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Evolution of geographic variation in thermal performance curves in the face of climate change and implications for biotic interactions

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We review the recent literature on geographic variation in insect thermal performance curves (TPCs). Despite strong thermal differences, there is often no change in TPCs across geographic gradients. When shifts occur, these are mostly vertical (indicating an overall shift in performance across temperatures, that is, countergradient or cogradient variation) and less horizontal (reflecting thermal adaptation). Based on this, using a space-for-time substitution approach, we generated likely evolutionary scenarios of TPC evolution to simulate the outcome of biotic interactions under future warming. We illustrate how taking evolution of the TPCs into account may strongly impact the predicted outcome of biotic interactions under climate warming. Importantly, both the type and the magnitude of the TPC shift was identified to be crucial to determine who will be winners and losers of biotic interactions.

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Introduction

Understanding how performance changes with temperature is crucial to assess the potential of populations to deal with current and future thermal regimes [1]. The relationship between a performance trait and temperature is known as the thermal performance curve (TPC). TPCs of insects typically have a rising part until the temperature where the best performance is reached (i.e. thermal optimum, or T_{opt}). Above this temperature, performance steeply decreases until reaching the critical thermal maximum (CT_{max}), where performance becomes zero (Figure 1).

Populations across geographic gradients may experience strongly different thermal regimes. This holds both at the macrogeographic scale, for example along latitudinal and altitudinal gradients, and at the microgeographic scale, for example along urbanization gradients [2]. As a result, TPCs can strongly depend on the populations' geographic origin [3]. Studying the evolution of TPCs across geographic gradients is getting renewed interest to predict responses to climate change [1,3]. Using a space-for-time approach [4], the current TPC at a warmer site can indeed be used as a proxy to predict the TPC at a colder site under a given warming scenario.

Although it is increasingly accepted that the fate of populations to persist locally depends not only the ability to deal with warming *per se*, but also on the ability to deal with biotic interactions under warming [5], this has been much less studied. Very few studies indeed directly addressed how biotic interactions change along temperature-associated geographic gradients (e.g. [6,7]). Importantly, the outcome of biotic interactions such as consumer–resource interactions [8–10] and interspecific competition [11,12] at a given temperature can be predicted based on the TPCs of the interacting species. For example, comparing the TPCs for swimming speed of a predator and its prey, the predator attack speed was found to be lower than the prey escape speed below a certain temperature, which was suggested to be the reason of the mostly unsuccessful predator attacks below that temperature [10]. Therefore, geographic patterns of TPCs of interacting species may inform on geographic patterns of their interaction, and using a space-for-time approach also on the evolution of biotic interactions under future warming.

We here review recent work on TPCs across geographic gradients in insects and describe emerging patterns. Based on this review we then generate hypothetical scenarios of evolutionary changes in TPCs of two interacting species to infer possible patterns in the outcomes of their interactions in the face of future warming. We particularly highlight how evolution of the TPCs, often ignored in such studies, may affect the predictions of the outcome of the interaction between species in the face of climate change.

General geographic patterns in TPCs

Shifts in ectotherm TPCs along geographic gradients can show three, not mutually exclusive, patterns [13] that are visualized in Figure 1:

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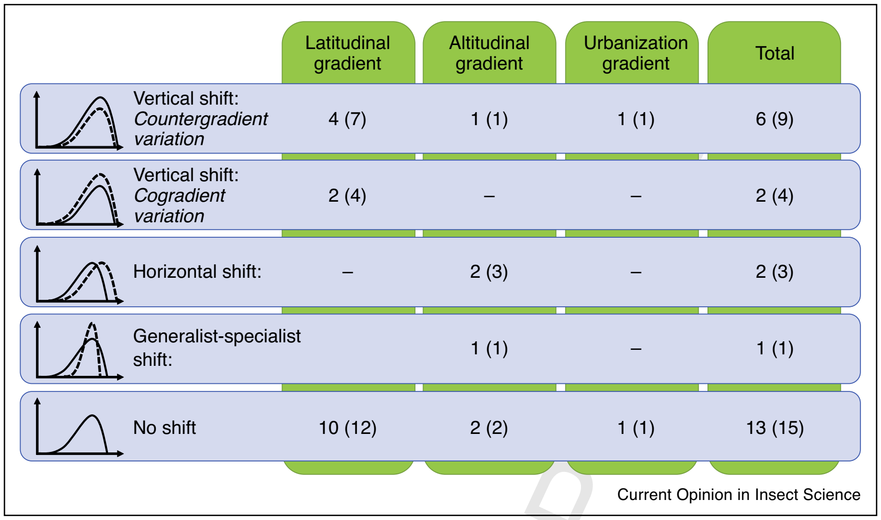
Figure 1



Schematic overview synthesizing the documented shifts in thermal performance curves (TPCs) along geographic gradients in insects. Numbers outside brackets give the total number of studies reporting a certain shift, numbers within brackets give the total numbers of traits showing a certain shift. Note that several studies reported different mode of TPC shifts for different traits (measured in the same study), resulting in an inflated 'total' number of studies (i.e. the total number of studies included in this review was 18, instead of 24).

(i) A 'horizontal shift' occurs when warm/cold-adapted populations perform better at higher/lower temperatures. This pattern is often associated with local thermal adaptation, where the maximum performance is achieved at the temperature the population is adapted to (T_{opt}), and is driven by a trade-off between performance at higher and lower temperatures [14].

(ii) A 'vertical shift' occurs when populations outperform across temperatures. This may take two forms. The scenario where populations inhabiting colder regions outperform those from warmer regions is termed countergradient variation (CnGV), as the genetic influence opposes the influence of the thermal environment. This shift, often documented for growth or development rate, is associated with stronger time constraints experienced in colder environments [15,16]. The opposite scenario where warm-adapted populations outperform cold-adapted populations along the thermal gradient, is called cogradient variation (CoGV). Although the underlying drivers of this pattern are not clear, it is often detected for morphological traits [16].

(iii) A 'generalist-specialist shift' occurs when populations adapted to more stable thermal environments have a narrower thermal performance breadth (i.e. the temperature range where performance can occur) and higher maximum performance than populations adapted to more variable thermal environments [17,18]. This trade-off is suggested to be driven by structural constraints in the thermal flexibility and stability of enzymes [19].

Many studies have been testing geographic patterns in only the extreme values of the TPC: the minimum (CT_{min}) and the maximum (CT_{max}) temperature where performance becomes zero. Recent studies on insects confirm the general patterns that CT_{min} is lower in high-latitude than in low-latitude populations, while CT_{max} shows no or only a weak latitudinal pattern (reviewed in [20]; but see e.g. [21,22]). Along altitudinal gradients, the emerging pattern is that of a higher CT_{max} at warmer, lower altitudes, and vice versa for CT_{min} (e.g. [23,24]). It is important to note that the geographic patterns in the extremes of the TPC do not automatically inform about the type of shift in the entire TPC. For example, TPCs with a different CT_{max} may still have the same T_{opt} and vice versa.

Geographic patterns in insect TPCs

To identify geographic patterns in insect TPCs, we selected recent intraspecific studies with at least two geographically separated conspecific populations, that assessed performance at ≥3 constant temperatures (the minimum requirement for constructing TPCs). We follow the definition of performance traits as biological rate processes with a time-dependent component [25]. We specifically focused on performance traits directly relevant for the outcome of biotic interactions in the short term (within a generation), thereby excluding cross-generational numerical effects.

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