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Climate change and biological control: the consequences of increasing temperatures on host–parasitoid interactions

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The relative thermal requirements and tolerances of hymenopteran parasitoids and their hosts were investigated based on published data. The optimal temperature (T_{opt}) for development of parasitoids was significantly lower than that for their hosts. Given the limited plasticity of insect responses to high temperatures and the proximity of T_{opt} to critical thermal maxima, this suggests that host–parasitoid interactions could be negatively affected by increasing global temperatures. A modelling study of the interactions between the diamondback moth and its parasitoid *Diadegma semiclausum* in Australia indicated that predicted temperature increases will have a greater negative impact on the distribution of the parasitoid than on its host and that they could lead to its exclusion from some agricultural regions where it is currently important.

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Introduction

Elevated concentrations of greenhouse gases in the atmosphere are leading to measureable increases in temperatures at the Earth's surface. This is likely to result in more extreme variation in local temperatures and increased frequencies and durations of heatwaves, periods of drought and extreme precipitation events. Climate change imperils global food security by compromising agricultural production, contributing to elevated food prices and increasing the risks of hunger and malnutrition [1]. Together, current agricultural practices and the conversion of land for agricultural production are responsible for approximately 30% of greenhouse gas emissions [2], exacerbating the problems that climate change poses to agriculture and leading to calls for a clear foundation for the sustainable intensification of agricultural practices [2,3]. The prevailing effects of climate change have already caused organismal range shifts and population changes, and they are increasingly considered to pose a risk to species extinctions [4].

The biological control of pests of food crops is a key ecosystem service that underpins sustainable approaches to their management, thereby providing significant fiscal and environmental benefits [5]. Classical biological control, the introduction of a natural enemy of an injurious organism from its region of origin into the region invaded by the pest, has its modern foundation in the establishment of *Rodolia cardinalis* and *Cryptochaetum iceryae* in Californian citrus groves to control the invasive scale insect, *Icerya purchasi*. Since then many successful classical biological control programs have been implemented [5], notable examples include the control of cassava mealybug (*Phenococcus manihoti*) in sub-Sharan Africa by introduction of the encyrtid parasitoid *Epidinocarsis lopezi*) [6] and management of the diamondback moth (*Plutella xylostella*) in many locations by introduction of one or more members of a parasitoid complex [7]. The impacts of climate change on host–parasitoid interactions, whether natural enemies have been deliberately introduced into new regions or whether the agents are indigenous and biological control is being supported by conservation practices, will be modulated by direct effects on the organisms involved (*e.g.* through effects on physiology and metabolism), the responses of those organisms and subsequent tri-trophic interactions. Parasitoids, which represent the third trophic level, are likely to be significantly affected by climate induced perturbations to these systems and understanding what these effects might be is of critical importance.

Thermal biology and host–parasitoid interactions

Insects are ectotherms and their body temperatures reflect the temperatures that they experience in their local environment. Insect metabolism, growth, movement and reproduction are temperature-dependent and we can begin to understand the likely impacts of climate change on host–parasitoid interactions by considering how temperature might affect relative fitness. By measuring a surrogate for fitness or 'performance' (*e.g.* development rate), the response of insects across a

Table 1

Published studies reporting development rate data from which the critical thermal limits of parasitoids and their host insects were estimated

Host				Parasitoid						
Species (Order)	CT_{min}	T_{opt}	CT_{max}	Species (all Hymenoptera)	Host stage attacked	CT_{min}	T_{opt}	CT_{max}	Temp range (°C)	References
Heliothis virescens (Lepidoptera)	13.0	31.5	35.0	*Trichogramma acacioi*	Egg	9.9	25.0	30.0	20–30	[16,17]
Diaprepes abbreviatus (Coleoptera)	11.0	26.0	30.0	*Fidiobia dominica*	Egg	9.6	27.6	30.0	9–36	[18,19]
Diaprepes abbreviatus (Coleoptera)	11.0	26.0	30.0	*Haeckeliania sperata*	Egg	11.3	31.0	35.0	9–36	[18,19]
Diaprepes abbreviatus (Coleoptera)	11.0	26.0	30.0	*Aprostocetus vaquitarum*	Egg	15.8	30.9	33.0	5–40	[20,19]
Diaprepes abbreviatus (Coleoptera)	11.0	26.0	30.0	*Quadrastichus haitiensis*	Egg	16.0	32.0	33.8	5–33	[21,19]
Ceratitis capitata (Diptera)	10.0	35.6	47.0	*Aganaspis daci*	Larva	8.5	25.0	35.0	15–35	[22,23]
Bactrocera invadens (Diptera)	9.7	30.0	35.0	*Diachasmimorpha longicaudata*	Larva	9.0	20.0	31.0	15–35	[24,25]
Bactrocera invadens (Diptera)	9.7	30.0	35.0	*Fopius arisanus*	Larva	8.0	20.0	35.0	15–35	[24,25]
Thecodiplosis japonensis (Diptera)	5.0	27.0	30.0	*Platygaster matsutama*	Larva	4.2	24.8	30.0	12–30	[26,27]
Thecodiplosis japonensis (Diptera)	5.0	27.0	30.0	*Inostemma seoulis*	Larva	8.4	26.5	30.0	12–30	[26,27]
Plutella xylostella (Lepidoptera)	7.4	30.0	38.0	*Diadegma semiclausum*	Larva	6.0	20.0	30.0	10–30	[28,29]
Spodoptera exigua (Lepidoptera)	13.0	32.0	35.0	*Microplitis manilae*	Larva	11.0	28.0	33.0	17–32	[30,31]
Macrosiphum euphorbiae (Hemiptera)	5.0	20.0	27.0	*Aphidius ervi*	Nymph	12.0	20.0	28.0	12–28	[32,33]
Apolygus lucorum (Hemiptera)	3.5	32.0	40.0	*Peristenus spretus*	Nymph	7.3	23.0	33.0	15–35	[34,35]
Diaphorina citri (Hemiptera)	10.5	30.0	41.0	*Tamarixia radiata*	Nymph	−3.6	25.0	36.0	15–35	[36,37]
Sitobion avenae (Homoptera)	4.0	29.0	30.0	*Aphidius rhopalosiphi*	Nymph	3.5	25.0	27.0	10–25	[38,39]
Diatraea saccharalis (Lepidoptera)	8.0	30.0	35.0	*Trichospilus diatraeae*	Pupa	9.4	25.0	31.0	16–31	[40,41]

range of temperatures can be estimated and used to construct Thermal Performance Curves (*TPCs*) [8••]. Typically, such curves increase gradually with temperature from the critical thermal minimum (CT_{min}, lower thermal limit of performance) to a maximum (T_{opt}, temperature at which performance is maximized) and then decline rapidly as the critical thermal maximum (CT_{max}, upper thermal limit of performance) is approached [8••]. Interpretation of *TPCs* and the implications for how organisms might be expected to respond to changes in temperature need to be exercised with care as responses to temperature of a given species typically vary between different ontongenic stages, fitness traits and individuals that have been held at different temperatures prior to the start of studies [8••,9••]. Nevertheless, provided that their constraints are appreciated and if they are constructed from appropriate data, *TPCs* can provide significant insight into the thermal biology of ectotherms and how they might respond to increasing global temperatures.

Much of the research that has investigated the responses of parasitoids to extreme temperatures has focused on lower thermal limits, with more recent studies considering how warmer conditions could lead to the decoupling of phenological synchrony between parasitoids and their hosts based on differences between these lower thermal limits [10•]. Differences between the *TPCs* of parasitoids and their hosts will result in different responses to given temperature conditions, resulting in changed relative development rates that will affect their population biology. If the critical parameters of the *TPC* for a parasitoid are lower (to the left) than those of the corresponding *TPC* for its host then increased temperatures are likely to have a greater impact on the parasitoid than on its host. The upper thermal limits for insects tend to vary much less than the lower thermal limits in response to acclimation or acclimatization, they are restricted to a narrow range that is typically close to T_{opt} and their evolution appears to be tightly constrained [9••]. Consequently, rising global temperatures are likely to pose significant problems for insects. In host–parasitoid interactions the relative nature of host and parasitoid *TPCs* will have profound consequences for the outcomes of these relationships.