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Effects of global change on insect pollinators: multiple drivers lead to novel communities

Nicole E Rafferty[1,2]

Global change drivers, in particular climate change, exotic species introduction, and habitat alteration, affect insect pollinators in numerous ways. In response, insect pollinators show shifts in range and phenology, interactions with plants and other taxa are altered, and in some cases pollination services have diminished. Recent studies show some pollinators are tracking climate change by moving latitudinally and elevationally, while others are not. Shifts in insect pollinator phenology generally keep pace with advances in flowering, although there are exceptions. Recent data demonstrate competition between exotic and native bees, along with rapid positive effects of exotic plant removal on pollinator richness. Genetic analyses tie bee fitness to habitat quality. Across drivers, novel communities are a common outcome that deserves more study.

Addresses
[1] Department of Biology, University of California, 900 University Ave., Riverside, CA 92521, USA
[2] Rocky Mountain Biological Lab, P.O. Box 519, Crested Butte, CO 81224, USA

Corresponding author: Rafferty, Nicole E (nicole.rafferty@ucr.edu)

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Introduction

Global change is affecting insect pollinators in profound ways. Climate change, exotic species introduction, and habitat loss are affecting all major aspects of the biology of insects that pollinate plants in both natural and agricultural communities, altering their distribution, phenology, abundance, physiology, and morphology [1–5]. The consequences of these effects are complex, perturbing plant–pollinator interactions in subtle but important ways and in some cases resulting in local extinction [2]. Despite the complexity, understanding these consequences is critical: just as the vast majority of flowering plants depend on insects for pollination [6], we rely in large part on insects to pollinate our crops, a valuable ecosystem service [7].

Among the many insect taxa that serve as pollinators, bees, flies, butterflies, and moths have received the most study in the context of global change. Within these taxa, bees are key pollinators of both crop plants and wild plants [8], and studies on bees have dominated the literature on plant–pollinator interactions under global change. Because bees rely heavily on floral resources both for their own sustenance and to provision their offspring, their fitness is strongly determined not only by the direct effects of global change but also by the influence of global change drivers on flowering plants.

Here, I consider the effects of several global change drivers on insect pollinators, with an emphasis on what we know about the effects on native bees. First, I discuss how climate change is affecting insect pollinators, as this is a topic of active research that illustrates a suite of responses. Second, I review the effects of exotic species, both insect and plant taxa, on insect pollinators. Third, I consider another global change factor, habitat alteration and loss, and its effects on insect pollinators. Throughout, I consider both direct effects on pollinators and effects that are mediated via plants and other interspecific interactions. Given biotic pollination is by definition a multitrophic interaction, greater consideration of how global change alters species interactions is needed to improve conservation and management of pollination services.

Effects of climate change

The responses of insect pollinators to climate change have been relatively well-studied, although much remains to be resolved. For the most part, experimental studies of climate change factors on insect pollinators have focused on temperature [9–12], an important determinant of developmental rate [13]. Manipulations of other factors, such as carbon dioxide [14] or precipitation [15], have been applied to plants with subsequent measures of pollinator responses to altered floral traits. Complementing experimental approaches are long-term data, historical observations, and museum specimen records that can be correlated with ambient temperatures and other climate variables to describe insect responses [1,16].

Among the most striking consequences of climate change have been shifts in the spatial distributions of insect pollinators. Given the rapid life cycles and high mobility of most insect pollinators, are they able to keep pace with anthropogenic climate change by tracking environmental conditions over space? Evidence is mixed. On the one hand, Kerr *et al.* [4••] discovered bumble bees (*Bombus* spp.) across two continents have not tracked warming temperatures, as evidenced by a failure to expand their northern latitudinal range limits. On the other hand, several studies have shown that bumble bees have moved upward in elevation in montane ecosystems [4••,17,18], and some butterflies have shifted up in altitude [19]. Both a nymphalid butterfly (*Polygonia c-album*) and a lycaenid butterfly (*Aricia agestis*) in Britain have greatly expanded their ranges northward in association with warming [20,21]. A key question that has been not been considered for most taxa is how these spatial shifts affect interactions with floral resources and thereby influence both pollinator fitness and patterns of pollen flow and reproductive output of plants. Differential shifts among taxa will almost certainly translate into modified communities, especially as perennial plants are likely to lag behind their pollinators. In addition, it remains largely unknown whether traits or phylogenetic relationships can explain variable spatial responses among taxa (but see [4••,22]). To understand constraints on the distributions of insect pollinator populations and predict how distributions will be affected by climate change directly and via effects on host plants and other species with which pollinators interact, species distribution models can be a useful tool [23,24].

Shifts in the phenologies of insect pollinators are another conspicuous signal of climate change. Multiple species of bees have significantly advanced their phenologies [1], as have many butterflies and moths [25,26]. Among lepidopterans, variable responses can be partially explained by traits such as diet breadth [26]. In contrast to spatial shifts, the consequences of climate change-induced temporal shifts for plant–pollinator interactions have received much attention. Community-level analyses indicate bees and the plants they pollinate are advancing at similar rates [1], whereas butterflies and their nectar sources show different sensitivities to temperature [27•]. In general, experimental studies suggest phenological mismatches are unlikely to lead to complete decoupling of interactions among insect pollinators and plants [28,29]. In part this outcome is not surprising: plant–pollinator interactions tend to be generalized [30] and nested, with specialists interacting with generalists [31], and high rates of interaction turnover [32]. However, there are examples of specialized plant–bee interactions that are likely becoming disrupted as phenologies shift [33,34]. Even subtle phenological mismatches are likely to have consequences for interaction strengths, fitness, and the evolution of life histories [35]. Whereas the consequences of mismatches for plants have been commonly measured in terms of seed production [29,36], the consequences for pollinators have gone unquantified [37]. Also in contrast to the situation for insect pollinator phenology, where few studies have linked responses to traits or phylogenies, flowering phenology responses to climate change have been associated with traits such as flowering season, life history, and pollination mode [38,39] and exhibit phylogenetic signal across continents [40]. Together, these gaps in understanding point to a need for more studies at the community level; a community approach should simultaneously create opportunities for trait-based analyses and enable the consequences of phenological mismatches from the pollinator perspective to be quantified.

Other aspects of climate change that have been demonstrated to affect insect pollinators via flowering plants include elevated carbon dioxide and decreased precipitation. Plants grown under elevated carbon dioxide can have altered floral traits, such as nectar composition [14] and pollen protein concentration [41]. In turn, these altered traits can influence the fitness of insect pollinators; Hoover *et al.* [14] found that *Bombus terrestris* workers exhibited reduced longevity when fed synthetic nectar mimicking that of flowers produced under elevated carbon dioxide, and Ziska *et al.* [41] posit that reduced protein in goldenrod pollen could negatively affect bees. Experimental drought had variable effects on floral volatiles but consistently reduced flower size and floral display across four species, resulting in different communities of bees, flies, and butterflies visiting the flowers in the drought treatment [15]. In general, a tight link between the direct effects of climate change on floral resources and the consequent effects on insect pollinators has yet to be made. In part, this is because it is difficult to isolate the effects of complex floral responses on mobile insects, particularly in the field and at the population and community levels. As molecular genetic techniques and technologies that allow automated identification of individual bees, for example as they pass over radio frequency identification readers, are refined, larger-scale field-based studies of pollinator fitness and foraging responses should become more feasible.

Effects of exotic species

Human-aided transport and introduction of exotic species is a major driver of global change, reshaping fundamental ecological relationships [42]. Focusing in on exotic insect pollinators, we know the most about the impacts of non-native bees on native bees [43]. Non-native bees include long-established domesticated honey bees (*Apis mellifera*), more recently-introduced commercial pollinators, such as *Bombus terrestris* [44], and accidental introductions of species such as *Hylaeus communis* [45]. Alien pollinators can compete with native pollinators for resources, potentially reducing their fitness, altering patterns of pollen flow, and ultimately changing community structure to the disruption of ecosystem services [46,47]. Not surprisingly, the best-studied interactions between exotic and native bees involve honey bees. Building on prior experimental work that demonstrated competition for floral resources

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