Mechanistic models for predicting insect responses to climate change
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Mechanistic models of the impacts of climate change on insects can be seen as very specific hypotheses about the connections between microclimate, ecophysiology and vital rates. These models must adequately capture stage-specific responses, carry-over effects between successive stages, and the evolutionary potential of the functional traits involved in complex insect life-cycles. Here we highlight key considerations for current approaches to mechanistic modelling of insect responses to climate change. We illustrate these considerations within a general mechanistic framework incorporating the thermodynamic linkages between microclimate and heat, water and nutrient exchange throughout the life-cycle under different climate scenarios. We emphasise how such a holistic perspective will provide increasingly robust insights into how insects adapt and respond to changing climates.

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Correlation versus mechanism in modelling insect responses to climate change
Biology has entered the age of data. Our access to information, and its rate of accumulation, is unprecedented. The sheer resolution of data available for use has led to new statistical methods and computational techniques that are able to describe and predict complex relationships between variables [1,2]. Correlative approaches for analysing detailed data are important tools in a variety of applications. However, when projecting to novel scenarios, correlative models make one crucial assumption: that the relationships inferred from observed data will hold beyond the range of our observations. This issue is of particular concern when trying to predict species’ responses to climate change, which will present novel environments to organisms [3,4**,5].

To make predictions of insect responses to climate change we require models that behave realistically under novel scenarios [4**]. Mechanistic models can be defined as those that explicitly incorporate a system’s sub-processes to predict a response, as opposed to a model concerned with the statistical description of a phenomenon [6]. For this reason, mechanistic models are less vulnerable to the well-known pitfalls of extrapolation (Figure 1). The main trade-off is that we require an in-depth knowledge of the components relevant to predicting a particular system, such as classical mechanics in Figure 1. Predicting insect responses to climate change requires an understanding of how their underlying physiology, homeostatic requirements, and adaptive potential mediate their responses to changing environments.

Various processes occurring at molecular or ecological levels are involved in how organisms respond to climate, but each can be expressed in the universal currencies of energy and mass, which must be conserved irrespective of the scale of inquiry. Insect behaviour is largely driven by a need to meet certain homeostatic requirements. Stoichiometric homeostasis causes insects to preferentially select food that contains more of a required nutrient [7,8]. Likewise, ectothermic insects must defend their thermal target by behaviourally regulating body-temperature through the selection of different microhabitats [9–11]. Nutritional and thermal demands also interact strongly with water requirements [12]. The ability to meet these requirements determines rates of development, growth and reproduction, which obey universal energetic constraints across a wide range of insects and life-stages [13,14,15*,16*]. Such potential rates interact with the seasonal windows for development, growth and reproduction, necessitating appropriate phenological responses [17,18]. In turn, generation times and reproductive output affect rates of evolution and an insect’s ability to adapt to new selection pressures [19]. Although insects have significant adaptive ability compared to other animals, they must nonetheless obey these fundamental constraints.

Here we outline some important considerations when developing mechanistic models aiming to predict insect
Mechanistic models can be particularly useful for prediction under novel circumstances. Using the observed trajectory of a grasshopper in flight, extrapolation by a correlative model makes an unrealistic prediction of the grasshopper’s future position. Building the laws of motion into a mechanistic model, such as gravity and air resistance, improves the prediction and applies anywhere these physical rules operate, for example, on a novel planet. Likewise, building in known biological processes into mechanistic models will improve predictions of species’ responses to novel climatic circumstances.

responses to environmental change. Key issues include stage-specific considerations of insect life-cycles, the microclimates they inhabit, and their adaptive potential. Most of these issues were emphasised 85 years ago by Uvarov in his manifesto on insects and climate [20], which distilled 1100 papers on the responses of insects to climate. Here we aim to show how, with the application of new thermodynamically-based modelling approaches, Uvarov’s vision can now be more readily achieved.

Microclimates: the environmental stage for the insect energy budget

The ecological diversity of insects is reflected in the range of microclimates they inhabit which in turn influence insect physiology [21]. These microclimates vary greatly and may act as buffers or amplifiers of weather conditions [22,23**,24]. Within soil, microclimate conditions vary with depth and soil type, whereby soil microclimates can buffer above-ground conditions even at near-surface soil layers [21,25]. The interactions between insects and biotic habitats such as plants generates highly variable microclimates, which are often dominated by host plant physiology rather than weather conditions [26].

Microclimatic conditions can be measured directly but manually collecting such data at ecologically relevant temporal and spatial scales is usually unfeasible [5,27**]. Alternatively, we can exploit the physics of energy and mass exchange, as well as historical and projected climatic data, to estimate microclimates across large scales of time and space [28]. Behavioural strategies regulate the selection of microclimates and determine heat and water budgets [23**]. With enough information, a model that combines microclimatic options and behavioural strategies can be constructed to infer an organism’s heat and water budget and, thus, vital rates through time (Figure 2) [29*].

Matching the microclimate to the life-cycle stage

Life-stages of insects differ in mobility, and thus exposure to microclimate variability. The survival of immobile life-stages, such as eggs or pupae, is closely tied to their microenvironment, which may be behaviourally selected by preceding life-stages [30]. The microclimatic variation between successive stages in a life-cycle must be adequately captured in mechanistic models, including stage-specific sensitivities and fitness measures [31–33,34*]. Additionally, as the body size of adult insects is usually fixed by pupation, nutrients acquired during the larval stage strongly determines reproductive output, and adult fitness in general [35,36].

A range of physiologically-based models have been developed that use statistical descriptions of observed growth and development to predict stage specific responses [37–43]. Detailed species-specific models derived from statistical descriptions of experimental data or of particular microclimates can be highly successful [44]. More generality and robustness to novel conditions can potentially be achieved if models are developed from general theories about metabolism which are grounded in thermodynamic principles. A promising approach is to develop models based on Dynamic Energy Budget (DEB) theory that integrate the dynamic processes of growth, development, maintenance and reproduction throughout the life-cycle as a function of temperature and food availability [45]. At each stage the organism’s energy and mass budget depends on the conditions experienced in previous stages. Such models have been used to explain species-specific phenomena [16*] and also general energetic patterns within stages that hold across species [14,46]. A key advantage of the DEB framework is its generic nature, leading to its application to hundreds of diverse species from bacteria to vertebrates [47].

Evolutionary responses to changing climates

Although insects possess varied behavioural and physiological mechanisms to help them mitigate the effects of changing environments [48*], the capacity for adaptation via evolution will further determine a species’ success. Attempts to understand the evolutionary responses of insects to changing environmental conditions, including climate change, have focussed on various life-history responses or traits such as thermal resistance [49,50].
Figure 2

Model predictions for *Heteronympha merope* include growth trajectories and microclimate estimates under four simulation scenarios (top-left: baseline; top-right: warming; bottom-left: larger body-size; bottom-right: warming and larger body-size). The simulations were implemented in the R package NicheMapR. Body temperatures of the different life-history stages within their respective microclimates were determined at each hour of the simulation, and temperature-dependent physiological rates, including growth and maturation (development), were estimated from published datasets (Barton et al. in prep). Development and growth through the annual life-cycle of *H. merope* is tracked throughout the simulation, shown in the corresponding growth trajectory figures, in which the solid blue line represents the food water content as driven by soil moisture (dips in the line represent dry spells). The active stages (larvae and imago) were allowed to thermoregulate behaviourally within their microclimates. Hours in which predicted body temperature could facilitate sustained activity are indicated by the grey line in the microclimate figure. The points where the chosen depth drops 15 cm (brown line) indicate retreat to deep, humid conditions until the next rainfall event. Shade selection (dark green line) in the nocturnal larval stages acts to make the animal warmer and is thus reduced under warming, in contrast to the diurnal adult stage. Predicted body temperatures in these different states (red line), as well as the corresponding air temperature (at 1.2 m high, light blue line) for each, hour are also shown.

Typically, such traits are assessed for variation across and within populations, using quantitative genetic approaches to assess the heritability of traits and how far they can be shifted under directional selection. Between-population studies tend to focus on the extent to which population variation is genetically determined, through transplant experiments or, more commonly, comparisons in common environments.

Mechanistic models can be used to identify the types of traits and environmental conditions that should be assessed in determining whether insects are able to adapt through evolution under climate change [51]. Models can then explore the role of heritable variation and likelihood of evolutionary shifts in survival and distribution under climate change [52,53]. Such models are expected to improve predictions, and lead to an understanding of
adaptive changes that are predicted to occur or that have already been observed.

Mechanistic models combining genetic variation and predicted impacts of climate change can also be used to explore cases where evolved responses might be expected, but have not yet occurred. Such evolutionary delays to adaptation may occur in plant-insect systems that are dependent on phenological synchrony between insects and their host plant, where each trophic level has specific sensitivities and evolvability under climate change [54,55]. These sensitivities can be better quantified by recent advances in the molecular basis of temperature responses, which feed into mechanistic models that predict seemingly complex phenological responses with the regulatory dynamics of only a small number of genes [56].

Mechanistic models may also be useful in identifying the types of traits likely to exhibit evolutionary constraints and reduced adaptive potential under climate change. Insect traits are expected to show reduced narrow-sense heritability and evolvability as they approach extremes within this space, unless there are some major adjustments in an organism's development. Low evolvabilities occur commonly for traits scored in insects [57] but they are rarely considered from the perspective of potential limits [58]. Conversely, by identifying limits to evolutionary changes in development, voltinism and thermal performance, evolutionary studies can help define the parameter space within which traits can be altered, or where traits are invariant and result in vulnerability [59]. Trait limits associated with climate change vulnerability should be testable through a phylogenetic framework [60]. Such analyses have highlighted lineages where evolutionary shifts are expected to be achievable as opposed to being constrained due to phylogenetic inertia [58].

**Mechanistically modelling insect responses to changing climate: an example**

To predict how insect phenologies and life-cycle bioenergetics will respond to changing climates, mechanistic models must ideally account for the microclimatic, stage-specific, and evolutionary processes discussed above. To illustrate how this can be achieved, we provide an example analysis of from a model we are developing for the Common Brown butterfly, *Heteronympha merope* (Figure 2). This species has an annual life-cycle, and we aim to predict how changes in climate might alter the timing of adult emergence, and whether evolution to a larger adult body size leads to further shifts in phenology.

To begin, the microclimates of each life-history stage are estimated using the NicheMapR package (https://github.com/mrke/NicheMapR/releases). Although the larval and imago stages can behaviourally buffer themselves against unfavourable environments by seeking shade and moving underground to more suitable hydric and thermal conditions, the egg and pupal stages remain at a fixed location. With our estimates of microclimate conditions, the life-cycle energetics (developmental, growth, condition, and reproduction) of the Common Brown are then captured by an insect DEB model (detailed in [16]). The effect of evolution to a larger body size (and associated life-history trade-offs [61]) is compared assuming inheritable genetic variation for size available to selection. Finally, climatic conditions under a moderate warming scenario are tested by adding 3 °C to the air temperature data from which microclimates are derived.

We see a strong effect of warming on earlier larval stages because these stages have a greater sensitivity to temperature, despite their capacity to behaviourally thermoregulate (Figure 2) [62]. Large shifts in phenology are observed, with pupation occurring earlier in the year under warming [63]. The adult consequently emerges earlier in spring in the warming scenario, potentially reducing survival to the next suitable oviposition time in autumn because of life-span constraints. The effect of warming on soil moisture early in the year is also particularly pronounced. However, there is no major predicted phenological effect of a 1.7-fold increase in body size.

**Concluding remarks**

In 1931, Uvarov wrote that predicting insect responses into the future ‘can be done only on the basis of a most intimate knowledge of the pest and of its relations to its environment, i.e., of a thorough understanding of the whole bewildering complex of environmental factors and of the responses thereto of the insect’. Mechanistic models based on fundamental and general physical principles go some way to incorporating this complexity, and can be particularly powerful at capturing the direct impacts of climate.

One impediment to mechanistic modelling is the large biological data requirement for model parameterisation. This burden will lessen as methods emerge for more efficiently phenotyping individuals, which will lower the costs of obtaining required inputs for the model. For example, the thermal response of insect eggs to temperature gradients and diurnal cycles can be explored experimentally through rearing them in thermocyclers [64]. Insects in particular will benefit from such technologies due to their small size and fast development times.

Biotic interactions and evolutionary responses loom as an additional challenge in the complex puzzle of insect responses to climate change. But, as Uvarov also said, ‘It is possible to imagine an insect with no natural enemies and without any need to compete for food, shelter,
etc., . . . but an insect living under natural conditions and yet free from climatic influences is an absurdity' [20]. Capturing the direct climatic responses with the kind of detail we illustrate in our example above permits us to at least define the boundaries of the problem — that is, to lay out the ‘thermodynamic edge pieces’ of the puzzle [65]. We are then in a stronger position to tackle other kinds of interactions that may be needed for sufficient realism. For these reasons we expect mechanistic models, and the underpinning science on which they are built, to become increasingly important tools for predicting and understanding insect responses to climate change.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

● of special interest

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A comparison of different mechanistic models for insect growth.


A whole life-cycle Dynamic Energy Budget (DEB) model applied to holometabolous insects for the first time. Insects posed unique problems to the standard DEB framework that were addressed in this study.


A comprehensive discussion of the importance of microclimate heterogeneity to small organisms. The authors provide general rules for how macroclimates are translated into microclimates.


A review of recent advances in insect microclimate-based macrophysiology in the context of macrophysiological forecasts of the impacts of warming.


Through the development of a species-specific biophysical model, the authors show the importance of biophysics and behaviour for studying biodiversity consequences of global climate change at multiple spatial and temporal scales.


This study shows how the use of macroclimate temperatures (rather than microclimate temperatures) can cause the overestimation of warming tolerances in insects, resulting in errors when predicting persistence and distribution shifts under changing climates.


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A review of the role of different types of plastic responses in insects within the context of climate change.


This study demonstrates how mechanistic models of insect populations dynamics can account for unobserved properties and constraints, such as differences between laboratory and field conditions, to derive reliable inferences on the environmental dependence of insects.


An example of how modern techniques can reduce the cost associated with obtaining data inputs required for the parameterisation of mechanistic models.