The Role of Resources and Risks in Regulating Wild Bee Populations

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Abstract

Recent declines of bee species have led to great interest in preserving and promoting bee populations for agricultural and wild plant pollination. Many correlational studies have examined the indirect effects of factors such as landscape context and land management practices and found great variation in bee response. We focus here on the evidence for effects of direct factors (i.e., food resources, nesting resources, and incidental risks) regulating bee populations and then interpret varied responses to indirect factors through their species-specific and habitat-specific effects on direct factors. We find strong evidence for food resource availability regulating bee populations, but little clear evidence that other direct factors are commonly limiting. We recommend manipulative experiments to illuminate the effects of these different factors. We contend that much of the variation in impact from indirect factors, such as grazing, can be explained by the relationships between indirect factors and floral resource availability based on environmental circumstances.

INTRODUCTION

Bees are a critical group of pollinators in many ecosystems, contributing to seed production in a wide diversity of wild plants (85). They are also the dominant pollinators for the portion of human food derived from animal-pollinated plants (60). While honey bees are the primary managed pollinator in agriculture, their decline in some countries (3, 86) has focused considerable attention on native, unmanaged bee populations as major contributors to agricultural pollination (41, 133). If honey bee populations decline further or cannot be increased to sustain the worldwide expansion of bee-pollinated crops (2), then it will be important to understand how to maintain pollination services of wild bees where they already predominate (104, 134) or to enhance their services where they make only modest contributions (62). Declines in populations of bee species other than honey bees, however, have been reported from several countries (6, 22). While maintenance of bee abundance assures the continuation of pollination services, bee diversity can improve reproduction in individual crop (41, 47, 119) and wild plant species (37, 105). Evidence also supports the positive role of pollinator diversity in maintaining plant community diversity (32).

Habitat loss is the most commonly cited factor affecting both pollination services and bee population and community declines (131). Recent work has modeled pollination as an ecosystem service dependent on landscape factors (61, 66), but studies of bee population responses rather than ecosystem services have produced complex or inconsistent results (13). A meta-analysis of the influence of disturbance factors on bee populations found that only extreme habitat loss produced statistically significant negative impacts on bee abundance and richness, and found great variation of bee population and community responses to different types of disturbance (131). We posit that factors such as disturbance have only indirect effects on bee populations and that improving our knowledge of direct effects (i.e., how they function and how they relate to indirect factors) will greatly improve our ability to augment wild bee population abundance and diversity. Here, we review what is known about factors hypothesized to have direct effects on bee populations and discuss whether varied responses to landscape factors may be due to their conflicting influence on these direct factors.

At a basic level, we expect that the factors that control bee populations are simple and direct. Individual species abundances should increase with food and nesting resources but be reduced by risk factors, such as predation. Niche differentiation of food and nesting resources should promote bee diversity, but individual risks and risks that affect the community as a whole, such as pesticides, should reduce it (55). **Figure 1** shows a conceptual model of the interactions between species traits and factors assumed to have direct effects on bee populations. Diet breadth determines which components of local resources a given species perceives as food (16, 71). Foraging range, because it correlates with body size (42), describes both the geographic area in which resources can be used and the amount of a resource that must be collected to provision offspring (76). Life-history traits include level of sociality and nesting habit (excavating belowground, excavating aboveground, or utilizing preexisting cavities), which influence bee population responses to disturbance (129). Factors with direct effects (food abundance and timing, nesting resources, and incidental risk) (**Figure 1**) should most clearly influence population size.

The indirect factors shown in our conceptual model, invasive species, habitat complexity, and land management, are a subset of potential categories. Others include habitat fragmentation, climate change, and anthropogenic disturbance, which may overlap in various ways. The key point is that indirect factors work by influencing the direct drivers of bee population growth. In order for indirect factors to produce consistent results, they must have consistent effects on the direct factors. First, we consider direct factors themselves and the extent to which their population effects are known. We point

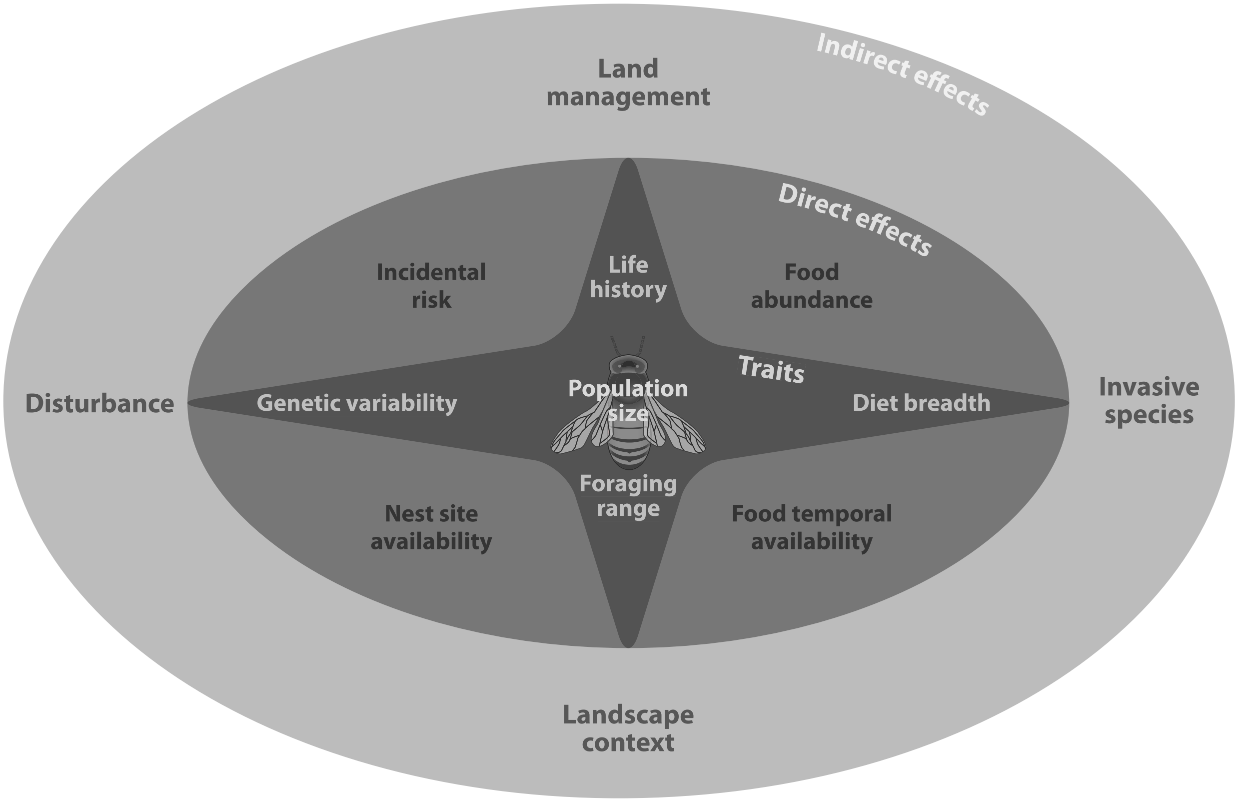

Figure 1

Direct and indirect effects. Bee populations are driven by direct effects and modulated by species traits. Indirect effects act by their influence on underlying direct factors.

out where important interactions between direct factors occur that modify their expected effects when acting individually, requiring joint consideration of these factors to understand their influence on bee populations. We argue that better understanding of direct effects and their interactions is needed for predictive models that focus on indirect factors. Ultimately, this information will be useful for creating prescriptive management plans to achieve specific population and community outcomes for bee community structure and function in pollination services.

DIRECT EFFECTS

Food Quantity and Temporal Distribution

Floral nectar and pollen are the primary energy source for most bee species, comprising both larval and adult diets (69). They are offered only by flowers, many of which present their rewards briefly. Pollen and nectar themselves are susceptible to abiotic conditions and consumption by other biotic communities, such as yeasts (45). Nonoverlapping phenologies of bees and flowers and lack of fit between bee food-gathering structures and flower parts can limit flower availability in a habitat. Widespread pollen specialization among bees, which can range from 15% to 60% of bee species in different biogeographic regions, further limits the potential bouquet of flower species available to a particular bee species in a particular habitat (71). Therefore, floral resource availability is hypothesized to be a major driver of population abundance and community diversity of bees.

Floral resource limitation of bee populations has been inferred by reproductive output of social colonies or solitary nests, positive correlations of either bee abundance or

Oligolectic: refers to bees that use a limited subset of available pollens, usually in a single plant family, to provision their offspring

bee diversity with floral resource abundance or diversity, and negative correlations between bee species thought to compete for food. Studies of oligolectic (pollen specialist) bees permit the simplest analyses of these relationships because resources are relatively easy to calculate and foragers are easy to find by observing their host plant. *Andrena hattorfiana* (Andrenidae) population size in southern Sweden correlates strongly with population sizes of their host plant, *Knautia arvensis* (65). The researchers calculated that each offspring requires the floral resources of two entire plants for complete development. A second specialist bee, *Calliopsis pugionis* (Andrenidae), was estimated to need a single plant to provide the pollen resources for 1,600 brood cells (122). Such estimates based on a resource economy offer tools for managing habitat to support viable populations of these species, as exemplified by Muller et al. (76).

Detailed studies of oligolectic bees also offer insights into the mechanisms and timing of resource limitation. *Dieunomia triangulifera* (Halictidae) foraging on its host, *Helianthus annuus*, took longer foraging trips and carried less pollen as resources declined seasonally and daily (72). Estimates of floral resource availability combined with foraging patterns and brood provision sizes predicted that individuals foraging early in the season when flowers were scarce would need a foraging radius of 8 km, but at peak bloom that radius declined to less than 1 km. Even with adequate floral resources present in the local landscape, the distance between them and bee nests can greatly influence bee productivity. When two specialist cavity-nesting species, *Hoplitis adunca* and *Chelostoma rapunculi* (Megachilidae), were placed at increasing distances from their host plants, provisioning rates dropped 23%–46% (140). While these studies support the influence of local floral abundance on reproductive success, it is notable that females of both *D. triangulifera* and *C. pugionis* mentioned above did not maximize their number of daily foraging bouts and did not forage every day (72, 122). Reduced foraging may reflect slower rates of oocyte maturation than of brood provisioning (95).

Resource limitation of reproductive output and population size of generalist species has also been tested but by using proxies for resource abundance because it is difficult to both specify and quantify all possible plant species that generalists might use. Brood cell production in *Osmia lignaria* (Megachilidae) in an agricultural landscape in California varied with the proximity to natural habitat at larger spatial scales (130). Similarly, snapshot estimates of local floral density and bee population abundance are often positively correlated (19, 88), and food supplementation of captive bumble bee colonies foraging in natural settings sometimes boosts reproductive success (84). There are exceptions to these findings (27), however, especially for bumble bees (20, 29, 40).

This correlative approach requires special attention to geographic and temporal scales of the study. Because current bee populations derive from resources present in the prior generation (weeks to more than a year previous) (23, 70), cross-site correlations based on snapshot estimates should be positive only if resource variation within sites across time is relatively low compared with cross-site variation. Areas under consistent farm management or with predictable rainfall are more likely to produce these conditions than highly variable communities, such as deserts, where different plant species have different rainfall requirements and often bloom intermittently and asynchronously (8). Evidence for temporal lags between resource levels in one year and bee abundances the following year is limited, partly because it is rarely considered (72, 88). The observation that founding bumble bee queen density correlates to floral resource density early in the spring in subalpine meadows, but not later in the summer (28), demonstrates that time lags can also result from short term fluctuations in floral resources. It seems likely that densities of eusocial bumble bees, which start colonies annually from a single foundress, track the availability of floral resources in the proximity of nest sites during the brief period of colony founding rather than later in the season when weather and flowers are less variable and foragers more plentiful. In general, short-term time lags should be more likely in population response to floral resources by multivoltine species, while univoltine species and first-generation multivoltine species should show evidence of interannual lags in population abundance.

Because bees are mobile, correlations between local floral density and forager density do not necessarily indicate resource limitation of population size but could reflect patterns of aggregation around pulses of rich resources, such as might be predicted by an ideal, free distribution of consumers relative to prey (91). Therefore, correlations between flower abundances relevant to a particular bee population may occur over a broader spatial or temporal scale than is typically studied. For example, local abundance and diversity of bumble bee species on grasslands in Iowa were better explained by floral resource abundance in the grasslands within a radius of 500–700 m of the site than by the same index of local floral resources (46). Large pulses of floral resources from oilseed rape crops strongly predicted bumble bee forager abundances on planted forage in German landscapes (126), and different bumble bee species responded to the proportion of these large patches of synchronously flowering crops at spatial scales ranging from 250 to 3000 m (127).

Timing and composition of bloom are also critical to bee species in ways that relate to species-specific traits such as diet breadth and flight season. Continual resource availability over the whole active season is needed by most social and multivoltine species. Although many studies find that the abundance of natural habitat is positively associated with bee populations, bee abundance and richness decline with increasing cover of the predominant natural vegetation type in the eastern United States—forest (132). Temperate deciduous forests can provide good springtime floral resources for bees, but the forest tends to lack both flowers and bees in the summertime (44). During one study of the impact of logging on bees in New York state, no flowers were seen in the control forest plot during the summer over two study years and only a single bee specimen was taken, in great contrast to logged plots, which had both bees and flowers (94). Therefore, the amount of natural habitat is not necessarily a blanket predictor for bee abundance and diversity.

The quality and composition of floral resources interact with species-specific traits to determine population abundances across sites. For example, bumble bee forager abundance in small plots within a 50 × 50 m swath of Norwegian grassland was determined largely by the presence of highly rewarding tubular flowers and not overall floral richness (43). Individual bee species responded to different measures of floral resource availability (88), suggesting that the diverse floral communities support diverse bee species by offering resources that benefit species differently.

Multivoltine: refers to species that produce more than one generation per year

Univoltine: refers to species that produce a single offspring generation per year

Nesting Resources

Bees use nests to protect adults and developing larvae from predators, parasites, environmental extremes, and incidental harm. The majority of species excavate simple tunnel systems in soil, but others require particular structures or resources that are potentially in limited supply, including mud, leaves, resin, pith, dead wood, narrow cavities, and large protected chambers (69, 96). Demonstrating that nesting resources are limiting is challenging because they are likely to correlate with local vegetation structure and thus floral resources as well. Ideally, nest site limitation should be demonstrated by associating an increase in nesting resources with a subsequent increase in population sizes of bees, without changing other important variables. We are unaware of any studies that have documented convincingly bee population response to augmented nesting resources independent of floral resources. The main evidence for nest site limitation is inference drawn from bee population sizes compared with estimates of nesting resources in unmanipulated (by the researcher) landscapes.

Stingless bees (Meliponini), which nest in tree cavities or hollow areas in the ground, use plant resins for nest construction (96). Because large cavities and resin-producing plants are more likely to occur in mature tropical forest than in agricultural areas, it is likely that the distance to forest constrains stingless bee populations. Ricketts (93) found that stingless bee abundance in coffee plantations declined with distance to forest, and suggested that nest site limitation was a potential mechanism. Eltz et al. (30) found that stingless bee nests were associated primarily with very large tropical forest trees, but that nest density was better explained by pollen resource availability than by nest availability in forests with different histories of disturbance.

Many bee species in the family Megachilidae (and some Colletidae) routinely nest in narrow cavities in wood, soil, or plant stems and separate their brood chambers with leaf pieces (*Megachile*), resin (*Heriades*), or mud (*Osmia*). Because they show great selectivity for cavity size (103) and leaf type (48), and because mud may be seasonally or locally rare, there is great potential for nest resource limitation. Numerous studies have used artificial cavities to record the presence of cavity-nesting bees (e.g., 63). Although trap nests provide evidence for the occurrence of species that will use them (125), inferring either population size or population change by this method is problematic. Trap nests compete for nesting female bees with natural cavities, and it is difficult to assess natural cavity availability (but see Reference 89) or the relative attractiveness of trap nests compared with natural cavities. In one study that captured numerous cavity-nesting bees by other methods, only a single bee was caught among 20 trap nests across 10 sites (36). One study used mark-recapture methodology with trap nests to estimate local population size (109) by comparing the number of marked bees released from and recovered in trap nests with those that colonized the trap independently. Given that bees show strong philopatry to natal nests (109), marked bees would have to be released away from nest sites, not in them, to permit equal sampling probability of marked and unmarked bees.

If narrow cavities are limiting resources, then providing trap nests at sites over time could increase population size. Ideally, this would be demonstrated by comparing estimates of bee abundance in trap nests with bee abundance sampled independently by other methods. Unfortunately, we are unaware of any studies that do this, but some find correlations consistent with nest site limitation. Moretti et al. (74) found that recent low-intensity fires in Switzerland had a differentially favorable impact on bee species that excavate dead wood or nest in preexisting cavities, consistent with the idea that a flush of nesting material resulting from fire releases particular guilds of bees from nest site limitation. One study inferred population increase through trap nest augmentation at study sites over five years by recording a 35-fold increase in the number of offspring reared from trap nests over time (110). Because bees reared in trap nests were returned to the trap nests for emergence each year, however, it is unclear if this represents population increase in general or just an increase in trap nest use driven by philopatry. In the sixth year of that study, bees were not returned to the trap nests, and trap nest occupancy, then composed of only nest-searching bees reared in the habitat, dropped by 80%–90%, to nearly the level at the beginning of the project. Thus, the 35-fold increase in brood cells over five years appears to be applicable only to the descendents of the first generation of trap-nesting females unless the trap nest population actually comprised most of the local population.

Cane et al. (15) inferred nest site limitation for cavity-nesting bees through field population estimates of the pollen specialist *Hoplitis biscutellae* (Megachilidae). They found that the bee was several times more abundant at its host plant, creosote bush, in urban desert fragments than it was in nearly pure stands of its host in nearby open desert and postulated that cavities were more available in urban areas than in natural desert.

Bumble bees nest in larger aerial or subterranean cavities, often vacant rodent burrows.

McFrederick & LeBuhn (68) found that bumble bee forager density was positively associated with rodent hole density. Similarly, Potts et al. (89) found an association between cavities >2 cm in diameter and the abundance of large cavity-nesting bees in the family Apidae, mainly *Apis mellifera*.

Observational studies of bee guilds or individual ground-nesting species have found correlates of local nesting density with environmental variables such as soil moisture, ground cover, slope aspect, and soil compaction (e.g., 57, 89). Fewer studies have correlated estimates of population density with substrate characteristics. Julier & Roulston (52) found irrigation associated with squash bee density on farms. Potts et al. (89) found a strong association between bare ground and ground-nesting bee populations. Although provocative, correlative studies such as these do not provide clear evidence that manipulating only nesting resources would result in greater bee populations. Farm irrigation could easily correlate with flowering resources and be a greater driver than preferred soil texture. Similarly, bare ground could also be associated with floral characteristics. In the study by Potts et al. (89), bare ground was positively associated with fire disturbance, which has been shown in some studies to correlate with floral resources for pollinators as well (12, 74, 87).

Overall, there is good reason to expect that nesting resources are potentially limiting, but there is little compelling evidence to show the scale, frequency, or severity with which nest site limitation occurs. Studies are very much needed to show the conditions under which manipulating nesting resources changes bee populations independent of changes in vegetation or other potentially direct effects.

Incidental Risks

Incidental risks to bees include sources of mortality that disrupt the reproduction of individuals and therefore potentially contribute to population regulation. They include a variety of biotic and abiotic factors that differ among bee species and communities and therefore must be considered separately for each species, guild, or habitat. Incidental risks can be devastating locally but are highly variable over time and space, so it is more difficult to predict their effect on population size outside of a specific context, for example, bees inhabiting a particular cropping system. Here, we consider types of incidental risk that have received substantial research attention for their effects on bees.

Tilling. Agricultural tilling involves turning over and mixing the top layer of soil, usually on an annual or semiannual basis. Many insects, including both pests and beneficials, may be affected by this activity. Tilling potentially crushes subterranean insects and exposes vulnerable stages to predators and disease. Numerous studies have examined the effects of tilling on invertebrates, and the overall conclusion is that macroinvertebrates, such as beetles and earthworms, are particularly sensitive to tilling (58). Tillage practices across farms vary greatly, in both depth and type of plow (e.g., moldboard plow, chisel plow, and rotary tiller), and different tilling methods have species-specific effects, such as shown for ground beetle populations (102). Thus, results may be complex.

Many ground-nesting bee species place their brood cells <30 cm from the surface (67, 79). The newly produced offspring remain in diapause in their nests from the end of the previous flight season until the beginning of the next. Because agricultural tillage commonly reaches to a depth of 15–30 cm, tilling is likely to destroy part or all of some subterranean bee nests. To date, no researcher has reported on an experiment that tills through a nesting aggregation to measure mortality, as has been done for ground beetles (102).

There are two published studies of the effects of tillage on the density of *Peponapis pruinosa*, a specialist bee pollinator of squashes, gourds, and pumpkins (52, 104). In some respects, this species should be among the most sensitive to tilling: It has no noncrop host plants in much of its range and it prefers to nest in agricultural fields directly below its host plant at a depth that places its brood cells within common tilling range (52). Despite this apparent susceptibility, the two studies produced conflicting results, with Shuler et al. (104) finding reduced populations in tilled fields and Julier & Roulston (52) finding no difference. There are various possible reasons for this discrepancy. First, a sufficient reservoir of bees on-site may survive by nesting beneath the till zone or outside the till zone. Despite the apparent preference for *P. pruinosa* to nest within the crop, the bees sometimes nest outside the crop area in aggregations that can persist at a site for years (56). Many ground-dwelling bee species that nest in aggregations show strong philopatry (137), which could lead to increased bee occupancy in safe sites, once established, regardless of the relative preference for a particular site.

Second, one study (52) focused exclusively on pumpkins while the other included all cultivated yellow-flowered *Cucurbita* available in regional agricultural systems. Because pumpkin is cultivated as a late-season holiday crop, it may not flower before its specialist bees emerge. If early bees disperse rather than wait, farms with safe nest sites but late flowers may serve as regional source populations and depend on late emergence or immigration to maintain a specialist bee population. Distinguishing among these scenarios (surviving tilling, avoiding tilling through philopatry at safe sites, and dispersing toward resources at regional scales) is important because each scenario provides different guidelines for promoting and preserving bee populations. If bees often survive tilling, then well-timed resources may be the most important factor for keeping wild bees in agricultural systems. If they do not survive tilling, then regional untilled land will act as sources and tilled land as sinks, as proposed by Kim et al. (57).

Parasites/Disease. Bees support numerous parasitic guilds, including insects (Diptera, Coleoptera, Hymenoptera, and Strepsiptera), arachnids (mites), and protozoans. These parasites can be classified into those that attack adult bees, usually while foraging, those that attack brood, those that attack the stored provisions of brood cells (cleptoparasites), and those that usurp the nests of eusocial bees and produce only sexual castes using their host's worker castes, such as cuckoo bumble bees. Together or individually, these natural enemies could influence individual bee or colony survival and reproduction and eventually population dynamics and community structure. A detailed account of the ecology and evolution of parasites of social bees has been compiled by Schmid-Hempel (99). In their review of cleptoparasites and natural enemies of bees, Wcislo & Cane (124) indicate that the evidence for demographic effects of natural enemies is scant and we would argue that rigorous studies demonstrating that natural enemies regulate bee populations are still lacking. Parasite and pathogen effects on bee populations are known to be problematic in managed bees such as honey bees (118) and other domesticated bees, such as the alfalfa leafcutting bee, in which unnaturally high densities and environmental stresses can increase exposure and susceptibility to parasites and pathogens (50). Research effort into the population effects of natural enemies (top-down effects) in wild bees is small relative to that in managed bees. Nevertheless, it is likely to be important, as top-down control of herbivorous insect density is not uncommon (e.g., 31). In fact, it is one of the central pillars of the theory behind biological control of pest outbreaks (116).

The best test for the importance of top-down factors in regulating the populations of insects involves experimental manipulations of predator or parasite density and measures of prey or host response in terms of density or demographic rates (31). Because demographic responses result from a difference between birth and death rates, experiments that include a manipulation of resources can determine the relative importance of these two direct factors. In bees, these experiments are tricky because manipulation of floral resources and parasite density often requires caging, which is likely to affect the normal foraging and nesting behavior of bees. Studies that assess the effect of natural or experimental variation in parasitism in the field have the advantage of retaining the natural context for behaviors, but the disadvantage of confounding factors, such as resource availability and exposure to multiple natural enemies (e.g., 49). When conducted in a comparative framework, for instance, across sites varying in environmental factors, they can help to isolate important correlates to parasite success. Replication of these studies over several years can provide important data on the magnitude of temporal variation in demographic effects of parasites.

Experimental manipulation of both floral resources and parasites within enclosures surrounding nesting populations of a twig-nesting solitary bee, *Osmia pumila*, indicated a greater influence of resources than of parasites on overall brood cell production; 60% more brood cells were produced when floral resources were doubled versus 12% mortality caused by parasites when present versus absent (38). Importantly, parasitism rates rose to 25% of brood cells under sparse floral resources, five times higher than under rich floral resource environments. Solitary bee females are expected to experience a special sensitivity to parasitism under conditions of sparse resources because increased foraging effort causes a trade-off with protecting the nest from brood parasites (e.g., 122). This trade-off has not yet been demonstrated in the field, but if it proves common it suggests exacerbated negative effects on overall reproductive output when floral resources become limiting. Confirmation of this interaction between direct factors under natural conditions is desirable.

A study of natural variation in resource availability and parasitism rates by conopid flies, common parasites of foraging bumble bees in Europe, showed that parasitism explained less of the variance in population-level reproductive output (male production and the number of males per worker) than did resource availability (100). Social parasitism of free-living bumble bees by their parasitic congeners (*Bombus* subgenus *Psithyrus)* directly reduces colony success by ovarian suppression of workers and the production of their own reproductives (120). In some studies, rates of *Psithyrus* attack of field-placed captive colonies reached 100% and higher rates of attack occurred under the most favorable floral resource conditions, presumably related to the higher densities of *Psithyrus* in resource-rich habitats (20, 40). This interaction between social parasitism and floral resources is potentially important because it indicates that parasitism limits a colony's maximum reproduction under the most favorable resource conditions.

Social parasitism: the exploitation of a social colony structure for the production of offspring by an individual unrelated to the colony, often a different species

Brood parasitism of solitary bees directly reduces reproductive output by causing offspring mortality after the female has fully invested in that individual. Surveys of parasitism in natural populations of solitary bees indicate that parasitism rates can be high but vary widely among years. Parasitism of the solitary bee *Osmia rufa* by six species of cleptoparasites and parasitoids accounted for 17% of overall brood cell production averaged over 30 field sites and five years but varied significantly across years (110). In this study, average attack rates of trap-nesting solitary bee nests by cleptoparasites and parasitoids were related to habitat age, but not to the diversity of trap nesters. An investigation of a trap-nesting population of *Osmia tricornis* found that parasitism rates of brood cells varied little (12%–16%) over three years, but the rates of parasitism by any one species and its rank importance varied dramatically over years (121). Because the stage and mode of attack of different parasite species differ, avoiding parasites requires various strategies and adaptation to particular parasites may be hindered. Minimizing parasitism in captive populations also requires multiple strategies (7).

Internal protozoan parasites of bumble bees are potential factors in declines of bumble bee species, particularly in association with the commercial rearing and importation of bumble bees for greenhouse pollination (81). *Crithidia bombi* and *Nosema bombi*, two protozoan gut parasites prevalent in field and commercial bumble bee colonies, show potential for large-scale negative effects on bumble bee colonies and populations. *C. bombi*, though not highly virulent under field conditions (49), can have strong negative effects on colony size and reproduction when infected colonies experience starvation or other stressful conditions (10, 11). Negative effects of *C. bombi* infection on foraging performance of bumble bee workers suggest the potential for additional negative consequences in field conditions (80).

The effects of *N. bombi*, generally thought to be the more virulent of the two, have provided similarly variable results. Natural infection of captive bumble bee colonies in the field with *N. bombi* showed greater production of reproductive individuals than uninfected colonies (49). A study of greenhouse colonies experimentally infected showed no significant effects of *N. bombi* infection on colony performance (128), yet laboratory studies indicate almost total loss of fitness of queens and males in colonies infected early in the colony development cycle (82). A field study of experimentally infected colonies indicated significant negative impacts of *N. bombi* on colony growth and reproduction (83). Field studies are likely to provide the most realistic picture of parasite impacts on later colony development, but their ability to discern effects on queen survival and establishment is more limited. Genetic differences in effects and local adaptation of parasites to bee hosts increase the chances that exposure of wild populations of bumble bees to parasites of commercially reared bumble bees could create harmful epidemics. Well-controlled field experiments that track infection and colony development and reproduction under a variety of field conditions and that include species of conservation concern are needed to assess the environmental conditions under which *N. bombi* threatens the persistence of local populations.

Empirical research on bumble bee communities suggests that both parasite diversity and parasite load increase with local abundance of a species (26), as predicted by theory (90). In competitively structured bumble bee communities, lower-ranking species may benefit if parasites suppress population growth of the most abundant species, potentially enhancing community diversity. To our knowledge, no studies have examined the effects of parasitism on community structure of bees other than bumble bees.

Predators. Despite the ability of females of most species to sting, bees still suffer predation by numerous types of predators. These include vertebrates that consume larvae and/or honey (111), but most predators eat adult bees. Abundance of the European bee-eater, *Merops apiaster*, a bird that predominantly consumes flying insects, was positively correlated with the abundance of honey bee colonies, its primary prey, suggesting the importance of prey density on predator density. The bee-eater, however, consumed less than 1% of honey bee workers, suggesting that the prey was more important to the predator than the predator to the prey (34). Other major predators include flies, wasps, ants, and spiders. Species in the robber fly genus *Mallophora* consume adult bees of a wide variety of species (21). Many crab spider species perch on flowers and pose sufficient risk to bees such that bees alter their foraging behavior for an extended period of time to avoid the area where an encounter previously took place (25). Species in the wasp genus *Philanthus* (the beewolves) are voracious consumers of a wide variety of bee and wasp species. In one study, Stubblefield et al. (113) sampled more than 4,000 prey from a nesting aggregation of *Philanthus sanborni* and found that nearly all observed flower-visiting bee and wasp species in the area had been taken as prey. A study conducted near an aggregation of *Philanthus bicinctus* found that the predator had significantly reduced the local forager density of bumble bees, which further led to a significant reduction in pollination of a bumble bee–pollinated plant, *Aconitum columbianum* (24). Predation by ants is so common in some systems that it has been implicated in favoring behavioral shifts to sociality as a defense mechanism in the facultatively social allodapine bee *Exoneura nigrescens* (Apidae) in Australia (139).

Although all these studies show that predation is common and can have local population impacts, there is still little known about demographic effects on a larger scale and which direct (e.g., food availability and nest site selection) and indirect (e.g., landscape features or land management regimes) factors influence predation on bee populations.

Pesticides. Many pesticides and some herbicides and fungicides are toxic to bees and clearly pose a substantial hazard wherever they are used extensively, including agricultural and residential areas as well as woodlands that are treated for forest pests. They have been shown to cause sudden death of honey bee colonies since the nineteenth century (51) and may be related to recent honey bee declines (117). They have also been shown to reduce alfalfa leafcutting bee (4) and bumble bee (35) productivity and have been implicated in ecosystem-wide reductions of pollinator services (54). Pesticides have many sublethal effects on bees, including the impairment of foraging behavior (73), reducing the likelihood of returning to the nest (138), slowing larval development (1), and impeding learning (5). Given the abundance and diversity of pesticides found in honey bee colonies (77), it appears that bees regularly come in contact with pesticides in anthropogenic landscapes. Gauging the risks of pesticides is greatly complicated, however, by their diverse chemistry, retention times, and formulations (35) as well as the likelihood of species-specific effects on bees (101). Some species-specific differences may be caused by differences in physiology and behavior, such as the potential for concentrating or diluting pesticides in social colonies or adding risk through the use of leaf material in nest building (101). Although the most common means of testing is through laboratory feeding trials, it is difficult to extrapolate these results to likely impacts without better knowledge of field exposure or potential combined effects of mortality and sublethal effects on population growth (106).

Various studies use organic and conventional farms as contrasting treatments presumed to correlate with pesticide exposure (104, 130). Pesticide use on conventional farms is seldom quantified, however. In addition, some pesticides approved in organic farming have both lethal and sublethal effects on bees (101, 114). Thus, a lack of significant differences in bee populations between conventional and organic farming could be generated by a lack of experimentally robust treatment categories to specify pesticide risk. For studies on farms, we recommend making comparisons between treatments on large acreages of single crops (such as orchards) where a particular pesticide is being used. For manipulative experiments, the approach by Gels et al. (35) of monitoring colony growth of bumble bees under restricted but free-flying conditions with realistic field exposure is a promising middle ground between overly controlled experiments that may not represent realistic exposure and natural experiments where documenting actual exposure may be difficult. We hope that future pesticide exposure research will work with multiple bee species representing different ecological groups (social and solitary, leafcutters, and ground-nesters) toward the creation of population models of risk, as outlined by Stark & Banks (106).

INDIRECT EFFECTS

We define indirect effects as those arising from factors of broad general impact that influence bee populations primarily through subsequent changes in factors that have more direct impacts. For example, logging in most habitats is more likely to have a bigger impact on bees through changes in vegetation (94) than through direct mortality, although direct mortality is possible and could be substantial in tropical ecosystems. Indirect effects include many categories explored by other researchers as potential drivers of bee populations, including proportion of natural habitat in an area, distance to natural habitat, fragmentation, farming method, habitat complexity, disturbance level, grazing, agriculture, and habitat loss. Many of these factors were included in the meta-analysis of Winfree et al. (131), who showed the outcome (positive or negative) of different disturbance types on bee populations. Here, we focus discussion on the extent to which factors that cause indirect effects can be examined more simply as drivers of direct effects. To the extent that direct effects are relatively simple to measure and have predictable effects on bee populations, land manipulations that alter direct factors should result in relatively simple responses by bee populations. For example, in their model of land management's effect on invertebrate trophic levels, Woodcock et al. (135) found that the key predictor of species richness for both phytophagous and predatory trophic levels was sward architecture.

Land Management

Of land management practices, grazing has been examined most often for its impact on bee populations. Most studies of grazing have considered grazing intensity on a relative scale from light to heavy. Generally, increased grazing intensity negatively affects bee populations (53, 64, 136). In these cases, increased grazing is associated with decreased abundance or diversity of floral resources. In other studies, grazing has a positive effect on bee populations (18, 123), and in these cases grazing has a positive effect on floral resources. Thus, the evidence on grazing to date points mainly to a fairly simple effect on floral resources, but one study found that bare ground (a surrogate for ground-nesting bee nesting substrate) provided information beyond that provided by flower response alone (123).

Disturbance

The only particular disturbance type to date examined in several studies has been fire. Fire may have direct effects by burning bees (78), but this has never been quantified directly or inferred as a major effect. Instead, the impact on bees has been most clearly related to floral resources, which tend to flush in the first years after fire and then decline, along with bees, several years later (75, 87). One study found evidence of species-specific postfire effects on bees most likely generated by shifts in the herbaceous plant community that favored large social bees over smaller solitary species (78). In a study of fire and fire surrogates as management practices, Campbell et al. (12) found that either type of disturbance, but especially the two in combination, decreased tree canopy, increased herbaceous vegetation, and increased bee abundance. Similarly, in a study of the effect of logging (2–3 years after the disturbance), bees were most abundant where floral abundance was greatest in the most disturbed habitats (94).

Although disturbance does not always cause local reduction in abundance and diversity of bees (α-diversity), presumably because local resources in disturbed habitats provide equal or better resource opportunities for bees, disturbance can still have negative impacts through reducing diversity at larger spatial scales (β-diversity). Winfree et al. (132) noted that, although cleared land had higher abundance and diversity of bees than native eastern pine forests, several bee species used only pine forest habitat. Quintero et al. (92) reported little difference in local-scale diversity of bee communities between paired disturbed and undisturbed patches across a 50-km-long elevational and precipitation gradient of Patagonian forest. Anthropogenic disturbance appeared to homogenize bee communities over broad spatial scales, however. There was less than expected turnover in bee species across the gradient in disturbed than in undisturbed patches. Similarly, paired restored and remnant riparian habitats supported similar bee abundances and diversities, but approximately half of the species were found in only one type of habitat (127). Species traits are likely an important filter in determining which species thrive in more disturbed communities.

Landscape Context

The abundance or diversity of bees estimated in a local area may be related to the type, amount, or connectivity of land surrounding the surveyed area. It is seldom possible to estimate floral resources or their temporal distribution, nesting substrate, and incidental risks over a large area, or to calibrate habitat connectivity for the bee populations sampled. Thus, several direct effects may be confounded when landscape context is examined. The most common variable used in studies of bees is the amount of seminatural habitat surrounding the sampling area. Although this is often a significant predictor variable for bee populations (62, 108, 130), it sometimes is not (17, 132). It may yield a positive statistical interaction with other indirect factors (98) or do so in a species-specific or habitat-specific manner (17, 59). This is to be expected because it is seldom possible to quantify the direct effects in the system (but see Reference 107) and because different species respond demographically at different geographic scales (108). Given that habitat loss had only modest effects on bee populations, and then only in extremely degraded habitats (131), landscapes that appear highly degraded to humans may still provide the necessary resources for bees. Even urban landscapes can be relatively rich in bees. Berlin, Germany, for instance, has 262 bee species, half the total for the entire country (14). Interestingly, the habitat that seems most hostile to bees, such that distance to another type of habitat is of critical importance, is agriculture. As with food abundance, the relationship between landscape context and direct effects, as well as independent effects of connectivity, is best understood for specialist bees with easily discernible host plants. Franzen & Nilssen (33) followed 63 habitat patches containing the plant host of the specialist bee *Andrena hattorfiana* (Andrenidae) over four years and were able to document the relationship between floral resources, bee population size, habitat connectivity, and bee extinction and colonization events. Generalist species and whole communities are much more complicated to track and predict, but this work should stand as a model for how these types of parameters may combine to regulate bee populations.

One often discussed form of landscape context is habitat fragmentation. Although some studies report negative effects of fragmentation overall (reviewed in Reference 13), species-specific responses are also common, with some species thriving, others indifferent, and others declining (9, 13, 15). Species-specific traits, therefore, are important. For example, larger bees may be less sensitive to fragmentation than smaller species that cannot fly between fragments (e.g., 9). Cane (13) addressed fragmentation as influencing a combination of direct effects calibrated for each species. The effects of fragmentation can be further influenced by the matrix habitat surrounding them. For instance, pine plantations increase connectivity for most bee species between isolated patches of South American forest, but they seem to act as a barrier for at least one bee species (115).

Invasive Species

The effects of invasive plant and insect species on native bees have been thoroughly and recently reviewed (39, 112).The primary impacts are through changes in resources [i.e., how strongly invasive insects compete for floral resources (97) and how the intrusion of novel plant species into the plant community changes resource availability]. These effects are highly species specific, both on the part of the invader and on the part of the natives.

Summary

Despite the many types of variables considered as predictors of bee population size or diversity, there seem to be very few demonstrated underlying causes for the expected and unexpected results from diverse studies. Floral resource abundance and diversity, the most clearly demonstrated limiting factor among direct effects, are the most frequently implicated factors in studies of indirect effects. Convincing evidence for the primacy of other factors will require holding floral resource abundance constant, preferably through a manipulative study. Undoubtedly, there are cases in which nesting substrate or parasites or other direct factors limit population size, but there is little evidence at this point that those cases are common. Thus, we suggest that knowledge of landscape effects and management effects on flowers used by bees will likely predict the outcome of those factors on bee populations.

We also suggest that manipulative experiments are very much needed in order to understand when factors with potential direct effects do in fact limit population size. How much bare soil do ground-nesting bees need? At what density of bees in a habitat do cavities or plant stems become limiting? How often do parasites have demographic effects on bees? How much effect does tilling have on bees nesting in agricultural lands? These are some of the direct effects that are expected to regulate bee populations and be influenced by the categorical variables currently being tested, yet we know very little about how they work. Knowledge of these areas will help connect land management programs more directly to bee populations and provide an informed means to maintain pollinators for both wild plants and agriculture.

SUMMARY POINTS

1. Floral resource availability is the primary direct factor influencing bee population abundance as supported by a wide variety of observational and experimental evidence.
2. While plausible, little evidence supports nest site limitation of bees.
3. Studying the influence of resource availability requires selection of appropriate spatial and temporal scales in which to assess correlations between bees and flowers.
4. While parasites, especially newly introduced pathogens, potentially limit bee populations, little evidence exists for wild bee populations.
5. Parasitism acting directly can interact in synergistic or antagonistic ways with floral resource availability to influence individual and population performance.
6. Teasing apart important influences on bee populations requires separating indirect effects, such as fragmentation, from direct effects, such as floral resources.
7. Bee susceptibility to factors acting indirectly depends on species-specific traits such as foraging range and diet breadth.

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