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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.

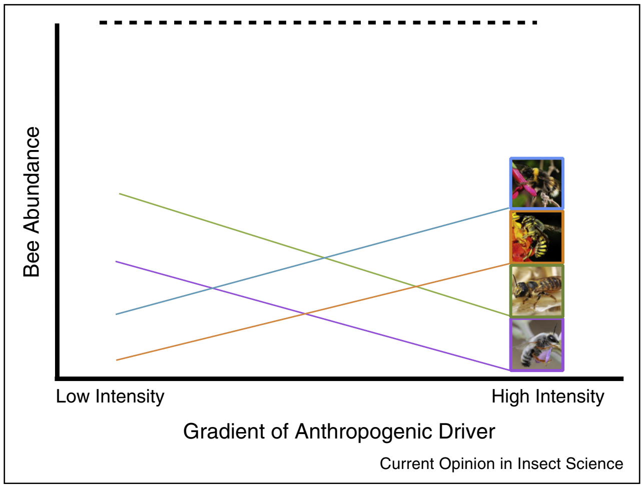
Variation in species-level responses

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