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Conserving host–parasitoid interactions in a warming world

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Anthropogenic global warming (AGW) represents a major threat to biodiversity at all levels of organization. Attendant changes with climate warming are abiotic effects such as changes in the duration and intensity of precipitation events, wind intensity and heat waves. Most importantly, AGW may unravel food webs by differentially affecting the biology and ecology of species involved in intimate interactions, where reciprocal selection forces are often strong. Amongst insects, plant–herbivoreparasitoid interactions fulfill this criterion, as many herbivores and parasitoids are highly specialized on specific food plants and hosts, respectively. Here, focusing on temperature-related effects of AGW, I discuss several potentially important eco-physiological herbivore and parasitoid responses to high temperatures. These include effects on plant traits such as volatile emissions and primary and secondary metabolism. In turn, how these will impact insect herbivores, their parasitoids, and thus trophic interaction webs is discussed. The possible direct metabolic effects of heat waves on insects are also described. I also argue that climate change does not affect biodiversity independently of other human-mediated environmental threats, including habitat loss and fragmentation, invasive species, and overuse of pesticides. Thus, the conservation of multitrophic interactions is critically dependent on reducing the impact of multiple anthropogenic stresses.

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Introduction

Climate change represents a profoundly serious threat to biodiversity across different levels of organization, from populations to species and communities, and from there up to ecosystems and biomes [1••,2,3•,4••]. At both global and regional levels, the current rate of temperature change, driven primarily by the human combustion of fossil fuels, exceed rates that have occurred in at least 2000 years and probably much longer than that [5]. Previous major climate change events have precipitated mass extinctions that led to the sudden demise of many marine and terrestrial biota [6,7]. Using area-extinction models, Thomas *et al.* [8•] predicted that the current warming episode might be the major factor in driving high extinction rates in the coming decades (for a rejoinder, see [9], and a response [10]). Moreover, warming is not the only stress associated with climate change; there are also many attendant changes in the incidence of heat waves, droughts, storms, wind and precipitation, all of which will have ecological consequences.

In addition to the recent warming episode, ecosystems across the biosphere are being altered in other important ways that negatively affect biodiversity. These include habitat loss and fragmentation, the introduction of species into non-native ecosystems, the widespread use of pesticides, other forms of pollution, and over-harvesting [11,12]. Consequently, natural systems are being challenged by multiple anthropogenic stresses, making it more difficult for species to adapt to recent changes in climate patterns. At present, and given the predictions of the IPCC, a major concern is that rates of warming in the coming decades will be so great that they will far exceed the ability of many species to evolve fast enough to be able to adjust ecologically and/or physiologically. Certainly there is abundant evidence that many species, including insects, are responding to the recent warming. For example various studies are reporting that species are adjusting various aspects of their life cycles, such as seasonal growth and phenology patterns, as well as by shifting their ranges pole-wards and/or to higher elevations [12,13]. The ability of species to shift their distributions is often limited, however, by other factors. These include physical barriers as a result of urban and agricultural expansion that inhibit the ability of many species to track warming by dispersing over landscapes to new suitable habitat patches. In fact, some commentators argue that current experimental set ups often underpredict plant phenological responses to climate change, a process which will hugely impact food webs and ecosystems [15•].

One vital aspect that must not be overlooked when predicting biotic responses to warming is that species do not exist in isolation: they interact with other species.

Importantly, adaptation involves processes that do not only occur at the species level but at the levels of interactions and communities. Ecologist Daniel Janzen [16] once argued that the 'most insidious sort of extinction [is] the extinction of ecological interactions'. Although conservation efforts often target individual species or their habitats, it is important to recognize that multiple interactions in food webs and communities underpin the functioning of ecological communities. These interactions may involve species competing either directly or indirectly for resources within the same trophic level, or include species in different trophic levels, where one is the resource and the other is the consumer. The loss of any link in these interactions can potentially precipitate an extinction cascade, particularly amongst organisms that are involved in intimate interactions such as species that are tightly co-evolved. Given that different species in food webs or trophic chains may also respond differently to climate change, warming has the potential of unraveling and/or destabilizing entire communities [3•,14,15•,17–20]. A recent model suggests that evolutionary rates in a changing world will greatly affect community-wide responses in the future [21]. Moreover, as a result of climate change and other human-mediated changes across the biosphere, we can expect ecological communities to change over time and for this to lead to unpredictable new assemblages as temperatures continue to rise [17,18]. Under these scenarios, mitigation of climate change and alleviation of other environmental threats is imperative if we are to ensure that the integrity of ecosystems, communities and trophic interactions are maintained.

Climate warming and herbivore–plant–parasitoid interactions

In this paper the effects and potential consequences of climate warming on trophic interactions involving plants, insect herbivores and natural enemies, here focusing on parasitic wasps (or parasitoids) are explored. Parasitoids are insects that develop on or inside the bodies of other insects, whereas adults are free living [22]. Many parasitoids, and especially those that develop internally in their hosts ('endoparasitoids') are very limited in the range of host species and stages that they attack, making them highly susceptible to changes in the abundance of these hosts [22–25]. If a host species or population disappears locally, then its parasitoids will disappear along with it. How climate warming will affect the persistence of tritrophic interactions is the subject of ongoing debate [10,17]. Warming-induced changes in the environment may affect various aspects of the biology and ecology of food plants and insect herbivores dependent on them [26] and this may affect natural enemies to the terminal end of the food chain, in particular specialist natural enemies. Because they have narrow host ranges and develop on finite resources, parasitoids are under greater resource-related constraints than just about any other organisms in nature [22–25].

The paper will be broken down into separate sections examining the effects of warming on the biology and ecology of the three trophic levels separately. Given that insects are ectotherms, the developmental program of insects is generally closely co-ordinated with changes in temperature. However, it is less well established how changes in temperature, as well as changes in the incidence of heat waves, droughts, precipitation regimes, and so on will affect tightly linked two and three-trophic level interactions. Moreover, plant tissues contain various concentrations of nutrients, with carbon (C), nitrogen (N), and phosphorus (P) being considered as the most important, as well as amino acids [26]. Although atmospheric CO_2 concentrations are deterministic at large scales, and are rising slowly at about 2–3 ppm annually, temperatures may fluctuate dramatically over short time scales. This makes the results of studies examining responses of plants and animals to enhanced CO_2 regimes open to conjecture; alternatively, simulating heat waves accurately reflects actual events. This paper focuses on temperature-related effects on plant–herbivore–parasitoid interactions.

Physiological responses of plants to warming and effects on insect herbivores and their parasitoids

There is ample evidence that warming alone clearly affects multitrophic interactions. The effects on insect behavior and performance may be indirectly mediated through the plant [27–29], or else high temperatures — for instance those expressed in heat waves — may directly affect the insects independent of direct effects on the plant [30,31,32••,33,34]. However, as they represent the basal end of the food chain, the response of plants to a warming climate is critical if we are to elucidate effects on higher trophic level consumers. As the climate warms, we may expect physiological and metabolic responses in both native and range expanding plants that will in turn potentially affect the behavior and performance of higher trophic levels associated with them (Figure 1). More specifically, the metabolic changes in plants may be borne out on traits such as primary and secondary metabolism which play a key role in insect nutrition and plant defence responses (Figure 1).

Plant quality is determined by concentrations of primary metabolites (e.g., C, N, P and amino acids) and secondary metabolites (or allelochemicals) whose primary function is considered to be defence against antagonists such as pathogens and herbivores [35–39]. High levels of allelochemicals for instance, in plant tissues can impair the development and hence fitness of herbivores, through increased rates of mortality, extended development time and reduced adult size [23,40–43]. The development of natural enemies such as parasitoid wasps is also known to