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Microclimate-based macrophysiology: implications for insects in a warming world

Grant A Duffy[1], Bernard WT Coetzee[1,2], Charlene Janion-Scheepers[1] and Steven L Chown[1]

Understanding the influence of microclimates is an increasing focus of investigations of global change risks to insects. Here we review recent advances in this area in the context of macrophysiological forecasts of the impacts of warming. Some studies have suggested that risk estimates may be inaccurate owing to microclimate variation or behavioural responses. Using modelled microclimatic data we illustrate this problem, demonstrating that soil microclimates on the Australian continent will warm in concert with global climate change such that the upper thermal tolerance limits of many insects will be exceeded across much of the continent. Deeper microclimates will be cooler and more hospitable, emphasising the importance of behavioural adaptation and movement amongst microclimates as a response to environmental warming.

Address
[1] School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

Corresponding author: Duffy, Grant A (grant.duffy@monash.edu)
[2] Current address: Organisation for Tropical Studies, Scientific Services, Kruger National Park, Mpumalanga 1350, South Africa.

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Physiological tolerance data can provide valuable insight into how organisms will respond to global climate change. Macrophysiological techniques [1] are particularly useful for examining the ecological implications of forecast global change, and, due to the prominence of insects in the physiological literature, can be readily applied to this group. The extent to which various physiological traits have been used for macrophysiological studies of insects is variable (see [1] for a general review of macrophysiology), with studies focusing on thermal physiological traits being by far the most prevalent (e.g. [2–4,5••]).

The prominence of work on thermal physiology, coupled with the climatic changes predicted under future climate scenarios (most regions are expected to experience warming, with extreme heat events becoming more common [6]), means that applying macrophysiological techniques to upper thermal traits is an important starting point in predicting insect responses to global climate change. Here, therefore, we focus on insect upper thermal tolerances, reviewing recent developments in thermal physiology and highlighting the importance of microclimates in macroecological studies of small ectotherms.

Macrophysiological modelling of insect thermal tolerances

Thermal tolerances are mechanistically determined through the complex interaction of various biochemical processes [7,8]. Recent developments in biologging mean that thermal performance curves of large ectotherms can now be measured *in situ* [9•], reflecting responses to natural environmental variability. Using these techniques on insects may not currently be feasible, but thermal tolerance traits are relatively straightforward to measure experimentally. Indeed, standardised techniques can provide ecologically meaningful measures of thermal tolerance that can be interpreted and applied in a climate change context. Understanding the full ecological implications of variation in thermal tolerance clearly requires assessments that incorporate several measures of fitness [10•]. Nonetheless, standardised measures of thermal tolerance, such as the critical thermal maximum and upper lethal temperature, which are measures of survival probability under given temperature conditions, are still by far the most common metrics in the physiological literature. The volume of available data, coupled with growing appreciation of and methods for comparing and generating cross-taxon data [11••], mean that these measures of tolerance are of considerable use in macrophysiology.

Importantly, the form of physiological traits may depend on methodological context. For example, the starting temperature and rate of temperature change for physiological assays are the subject of current debate, though it is generally accepted that these factors should reflect real-world environmental conditions to maintain ecological relevance [12]. Several other factors might also influence variation in thermal tolerance traits, depending on the life stage and taxon being investigated. Oxygen limitation has been proposed as a key determinant of upper thermal limits [13,14]. Although evidence to support this hypothesis has been found for aquatic insects, the open tracheal ventilation system of adult terrestrial insects means that oxygen limitation is unlikely to impact their thermal tolerances, at least when at rest [15]. Immature terrestrial insect life stages may show oxygen limitation of thermal tolerances due to the way in which oxygen demand, relative to supply capacity, changes over the course of each instar [16].

Other factors influencing thermal tolerance traits include the effects of individual condition [12] and life stage [17,18]. Acclimation [19] and hardening [20], forms of phenotypic plasticity, may increase thermal tolerance, but their effects tend to be relatively small in the case of upper thermal tolerance of terrestrial organisms [21,22••]. Physiological tolerances also vary as a function of the magnitude, fluctuation [23,24], and exposure time of a stimulus (e.g. discussion of thermal tolerance landscapes in [25]), and can be influenced by both temporal and spatial environmental variability [24–26]. Behavioural plasticity is a further significant factor to consider, especially because over the long term it may limit physiological adaptation [27]. Thus, phenotypic plasticity, adaptive responses, and interspecific interactions must be considered when using physiological tolerance data to determine broad-scale ecological patterns and responses to broad-scale change [5••,11••].

With potential confounding factors in mind, syntheses of thermal limit studies have been used to identify macrophysiological patterns of both upper and lower thermal tolerances of various terrestrial ectotherms [2,19,22••,28–30]. Lower thermal limits show a great deal of variability, decreasing with latitude [2,28] and varying substantially across taxa [29]. By contrast, upper thermal limits are more constrained. Critical thermal maxima and other measures of upper thermal tolerance vary little, relative to their lower counterparts, amongst terrestrial taxa and across environmental gradients, and show a fixed upper limit [20,22••,28–31] (though see [32••]). The maximum values of upper thermal limits in aquatic insects are similarly conserved [15]. Due to their relatively conserved nature, and the predicted 2–4 °C rise in global mean temperatures under future climate scenarios [6], upper thermal limits are of particular interest to macrophysiologists examining responses to global climate change.

Estimates of insect thermal safety margins and warming tolerances, made using macroecological-scale climate data (e.g. [3,4,5••,33,34]), suggest that many species have a thermal buffer of several degrees before their physiological limits are exceeded by warming. Tropical and subtropical species tend to have a narrower buffer than their more temperate counterparts. However, the warming tolerances and safety margins of most insects may actually be narrower than previously estimated once the effects of microclimates are considered [5••,18,35].

Insect microclimates

Microclimates are those conditions most relevant to small ectotherms, such as insects. The fitness effects of microclimates are mediated by behaviour and physiology and it is therefore climates at these small scales that play key roles in determining the local and broader distributions of insects [18,32••,36,37••]. Measuring microclimates at macroecological scales has, until recently, been challenging (though see [38•], e.g. of how biophysical models can be used for species-specific macroecological projections). Importantly, however, local studies, where microclimate has been measured *in situ*, indicate that microclimates differ from values taken from coarser-resolution weather station or interpolated climate data [1,5••,18,35,36]. For example, soil surface temperatures are often warmer than those indicated by standard climate data, but the thermal insulation effects of soil mean that subterranean temperatures decline with depth, generating significantly cooler microclimates below ground [32••]. Comparable microclimate heterogeneity has been recorded in forest canopy environments [36,39]. Therefore, the influence of microclimate must be considered when assessing the responses of smaller organisms, such as insects, to global change [38•,39,40].

Recent advances in environmental modelling mean that approximations of some microclimates are available at a global scale [41••,42]. The 'microclim' environmental dataset comprises multiple data layers, which represent the modelled environmental conditions of soil microhabitats at various depths in three generic substrata under multiple shade conditions. Modelled environmental data, which represent present-day conditions, has been validated against direct measurements across Australia [42] and the United States [41••]. Owing to the close correlation between land surface temperature and soil microclimates, relatively straightforward statistical modelling can be used to estimate future microclimate conditions. In consequence, macrophysiological techniques can be used to forecast the ecological implications of soil microclimates under future climate scenarios (Figure 1).

Microclimate-based macrophysiology

Macrophysiological approaches using microclimate estimates are demonstrated here using a case study of current and future Australian soil microclimates (Box 1). Although the approach used here is relatively straightforward, more complex scenarios can be explored by incorporating sensitivity analyses and additional traits of significance, such as the way in which desiccation sensitivity of particular life stages might alter forecasts based solely on thermal tolerance traits [43]. The scope for adaptation, in the sense of [11••], must also be considered when using macrophysiological techniques to forecast ecological outcomes spatially and temporally. The capacity of various mechanisms to alter physiological tolerances will depend upon the physiological trait or traits of interest and the magnitude, speed, and duration of change. For insects, a limit to