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Causes of variation in wild bee responses to anthropogenic drivers

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Anthropogenic change can have large impacts on wild bees and the pollination services they provide. However, the overall pattern of wild bee response to drivers such as land-use change, pesticides, pathogens, and climate change has been one of variability in both the magnitude and directionality of responses. We argue that two causes contribute to this variation. First, different species exhibit differential responses to the same anthropogenic drivers. Second, these anthropogenic drivers vary in type and magnitude that will drive variation in bee responses. For this second issue, we focus on land-use change, the most well-studied driver. We conclude by discussing how understanding species-level responses and the magnitude of land-use change can make bee conservation more effective.

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Introduction

Bees (Hymenoptera: Apoidea: Anthophila) are among the most ubiquitous and important pollinators of wild plants globally [1,2]. Furthermore, wild bee species, along with managed honey bees (*Apis mellifera*) and managed bumble bees (*Bombus* spp.), are important crop pollinators [3–5]. A few studies have shown regional [6] and local [7] declines in overall wild bee species richness. Declines in the best-studied genus, the bumble bees, is well-documented [8,9]. Given the ecological and agricultural importance of wild bees, these findings have raised concern among scientists, governments, and the general public. An array of anthropogenic drivers has been implicated in wild bee declines including pesticides, introduced pathogens, climate change, and land-use change [10–12]. Furthermore, multiple interacting drivers may have even stronger negative effects [12,13]. However, bee responses to anthropogenic drivers are far from universal, showing a range of magnitudes and directionalities [14–16]. For example, a recent review of bee responses to the largest global driver of species loss, land-use change, found that while a 42% of effect sizes showed a negative response, 45% were neutral and 13% were positive [17].

The purpose of this essay is to explore the causes of variability in responses of bees to anthropogenic drivers. We have three main objectives. First, we highlight recent research that explores variability in species and species-group level responses of wild bees to anthropogenic drivers. Second, we examine how variation in an anthropogenic driver itself mediates wild bee responses. We focus on the most well-studied driver, human land-use change, which is also the leading cause of species loss globally [18], and describe how careful consideration of the magnitude and type of land use can reveal patterns of bee response that are otherwise obscured [17]. Third, we demonstrate how focusing on the responses of particular types of bee species can make conservation and management of wild bees more effective.

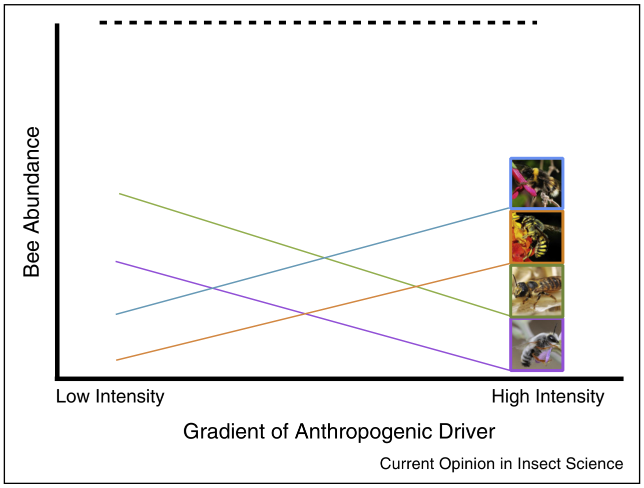
Variation in species-level responses

There are over 20 000 species of bees globally and they have a variety of life history traits and behaviors. It is therefore not surprising that different species show differential responses to the same anthropogenic drivers [19,20], and perhaps for this reason, also show different population trends over time [21••]. Recent species-specific studies move beyond simply assessing how aggregate wild bee abundance or species richness is affected by anthropogenic drivers (Figure 1), which had been the focus of the literature previously [17,22–24].

Pesticides

Pesticides are widely thought to be an important factor in wild bee declines [12], but bee species differ in their susceptibility to pesticides. A recent meta-analysis of lab-based, LD_{50} studies examined 18 bee species other than honey bees and found that species exhibit differential susceptibilities to direct application of insecticides [20]. These differences in acute susceptibility may be due to species-level differences in body size, hemolymph chemistry, and

Figure 1



Schematic representing how focusing solely on total wild bee abundance obscures species-specific responses to an anthropogenic driver. Each solid, colored line represents the abundance of an individual bee species across a gradient of intensity for a hypothetical anthropogenic driver. The dashed line represents total bee abundance across that gradient.

immune system function [reviewed in 20]. Different classes of pesticides have different levels of toxicity across bee species [20]. For example, Biddinger *et al.* [25] examined mortality of honey bees and *Osmia cornifrons* (Megachilidae) to five different pesticides and found bee species by pesticide type interactions. For example, the LD_{50} was met after applying 4 μg/bee of Acetamiprid to *O. cornifrons* compared to 65 μg/bee for honey bees but for Imidicloprid the LD_{50} was 3.8 μg/bee for *O. cornifrons* compared to 0.2 μg/bee for honey bees. The recent literature is increasingly finding sublethal effects as well, particularly for the systemic neonicotinoids [26]. Given the ubiquity of these insecticides, any species-level variation in susceptibility to neonicotinoids could have substantial ecological effects.

Behavioral and natural history variation among bee species will likely make species-level variability in response to pesticides even greater in field settings than in the lab, although few field studies have explored this yet. Different behaviors and natural histories will result in different likelihoods of exposures among bee species. For example, bee species that have flight times that overlap with pesticide applications, and species whose host plants are concentrated in the area of application will be most susceptible [27]. For systemic pesticides such as neonicotinoids, pollen typically has higher concentrations than nectar [28,29] and thus may have differential effects on species that are foraging for either resource. Landscape-scale studies are crucial to predict which bee species will be most susceptible to pesticides. In one of few such studies, Rundlöf *et al.* [30••] compared bee responses in landscapes with and without neonicotinoid-treated crops and found that bumble bee queen numbers and wild bee density was reduced with neonicotinoids while honey bee colony size showed no response.

Emerging pathogens from managed bees

The introduction of new diseases is a major concern for wild bees, with some species in decline likely due to pathogens, while others are unaffected. The best studied case concerns the bumble bee species in the subgenus *Bombus sensu stricto* which exhibited rapid declines in the midwestern United States [8]. This decline is associated with infection by the putatively introduced fungal pathogen *Nosema bombi*, which is commonly found in species in the subgenus *Bombus sensu stricto*. Spatially co-occurring species from other *Bombus* subgenera rarely host *N. bombi*, and these species are still relatively stable or increasing [8]. However, in the arctic and subarctic region of North America, some species in the subgenus *Bombus* show high *N. bombi* infection rates yet their populations are stable [31]. This example suggests that predicting which species will be most affected by emerging diseases will be challenging. Models with other insects suggest that diseases are most likely to affect species that are closely related to the hosts that harbor the new pathogens [32]. Thus given the ubiquity and global transport of honey bees, there is particular concern about their transmitting pathogens to others species of Apidae. Honey bees and bumble bees have been separated for over 70 million years [33], yet honey bee pathogens detrimentally infect bumble bees in laboratory settings [34–37] and vice versa [38•]. Honey bee pathogens have been found in multiple species of wild bees, but almost nothing is known about whether these pathogens have negative effects on wild species other than *Bombus* [39]. As domesticated bumble bees and honey bees are the most likely means by which these pathogens reach new locations, increased monitoring and control of these colonies is needed to protect wild bees [38•].

Climate change

Climate change will undoubtedly have differential effects on different bee species, as it does for other taxa [14]. A central focus of climate change research for bees has been potential asynchrony between bloom times and bee emergence [40]. Floral specialist bees could experience phenological mismatch differently from generalists. Two contrasting predictions have been made about this. First, some ecologists have predicted that specialist bees are at greater risk because if they emerge before or after their host plant blooms, they will be unable to forage [40]. However, some studies making this prediction are problematic as they confound rarity and sampling effects with true specialization [41]. Although there are well-known specialist (oligolectic) bee species [42], it is also true that species that appear to be specialists in a given study may not be specialists when more individuals are sampled, or when greater temporal and spatial scales are considered

[43]. Second, it has been proposed that specialist bees will be buffered against climate change because they have been selected to use the same cues for emergence that their host plants do; thus while these bees might change their phenology with climate warming, they would remain synchronized with their host plants [44,45•]. Generalist species will likely be little effected by asynchrony as they can visit numerous plant species as has been demonstrated in some studies [46,47].

Physiological differences among bee species might also make them differentially affected by climate change. For example, as temperature increases, species that overwinter as adults lose more body mass during winter diapause which is likely due to greater metabolic rates and energy expenditure during winter [48]. This suggests that these species are more likely to negatively affected as the climate warms. In the same experiment, Fründ *et al.* [48] found that these effects were more pronounced in earlier emerging bees, suggesting that, as is the case for other taxa, early spring species will be the most affected by climate change [49].

Land-use change

Land-use change is one of the most important and best-studied anthropogenic drivers of bee declines, and response to land use varies strongly across bee species. One group of bee species, the floral specialist bees, consistently shows stronger declines with land-use change as compared to more generalist species. Often the decline of specialist species can be linked specifically to declines of their host plants [7,50,51,52••,53,54]. For example, in Europe, bee species that specialize on Fabaceae have experienced greater declines. This is due to changes in agricultural management, specifically a decline in planting Fabaceae as cover crops [52••]. Specialist bees have shown to be disproportionately negatively affected in urban systems as well [53]. Conversely, populations of specialist bees can increase with land-use change if their host plants increase. In Europe, bee species that specialize on Rosaceae have increased along with increased plantings of Rosaceae crops [52••]. Some species have likely expanded their range following plantings of their host plant [55]. Therefore, while specialist species as a group are more negatively affected by land-use change than generalists [51], these responses are species-specific and dependent on changes in host plant abundance.

By contrast, other traits associated with species or groups of species do not strongly predict response to land-use change. No consistent patterns have been found for body size [53,56], nesting guild [7,53], or sociality [50,57]. This may be due to the statistical difficulty of separating the causal role of traits that are correlated across taxa [51]. For example, the well-studied genus *Bombus* (the bumble bees) are social, large, and polylectic, making it more difficult to determine which trait drives their responses to land-use change.

Variation in anthropogenic drivers: the case of land-use change

Another reason for the high variability in responses of bees to anthropogenic drivers is the variation in the anthropogenic drivers themselves. In this context, the relevant variation in responses includes not only that across bee species, but also in aggregate bee richness and abundance. We focus here on a single driver, land-use change, as this is the best studied of the anthropogenic drivers. Variation in land use has been found to influence the response of wild bee communities in two ways. First, the magnitude of the land-use change has strong effects on outcomes. For example, in systems where human land use is extreme (defined as some sites having $\leq$5% of natural habitat remaining), bee abundance and richness decline steeply [17]. However in systems with less extreme land use (all sites have >5% natural habitat), bee responses are mixed [17]. Importantly, in this review, 75% of the studies were done in systems with extreme human land use, which could bias the general impression that workers in this field have about how strongly bees are declining due to land-use change [17].

Second, bee responses vary with the type of land-use conversion studied. Bee abundance and species richness can increase with increasing urbanization and suburbanization [53,58]. Similarly, likely because many bee species are associated with open habitats, conversion of forest to more human-disturbed, open areas often increases bee abundance and richness [17]. Most studies of bee responses to land-use change have focused on conversion of natural habitat to agriculture, but within this broad category, different types of agriculture have differential effects [17]. For example in landscapes with red clover (*Trifolium pretense* L.), bumble bee queen densities were five time greater at sites with red clover than sites without [59]. By contrast to other studies that have demonstrated a negative effects of agriculture [e.g. 51].

Conserving wild bee communities

In this final section, we explore how the understanding of variability in species responses to anthropogenic drivers and variation in the drivers themselves can be applied to the conservation and management of wild bees. Understanding variation in species responses can provide valuable insight into an ongoing debate within conservation biology, which is: should conservation efforts focus on species that provide ecosystem services [61], or on the conservation of biodiversity per se, which generally emphasizes rare or threatened species [62]. A key question in this debate is whether the species that contribute ecosystem services such as pollination are also the important species driving patterns of biodiversity [63]. Recent studies suggest that only a small number of highly abundant wild bee species do the great majority of crop pollination [64•,65]. By contrast, rare species make up most of the biodiversity [65]. Specifically, a large synthetic study across 90 different field studies found 785 bees species visit crops yet 80% of pollination was provided by only 2% of those bee species, which were the more common species [64•].

Given that the important crop pollinating species and rare bee species might often be two distinct sets of species, it is crucial to understand how each of these groups responds to anthropogenic drivers as well as conservation actions. Few studies have examined whether these different groups respond differently to a given anthropogenic driver. Important crop pollinating bees have been shown to persist in agricultural landscapes [64•]. However, we know of no studies that have directly measured how well rare bees, as a group, persist in agricultural landscapes. It may be that common, crop-pollinating species that persist in agricultural landscapes are more robust to pesticides as these chemicals are ubiquitous on many farms. In support of this hypothesis, Brittain *et al.* [66] found that species richness declined with pesticide application yet pollination was not affected, suggesting that biodiversity and ecosystem services are not responding similarly to this anthropogenic driver. It is also important to determine whether conservation actions benefit both important crop pollinators and rare bees. The common conservation action of planting of pollinator habitat may benefit both important crop pollinators and rare bees [67]. However, no studies have examined whether conservation efforts that optimize conservation of one group results in trade-offs in the conservation of the other.

The variation in anthropogenic drivers themselves can have important implications for designing conservation actions, in particular to determining the most effective locations for conservation action. For example, the effectiveness of pollinator habitat plantings varies with the magnitude of land-use change in the larger landscape surrounding the planted site. When pollinator habitat plantings are placed in landscapes with very intensive human land use (<1% surrounding landscape in natural habitat within a 1000 m radius) few bees use the habitat plantings, likely because the potential colonist species pool is highly reduced [68••]. By contrast, in landscapes with extensive natural habitat (>20% surrounding landscape in natural habitat within a 1000 m radius) pollinator habitat plantings have little positive effect on bee communities because these landscapes already support diverse and abundant bees [68••]. The most effective location for pollinator habitat plantings are landscapes with intermediate levels of human land use (1–20%). In these locations, pollinator habitat plantings significantly increase bee abundance and richness [68••].

Conclusions

As global change intensifies, there is an increasing potential for negative effects on wild bees. The effect of this change will depend on bee species, and on the magnitude and type of anthropogenic driver. We have made significant progress in understanding how wild bee abundance and richness, in aggregate, respond to land-use change. However, few studies have directly addressed the impact of pesticides, pathogens and climate change on multiple wild bee species in field settings [but see 30••]. In addition, no studies have quantified the relative effects of anthropogenic drivers across species. Doing so will enable for more effective prioritization of conservation and management efforts. Finally, wild bees must respond to multiple anthropogenic drivers simultaneously and this may increase negative effects [12,13]. These more nuanced approaches will lead to more accurate assessment of bee responses and allow for more effective conservation of these ecologically and economically important organisms.

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We thank members of the Winfree lab for helpful comments. All photographs in Figure 1 are licensed under Creative Commons 3.0. Attributions from top to bottom are Alvesgaspar (*Bombus terrestris*), Alvesgaspar (*Anthidium florentinum*), Gideon Pisanty (*Megachile albisecta*), and Gideon Pisanty (*Megachile incerta*).

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