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The variable effects of global change on insect mutualisms

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Insect mutualisms are essential for reproduction of many plants, protection of plants and other insects, and provisioning of nutrients for insects. Disruption of these mutualisms by global change can have important implications for ecosystem processes. Here, we assess the general effects of global change on insect mutualisms, including the possible impacts on mutualistic networks. We find that the effects of global change on mutualisms are extremely variable, making broad patterns difficult to detect. We require studies focusing on changes in cost-benefit ratios, effects of partner dependency, and degree of specialization to further understand how global change will influence insect mutualism dynamics. We propose that rapid coevolution is one avenue by which mutualists can ameliorate the effects of global change.

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Introduction

Mutualism is a key outcome of many species interactions that provide the energy, nutrients, and services for ecosystems to function and persist. These interactions span a wide range of associations from highly specialized, pairwise, obligate interactions to large, diffuse networks in which many species interact to varying degrees [1]. Because of the importance of the many mutualisms involving insects, it is critical to assess how these interactions are impacted by anthropogenic disturbances because entomofaunal and floral composition are changing at alarmingly fast rates as compared to natural cycles [2•,3]. These human-induced alterations are forcing mutualisms to respond rapidly to large-scale global changes. A major challenge of global change ecology is to synthesize the effects of different types of disturbance on mutualisms.

In this review, we begin by briefly summarizing the most recent progress on how global change can affect defense, pollination, and dispersal mutualisms (Table 1). Because mutualisms commonly involve complex communities, we next explore how mutualistic network structure and dynamics can be affected by global change, specifically due to agricultural intensification, fire, and invasion. Against this backdrop, we conclude by discussing the characteristics of mutualisms that may help us predict insect responses to global change.

Diverse effects of global change on insect mutualisms

Global warming can have disparate effects on insect mutualisms depending on the geographic location and degree of warming as well as the mutualists' tolerances and temperature optima. For instance, mutualists can experience negative effects when temperatures exceed the thermal tolerance of at least one of the partners (but see Ref. [4] for a review on insect thermal tolerance). Some negative outcomes of warming include disruption of defensive mutualisms between aphids and ants [5], and potential mutualism abandonment in aphid-bacteria symbioses (reviewed in Refs. [6••,7•,8]). In contrast, positive effects of warming on insect mutualism can occur when temperatures approach the physiological optimum of the insect. Positive effects of warming have occurred in the defensive mutualism between ghost ants and mealybugs where ghost ants become more active and better defend their partners at higher temperatures [9]. Interestingly, all the above examples involve phloem-feeding hemipterans, emphasizing that there can be variable effects of global change even within insect groups with similar life habits.

Part of the reason that insect mutualisms vary widely in response is because multiple disturbances can covary, while at the same time, insects can also be indirectly affected by responses in other trophic levels. For insect-plant mutualisms in particular, the response of plants to global change will influence their associated insects. For example, two disturbances that can covary with warming

Table 1

Types of insect mutualisms and anthropogenic disturbances considered in this review (papers from 2017–2020). The type of mutualism, dependency, and degree of generalization as considered from the insects' perspective. This is not a comprehensive list of mutualisms involving insects

Type of mutualism	Partners	Dependency	Generalization	Disturbances considered	Ref.
Defensive	Ant-Hemiptera	Facultative	Mostly generalist	Warming	[5,9,29•]
				Invasion	[9]
				Habitat alteration	[28]
	Hemiptera-bacteria	Obligate or facultative	Mostly specialist	Warming	[7•,8]
Nutritional	Pollination	Obligate or facultative	Mostly generalist; brood-pollination is mostly specialist	Drought	[12]
				Fire	[40–42]
				Temporal mismatch	[15,16•,17–20,34]
				Spatial mismatch	[22,23,24•,34]
				Invasion	[21,44•,45–47]
				Habitat alteration	[36,37,39••,43]
				Agricultural intensification	[33,35•]
	Myrmecochory	Facultative	Mostly generalist	Drought	[11]
	Beetle-slime mold	Unknown	Specialist or generalist	Drought	[49]
	Ant-plants bearing EFN[a]	Facultative	Generalist	Elevated CO_2	[14]
	Insect-bacteria	Obligate or facultative	Specialist or generalist	Warming	[6••]

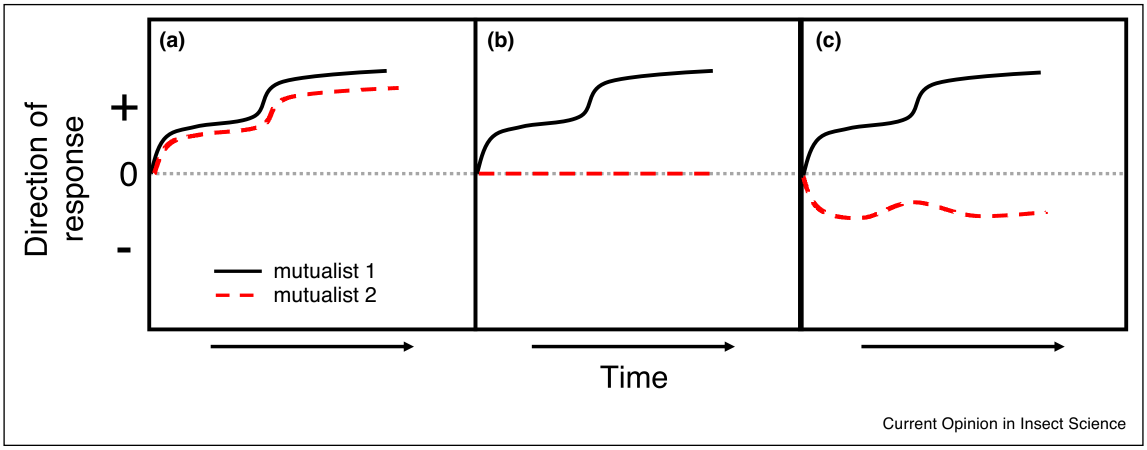
[a] EFN = extrafloral nectaries.

and directly affect plant fitness are changes in water availability and increases in atmospheric carbon dioxide (CO_2). Drought negatively affects plants, causing decreases in nectar production or quality [10] which, in turn, can reduce pollinator visitation, seed dispersal, and plant fitness [11,12]. In contrast, increased atmospheric CO_2 can enhance plant growth [13], and can lead to increased nectar production [10]. However, elevated CO_2 does not always translate into increased benefits for insect mutualists. For instance, elevated CO_2 may negatively impact ant protection and pollination mutualisms by reducing nectar quality [10]. Furthermore, elevated CO_2 may alter the timing of nectar production [14]. If the time shift in production of mutualistic commodities is large, this may cause temporal mismatches between mutualists. Thus, elevated CO_2 may be another cause of potential temporal mismatches between mutualists in addition to changes in temperature and snowmelt [15]. That said, the evidence for global change causing phenological mismatches between partners involved in pollination mutualisms is weak, as most studies have demonstrated little overall support for this prediction ([16•,17,18], but see Refs. [19,15]). Some authors have suggested that phenological mismatches may be unlikely because of the long evolutionary history of synchrony in the cues used by pollinators and plants [16•,20]; however, it remains to be tested if this is also the case for potential phenological mismatches driven by elevated CO_2.

In response to warming, drought, and habitat alteration, many species are changing their range to track suitable habitats, which could result in geographic mismatches between partners or disruption of the native mutualist community [e.g., Ref. 21]. The individual responses of the partner species will determine how range shifts influence mutualism persistence. When mutualists change their ranges in different ways, mutualism breakdown will occur if a mutualist partner is lost or cannot form new interactions. However, if partner species shift ranges in the same way or if one species can facilitate range expansion of its partner [22] (Figure 1a), the mutualism may persist as the ranges expand or contract across the landscape. Alternatively, if the partners fail to track each other (Figure 1b,c), insect mutualists can adopt new partners, but these new partners may be of lower quality [23,24•]·. Changes in range are expected to be accompanied by adaptation [25]; thus, the effect of range changes on mutualisms will depend not only on the immediate ecological responses, but also on whether mutualist partners adapt in parallel (Figure 1). We predict that locally adapted species may be more strongly impacted by changes in range and that changes in community context between locations will determine the likelihood of mutualism persistence following range shifts or expansions.

We also need to consider that most, if not all, mutualisms are context-dependent [26], and as such, the effect of global change on insect mutualisms is dependent upon the response of the entire community. For instance, global change could result in decreased natural enemy pressure in ant-herbivore defensive mutualisms because higher trophic levels can suffer more negatively from global environmental changes than lower trophic levels [27]. For instance, disturbed habitats with less forest cover have been shown to have fewer parasitoids [28]

Figure 1



Hypothetical responses by a pair of interacting mutualists adapting to global change. **(a)** Parallel responses to global change factors may keep the mutualism intact; however, **(b)** different magnitudes or **(c)** directions of response may lead to range or trait incongruences that decrease the efficacy of the mutualism. For example, in (a) shifts in the phenology of plants and pollinators in parallel can allow for the mutualism to persist. The changes in parallel could occur when the mutualists use similar environmental cues for their phenology, or when mutualists are able to coevolve rapidly or show plasticity in response to changes in their partners. In contrast, the mutualism might be threatened if, for example, a mutualistic partner changes its range, whereas the other partner does not respond (b). Additionally, mutualisms might be threatened if changes in each partner are in different directions, for example, when increases in temperature reaches the insect optimum but is detrimental for its symbiont (c). In cases b and c, mutualisms could persist only if mutualists can form interactions with other partners.

and increased temperatures resulted in fewer predators in a subalpine habitat [29•]. These studies suggest that the benefits of defensive mutualisms could decrease as less protection may be needed, potentially leading to mutualism breakdown. Additionally, the overall community composition and structure can have important implications for mutualism persistence (e.g. Refs. [30,31] making it necessary to assess how mutualist networks will be affected by global change.

Effect of global change on mutualistic networks

Accumulating evidence shows that complex, multispecies mutualisms are buffered from disturbances. At least part of this resilience is derived from species-rich mutualistic communities having more functional redundancy of partners. Recent work shows that increasing species richness and functional redundancy of experimental mutualist communities enhances mutualism persistence in the presence of exploitative species [32••]. Functional redundancy among mutualist partners within networks may also increase network stability in the face of other ecological stressors. For example, pollinators may survive disturbance if they can use multiple host plant species (e.g. Refs. [33,34,35•,36]). However, disturbance can decrease species richness (e.g. Ref. [37]) and increase asymmetry of networks [38] which, in turn, are predicted to reduce mutualism stability particularly when highly connected species are lost from the network (e.g. Ref. [32••]). In this case, coevolution of mutualistic partners can contribute to network stability through rewiring of the interactions after species extinctions [39••], suggesting that network plasticity may help to buffer mutualisms against disturbance.

The resilience of mutualistic networks, however, likely has limits and catastrophic events such as intense, frequent fires could have strong effects on mutualistic network structure. Fire frequency has been correlated with reduced pollinator diversity and high turnover rates in burned sites [40], and fire can cause changes in pollinator community composition [41]. Additionally, a post-fire assessment of floral visitor networks found that interaction strengths were stronger and more specialized in refuge areas [42], showing that flower-rich refuge areas can shelter networks from species extinction. Thus, refuge sites with high mutualist diversity may be pivotal to the persistence of networks in highly disturbed sites as they could reduce species extinction.

Although species loss is a key predicted outcome of global change, we also need to consider how mutualistic networks respond to the addition of novel species. Mutualistic networks are increasingly being invaded by alien species, but this seems to have a limited effect on network connectance, or the proportion of potential realized interactions among species. Because connectance is positively associated with the extinction threshold and species persistence [43], this suggests that alien species may not impact network stability. For example, although alien floral visitors have been shown to interact with more plants, native floral visitors have higher partner fidelity that could increase plant benefits, suggesting that native pollination networks may be buffered from the negative effects of invasion [44•]. Supporting this idea, some pollination networks have been shown to be stable despite the presence of alien pollinators [45,46]. Thus, invaders are not expected to completely supplant native pollinators, but the emerging patterns suggest that non-native species of plants and pollinators are increasingly becoming integrated into existing pollinator networks [47].

Although empirical data suggest that networks are generally resilient to disturbance and the introduction of new species, the question remains whether these complex mutualistic communities will continue to persist as global change escalates. Theory suggests that ‘tipping points’ and threshold responses could cause sudden, catastrophic changes in networks, and that these tipping points may be difficult to predict until they are already underway [48]. Furthermore, some types of mutualistic networks may be more vulnerable to collapse, particularly those involving specialized mutualisms that are more sensitive to disturbance. For instance, highly specialized beetle-slime mold spore dispersal networks may be more susceptible to extinction because erratic rainfall events threaten the supply of the slime mold spores on which the beetles feed [49]. Together, existing data suggest that while mutualistic networks may be resilient to the negative effects of global change, these networks can reach tipping points as global change proceeds, potentially leading to their collapse.

The future of global change for insect mutualists

Recent work underscores that insect mutualisms experience a wide range of potential effects caused by global change, making it difficult to provide general predictions across all mutualism types. This review also highlights that the effects of global change, either positive or negative, are going to be highly context-dependent and system-specific. This is an important point because it means that applying a broad statement about the effects of global change on insect mutualisms is not an appropriate avenue of discourse when planning for mitigation of the negative effects. Instead, what is needed are data specific to the particular insect mutualism under investigation. With this caveat in mind, we discuss some features of mutualisms that are likely to influence the response or magnitude of effect of global change.

Costs and benefits

Mutualistic outcomes are determined by the benefits surpassing the costs of providing a commodity in return. If the benefits increase with global change, for instance when plants are able to produce more rewards, then the mutualism may be reinforced. Alternatively, a decrease in benefits can lead to mutualism abandonment. For example, if disturbance reduces natural enemy abundance, this may lower the benefits of protection and increase the cost of defensive mutualisms. In some cases, a mutualist might be so limited by the mutualistic commodity that any reduction in the benefits received can result in an inability to respond to other environmental factors [50]. Few studies have measured the costs and benefits of mutualisms involving insects, especially with a focus on global change (but see Refs. [5] and [24•]). Although measuring benefits and costs in natural systems can be difficult, knowing how mutualistic traits might evolve or change in response to environmental conditions will be instrumental in predicting the effects of global change on mutualisms.

Partner dependency

The degree of partner dependency will likely determine the strength of species responses to disturbances. On one end of the dependency spectrum, strict obligate mutualists depend entirely on one another for survival and reproduction. As such, obligate mutualisms may be threatened by global change if mutualists cannot track the responses of their partners. Consequently, the maintenance of these mutualisms might depend on plastic responses or rapid adaptation of the partner with the shortest generation time. In instances in which the mutualists cannot respond quickly, we predict that local or global extinctions will occur (Figure 1b and c). Alternatively, in the cases in which a partner obligately lives within or on its mutualist, the symbiosis could facilitate simultaneous range or phenological shifts without a need for adaptation. In contrast to highly dependent mutualisms, facultative mutualists do not require the interaction for their survival/reproduction. If partners become extinct due to global change, facultative mutualists could obtain resources or services from other sources. Thus, facultative mutualisms should be more resilient to global change than obligate mutualisms.

Specialization level

Generalists are arguably favored after disturbance because they might be better able to use the narrow range of available resources or form new partnerships (e.g. Refs. [51•,52,35•]). In this sense, an obligate but generalized mutualism might be resilient to breakdown and extinction if alternative partners are available. In contrast, when mutualisms are so specialized that the interaction requires specific evolved traits, we expect increased mutualism abandonment or extinction on short timescales. On longer timeframes, specialized obligate mutualists might evolve traits that help partners respond in similar ways (e.g. Ref. [20]), and they may be better able to evolutionarily track each other’s responses (Figure 1a). These predictions do not likely apply broadly to all types of global change, especially when a disturbance can affect the partners in disparate ways (e.g. Ref. [6••]). Disturbances that can have asymmetrically negative effects on at least one partner may potentially lead to local extinctions (Figure 1c). Thus, being a specialized, obligate mutualist should be a major detriment to mutualism persistence with global change.

Coevolution

A key factor that could facilitate mutualism persistence is coevolution among partners (e.g. Ref. [53]), especially if it is rapid and allows tracking of the changes between partners (Figure 1a). Most of the research in this area has used theoretical network approaches to address the debate about the strength of coevolution in large mutualistic networks. Because of indirect effects, multi-species mutualisms may require more time than pairwise interactions to reach coevolutionary equilibrium after disturbances [54•]. In contrast, other work has shown that coevolution can buffer the negative effects of habitat destruction and climate change on mutualistic networks [39••]. Observational approaches such as tracking changes in trait values of interacting mutualists before and after a disturbance would be a first step in understanding the role of coevolution in mutualisms experiencing the effects of global change. Short-term evolution experiments using microbes or insects would also provide a powerful approach to study the role of coevolution in buffering mutualisms against disturbance.

Conclusions

In summary, the findings of this review suggests that we may not identify general patterns in how insect mutualisms response to global environmental change because these mutualisms are extremely variable. We advocate returning to a natural history approach that considers the set of features that make each mutualism unique, as well as examining how these interactions (co)evolve in changing environments. To push the field forward, we need to compare systems that vary in specialization and dependency and directly measure the benefits and costs involved in mutualisms experiencing different disturbance regimes. There is also a strong need to understand coevolutionary dynamics in mutualistic systems because global change is likely to place strong selection on mutualist partners. By doing so, these studies will allow us to integrate community and evolutionary ecology to advance our understanding of mutualism and global change.

Conflict of interest statement

Nothing declared.

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This study used citizen science data to evaluate the network properties of pollination mutualisms and analyzed which traits could make networks more stable in land under intense agriculture. They found that the presence of more generalist species allows for greater network robustness. This study provides evidence of traits that can enhance mutualistic network persistence with habitat alteration.

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This review summarizes both ecological and evolutionary effects of increased fire intensity and severity in insects. The authors discuss the effects of fire for insects of all trophic levels, including pollinators. They conclude that insects better able to disperse and have generalized diets and habitat choices will be more likely to survive fire events and colonize burned areas.

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This paper uses network analysis to understand how indirect effects influence coevolution in different types of mutualism networks. They conclude that networks with more species and more indirect effects will take longer for traits to evolve and this may slow species' responses to disturbance events.