4;[19]). It may be that agricultural habitat restoration programs, which tend to protect common species,[55] may be effective for the restoration of ecosystem services even if they are not effective for the conservation of biodiversity. It is striking, given the potential benefits of agricultural pollinator restorations to crop pollination, that no published study has investigated this question using actual cropping systems. A study investigating the restoration of pollination services to crops as a function of habitat restoration has been in progress in California since 2006

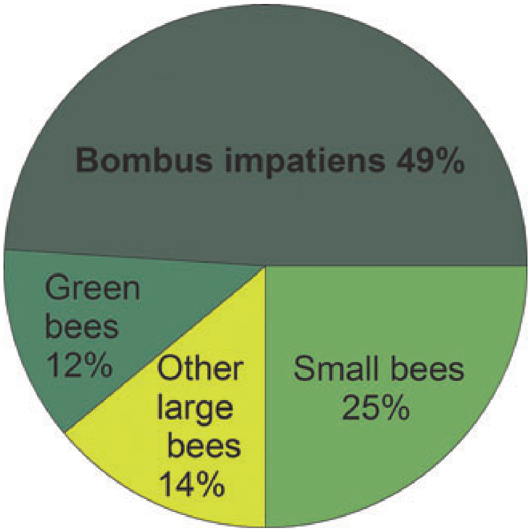

Figure 4. **Fraction of all watermelon pollen grains deposited on female flowers by the different components of the native bee community. "Small bees" included 28 species, "other large bees" 12 species, and "green bees" 5 species. Data averaged across the 23 farms reported in Winfree *et al.*[19]**

but is not yet completed (C. Kremen, Unpublished data). Several studies have shown the potential for crop pollination benefits by monitoring potted phytometers or noncrop plants situated near pollinator restorations. Seed set is higher in AES versus control (conventional) hay meadows for 2 of 3 potted, noncrop plant species.[233] Seed set of potted phytometers 300 m from a pollinator restoration falls to 1/3 the levels found within 100 m of the restoration; however, the difference was not significant.[261]

Bee restoration outside the agricultural context

Given the fact that restorations generally focus on the vegetative community, yet plants and pollinators are interdependent, it is important to know to what extent pollinator restoration follows naturally from vegetative restoration. There is only one published study of nonagricultural bee restoration, which found that bee communities on ancient and restored British heathlands were similar in species richness and dominant species identity. Species composition was not similar between ancient and restored sites, but composition was harder to assess as it also varied across sites within a restoration class and across time,[262] as it typical of bee communities.[124] In California, remnant riparian fragments and vegetatively restored sites have similar bee abundance and species richness, but species composition differs significantly between the restored and control sites.[263] In particular, ground-nesting species and floral generalists were more abundant at the restored sites. Pollination function also differed in that native plant species received fewer visits from native bees at restored sites.[263]

Summary and conclusions

Striking gaps in our knowledge of bee conservation and restoration became apparent in the process of writing this review. The following topics are particularly in need of scientific attention.

First, there is a great need for monitoring of bee populations to provide information about long-term population trends. Data from regions other than northwest Europe, and genera other than *Bombus*, are particularly needed. We also need studies that assess how different bee species are affected by land use change, so that conservation planners can prioritize the needs of the most sensitive species, while not basing conservation programs on the bee species that do well in disturbed areas. Studies from both temperate and tropical systems show that even when aggregate bee abundance and species richness are not negatively affected by land conversion, species composition can change dramatically,[85,88,94] indicating that species-level analyses are important. Last, there are almost no studies of bees and climate change and these are clearly needed.

Second, we lack basic information about the population biology of bees. To my knowledge, a life table analysis or population viability analysis (PVA) has not yet been done for any bee species. Solitary bees have unusually low fecundity for an insect, with studies reporting 2–30 eggs or offspring per female lifetime.[202,205,264,265] Presumably, this means that survivorship rates for juveniles and/or adults are unusually high. Studies that measure these rates and then perform sensitivity analyses to assess which life stages most strongly determine population growth rate would enable conservation plans to focus on the most critical aspects of bee biology. PVA could determine the population sizes necessary for bee species persistence as well as the land area required for reserves.

Third, we need to know what factors most often limit bee populations. This is a challenging question, but could perhaps be addressed in the restoration context using experimental additions of nest sites and/or floral resources. A related point is that we need more studies that measure bee reproduction as opposed to merely forager density. Forager density, reproduction, and genetic population size can be uncorrelated, at least for social bees.[110,140,266] Another problem is that bees are generally sampled at flowers, or using floral mimics such as pan traps, yet bees assess the attractiveness of a given flower patch relative to the alternative floral resources available in the larger landscape. Because researchers rarely have data on all the alternatives, this behavior can make studies based on forager density alone difficult to interpret, and even lead to erroneous outcomes such as concluding that bee abundance is highest in degraded landscapes, when actually the relative attractiveness of a standardized flower patch is highest in such landscapes.[248,261] Yet the great majority of published studies measure forager density as the outcome variable.

Fourth, given the funding and effort going into Farm Bill and AES-type restorations, we need more research evaluating the effectiveness of these restorations. I am not aware of any published studies of the efficacy of Farm Bill restorations in restoring bees. The research on AES restorations is strongly dominated by studies from the United Kingdom and the Netherlands, which presents a scope of inference problem insofar as these are among the most human-dominated agricultural landscapes in the world.[54] Determining the relationship between agricultural yield and bee density would also be very useful as it would allow land managers to use the model of Green *et al.*[251] to identify the optimal location for bee restorations.

Fifth, the success of habitat restorations in restoring ecosystem services to crops has not yet been studied and would provide important information for conservation planning and policy. Last, there are only two studies of bee restoration in nonagricultural settings. The paucity of studies makes it clear that much more work is needed in order to understand the restoration ecology of this critical functional group.

Acknowledgment

I thank Neal M. Williams, Scott Hoffman-Black, Daniel P. Cariveau, and William H. Schlesinger for helpful comments on an earlier version of the manuscript, Bryan N. Danforth and Stuart Roberts for sharing their knowledge of bee biogeography and bee conservation in the EU, respectively, and Wilhelmenia Ross for bibliographic help.

Conflicts of interest

The authors declare no conflicts of interest.

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