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Daily temperature variation and extreme high temperatures drive performance and biotic interactions in a warming world

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We review the major patterns on the effects of daily temperature variation (DTV) and extreme high temperatures (EXT) on performance traits and the resulting outcome of biotic interactions in insects. EXT profoundly affects the outcome of all types of biotic interactions: competitive, predator–prey, herbivore–plant, host–pathogen/parasitoid and symbiotic interactions. Studies investigating effects of DTV on biotic interactions are few but also show strong effects on competitive and host–pathogen/parasitoid interactions. EXT typically reduces predation, and is expected to reduce parasitoid success. The effects of EXT and DTV on the outcome of the other interaction types are highly variable, yet can be predicted based on comparisons of the TPCs of the interacting species, and challenges the formulation of general predictions about the change in biotic interactions in a warming world.

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Introduction

There is growing interest in the effects of daily temperature variation (DTV) and extreme high temperatures (EXT) on organisms [1••,2••,3]. The relationship between individual performance and temperature, the thermal performance curve (TPC), typically has an accelerating rising part before reaching an optimal temperature, and a quickly decelerating part above the optimum until CTmax, the critical thermal maximum [4••] (Figure 1). With EXT we here mean temperatures above the optimum and near CTmax that drastically reduce performance; EXT are rarely encountered as ectotherms are mostly living below their optimal temperature [5]. Note that what is an EXT may differ depending on the performance trait measured and the state of the organisms, for example their developmental instar [4••]. DTV and EXT are intrinsically linked as increases in DTV even at temperatures below the optimum will increase the probability of exposure to EXT [3]. There are two pressing reasons to focus on DTV and EXT. First, DTV and the strength, duration and frequency of heat waves are increasing worldwide and are expected to further increase in a warming world [6,7]. Second, biological consequences of DTV and EXT can be severe, and more important than, and reverse the effect of increases in mean temperature on fitness [8].

Recent reviews that synthesized the effects of DTV and EXT mainly focused at the level of individuals and populations [1••,2••,9]. Much less is known on effects of DTV and EXT at the level of species interactions. The temperature-dependence of species interactions is, however, among the most important structuring forces driving the response of species and communities to climate change [10,11], and a major driver of climate-induced extinctions [12]. It is widely appreciated that the direct effects of temperature on population growth rate of interacting species are important for biotic interactions. A recent review discussed how DTV and EXT can influence communities either by directly affecting the relative abundances of interacting species through demographic effects, or by disrupting the phenological matching among interacting species [1••]. Yet, how DTV and EXT shape species interactions within a generation through (functional) changes in performance rather than through (numerical, cross-generational) changes in demography is an underexposed topic. Performance traits can be defined as biological rate processes with a time-dependent component [13]; in the current context of short-term biotic interactions these include, for example, growth rate, running speed and activity of immune enzymes.

We here synthesize recent work on insects that deals with effects of DTV and EXT on species interactions in the short-term through changes in performance. We first give a conceptual background how DTV and EXT can shape performance traits relevant for the outcome of species interactions. We then present an integrated overview of recent empirical studies on how different biotic interactions are modified by DTV and EXT. Finally, we

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summarize and integrate the obtained insights and identify knowledge gaps awaiting to be studied.

Effects of DTV and EXT on performance

Effects of DTV on performance

The effects of DTV on performance traits may vary from negative to positive which can be understood from the TPC (Figure 1). The nonlinearity of a function, here the TPC, causes that the same deviation from a given mean will have a different effect on performance below or above that mean, also known as Jensen's inequality [14,15•]. Moreover, because of the asymmetrical shape of the TPC, the direction of the effect of DTV on performance will depend on the mean temperature and the magnitude of DTV [1••] (Figures 1 and 2). In the rising part of an exponentially increasing TPC (Figure 1a), increasing DTV will cause a stronger increase in performance when the temperature goes above the mean than the decrease in performance when the temperature goes below the mean, resulting in a net increase in performance compared to the performance when the temperature is kept constant at the same mean (cf. Jensen's inequality [14,15•]). In contrast, DTV has no effect on performance when the rising part is linear (Figure 1b). With the mean temperature getting closer to the optimal temperature, it will get more likely that extreme temperatures will be encountered during DTV which will tend to reduce the mean performance. Around the optimal temperature, DTV will reduce performance as during the cycle EXT will be encountered (Figure 1c, d). This may also occur with strong DTV at mean temperatures in the permissive temperature range below the optimal temperature (purple scenario in Figure 2a, b), a scenario often encountered in experiments where animals are periodically exposed to heat waves (e.g. [16,17•]). At mean temperatures above the optimal temperature, hence at mean EXT, DTV will typically lead to a strong decrease in performance (Figure 1e, f).

Studies on insects testing for effects of DTV on performance traits directly relevant for short-term biotic interactions are few, except for individual growth and development rate [2••]. As can be expected conceptually (Figure 1), the effects of DTV on performance can be variable. For example, DTV that remains in the permissive temperature range can result in accelerated development, slower development or no effect on development [2••]. Also for other performance traits, effects of DTV are not always present. For example, no influence of DTV on parasitoid encapsulation by *Drosophila* hosts was detected [18•].

The thermal response of biotic interactions results from the integration of the thermal dependence of performance traits of both individuals involved in the interaction [19,20]. Given that the effect of DTV on performance at a given mean temperature will depend on the local curvature of the TPC, interacting species may experience different changes in performance depending on differences in their TPC curvature at a given mean (Figure 2a,b). In support of this, strains of *Venturia canescens* parasitic wasps with a different shape of the TPC differed in how development rate was reduced under DTV [21].

Effects of EXT on performance

EXT typically negatively affect performance traits, eventually reaching zero performance at CTmax (Figure 1). Therefore, differences in CTmax between interacting species should be predictive of the outcome of their biotic interactions under EXT (Figure 2c,d). Several studies documented EXT-induced reductions in traits directly relevant for the outcome of biotic interactions: locomotor ability [22,23] and immune function [24•,25]. Yet, responses are not general. For example, opposing effects of EXT on different immune parameters have been documented: EXT increased the melanization response but reduced the number of hemocytes in velvetbean caterpillars (*Anticarsia gemmatalis*) [26].

EXT may also been reached during DTV at temperature means below or at the thermal optimum (Figures 1c,d, and 2a,b) and thereby affect performance traits. For example, a recent study showed that the production of winged offspring (a predator escape strategy) by the green peach aphid in response to predator presence disappeared under DTV that included EXT [17•]. Inclusion of EXT during DTV has also been shown to differentially shape development rate of a herbivore and its parasitoid, with as a result the host developing faster than the parasitoid [27].

Effects of DTV and EXT on biotic interactions

Competitive interactions

Explicit effects of EXT on competitive interactions have not been investigated. Yet, one recent study looked at effects of DTV including EXT on the outcome of competitive interactions between two *Anopheles* mosquito species [28•]. The competitive superiority of *An. arabiensis* increased at high DTV (that included EXT, cfr the purple DTV scenario in Figure 2a,b) as it could better deal with the EXT than *An. quadriannulatus*. This nicely illustrates how species' differences in CTmax may determine the outcome of their competitive interactions.

Predator–prey interactions

Predation rates typically increase with warming but decrease rapidly at EXT [20,29,30••]. This has been explained by a decrease in the search activity of the predators and an increase in the time needed to handle prey (i.e. longer handling time) [29,31]. For example, EXT reduced predation rates of ladybeetles on aphids [32,33] and of predatory dragonfly larvae on newt larvae [34]. The former was due because a decrease in search/attack rate at EXT [32].

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