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Abstract: 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 emphasize how such a holistic perspective will provide increasingly robust insights into how insects adapt and respond to changing climates.

Dear Dr Kostal and Sinclair,

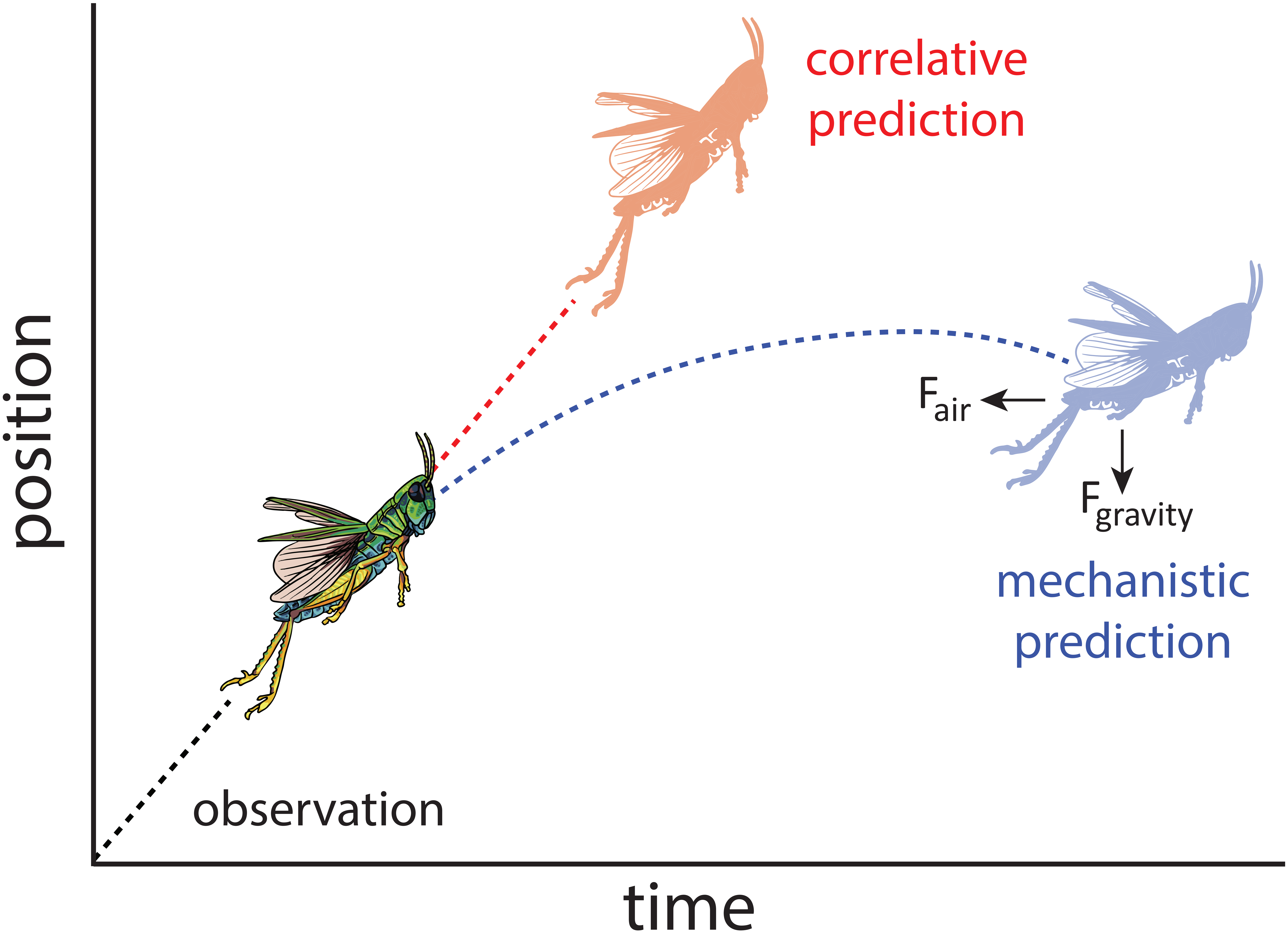
Thank you for considering our manuscript “Mechanistic models for predicting insect responses to climate change” for consideration in the Global Change Biology special issue of Current Opinions in Insect Science.

Our manuscript provides an overview of mechanistic models of insect responses to climate, emphasising the importance of understanding microclimates, the phenology of life cycles, the power of general theories of metabolism, and evolutionary responses.

We have made all changes to the MS suggested by you and by the reviewers.

We hope you find it suitable for publication in the special issue.

Sincerely,
Michael Kearney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***Highlights (for review)**

- Mechanistic models incorporate knowledge of subprocesses to predict higher level phenomena.
- We identify key subprocesses for mechanistically predicting insect responses to climate change.
- The insect microclimate, life-cycle, and evolutionary responses in this context are reviewed.
- An illustrative example for the Common Brown butterfly under climate change is presented.

COIS Review:

# Mechanistic models for predicting insect responses to climate change

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## Abstract

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 emphasize how such a holistic perspective will provide increasingly robust insights into how insects adapt and respond to changing climates.

## Correlation vs. 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 [3–5].

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 [13–16]. 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 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 1,100 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 [22–24]. 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 [31–34]. 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

While 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]. 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 invariable 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). While 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 heritable 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 – i.e. 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


1. Araujo MB, New M: **Ensemble forecasting of species distributions**. *Trends Ecol. Evol.* 2007, **22**:42–47.

2. Elith J, Graham C, Anderson R, Dudik M, Ferrier S, Guisan A, Hijmans R, Huettmann F, Leathwick J, Lehmann A, et al.: **Novel methods improve prediction of species' distributions from occurrence data**. *Ecography (Cop.).* 2006, **29**:129–151.

3. Veloz SD, Williams JW, Blois JL, He F, Otto-Bliesner B, Liu Z: **No-analog climates and shifting realized niches during the late quaternary: Implications for 21st-century predictions by species distribution models**. *Glob. Chang. Biol.* 2012, **18**:1698–1713.

4. Hill MP, Thomson LJ: **Species distribution modelling in predicting response to climate change**. In *Climate Change and Insect Pests*. Edited by Björkman C, Niemelä P. CABI (Centre for Agriculture and Biosciences International); 2015:16–37.

5. Battisti A, Larsson S: **Climate change and insect distribution range [Internet]**. In *Climate change and insect pests.* Edited by Björkman C, Niemelä P. CABI (Centre for Agriculture and Biosciences International); 2015.

6. Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C, Hartig F, Kearney MR, Morin X, Römermann C, Schröder B, et al.: **Correlation and process in species distribution models: Bridging a dichotomy**. *J. Biogeogr.* 2012, **39**:2119–2131.

7. Simpson SJ, Raubenheimer D: *The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity [Internet]*. Princeton University Press; 2012.

8. Lee KP, Simpson SJ, Clissold FJ, Brooks R, Ballard JWO, Taylor PW, Soran N, Raubenheimer D: **Lifespan and reproduction in Drosophila: New insights from nutritional geometry. [Internet]**. *Proc. Natl. Acad. Sci. U. S. A.* 2008, **105**:2498–503.

9. Heinrich B: *The Hot-blooded Insects: Strategies and Mechanisms of Thermoregulation [Internet]*. Harvard University Press; 1993.

10. Jones JC, Oldroyd BP: **Nest Thermoregulation in Social Insects**. *Adv. In Insect Phys.* 2006, **33**:153–191.

11. Kingsolver JG: **Thermoregulation and flight in Colias butterflies: elevational patterns and mechanistic limitations.** *Ecology* 1983, **64**:534–545.

12. Chown SL, Sørensen JG, Terblanche JS: **Water loss in insects: An environmental change perspective [Internet]**. *J. Insect Physiol.* 2011, **57**:1070–1084.

13. Maino JL, Kearney MR: **Ontogenetic and interspecific scaling of consumption in insects**. *Oikos* 2015, **124**:1564–1570.

14. Maino JL, Kearney MR: **Ontogenetic and Interspecific Metabolic Scaling in Insects [Internet]**. *Am. Nat.* 2014, **184**:695–701.

15. Maino JL, Kearney MR: **Testing mechanistic models of growth in insects**. *Proc. R. Soc. B Biol. Sci*. 2015, **282**:20151973.

16. Llandres ALAL, Marques GMGM, Maino JL, Kooijman SALM, Kearney MR, Casas J: **A dynamic energy budget for the whole life-cycle of holometabolous insects**. *Ecol. Monogr.* 2015, **85**:353–371.

17. Bradshaw WE, Holzapfel CM: **Evolutionary response to rapid climate change.** *Science* 2006, **312**:1477–1478.

18. Tauber MJ, Tauber CA: **Insect Seasonality: Diapause Maintenance, Termination, and Postdiapause Development**. *Annu. Rev. Entomol.* 1976, **21**:81–107.

19. Willi Y, Hoffmann AA: **Demographic factors and genetic variation influence population persistence under environmental change [Internet]**. *J. Evol. Biol.* 2009, **22**:124–133.

20. Uvarov BP: **Insects and climate**. *Trans. Entomol. Soc. London* 1931, **79**:1–232.

21. Willmer P: **Microclimate and the environmental physiology of insects [Internet]**. *Adv. In Insect Phys.* 1982, **16**:1–57.

22. Potter KA, Arthur Woods H, Pincebourde S: **Microclimatic challenges in global change biology**. *Glob. Chang. Biol.* 2013, **19**:2932–2939.

23. Woods HA, Dillon ME, Pincebourde S: **The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change [Internet]**. *J. Therm. Biol.* 2015, **54**:86–97.

24. Kuhrt U, Samietz J, Hohn H, Dorn S: **Modelling the phenology of codling moth: Influence of habitat and thermoregulation**. *Agric. Ecosyst. Environ.* 2006, **117**:29–38.

25. Ackerman RA: *Physical factors affecting the water exchange of buried reptile eggs*. Cambridge University Press Cambridge; 1991.

26. Pincebourde S, Woods HA: **Climate uncertainty on leaf surfaces: The biophysics of leaf microclimates and their consequences for leaf-dwelling organisms**. *Funct. Ecol.* 2012, **26**:844–853.

27. Duffy GA, Coetzee BWT, Janion-Scheepers C, Chown SL: **Microclimate-based macrophysiology: Implications for insects in a warming world**. *Curr. Opin. Insect Sci.* 2015, doi:10.1016/j.cois.2015.09.013.

28. Kearney MR, Shamakhy A, Tingley R, Karoly DJ, Hoffmann AA, Briggs PR, Porter WP: **Microclimate modelling at macro scales: A test of a general microclimate model integrated with gridded continental-scale soil and weather data**. *Methods Ecol. Evol.* 2014, **5**:273–286.

29. Bonebrake TC, Boggs CL, Stamberger JA, Deutsch CA, Ehrlich PR: **From global change to a butterfly flapping: biophysics and behaviour affect tropical climate change impacts. [Internet]**. *Proc. Biol. Sci.* 2014, **281**.

30. Eilers S, Pettersson LB, Ockinger E: **Micro-climate determines oviposition site selection and abundance in the butterfly Pyrgus armoricanus at its northern range margin**. *Ecol. Entomol.* 2013, **38**:183–192.

31. Kingsolver JG, Arthur Woods H, Buckley LB, Potter KA, MacLean HJ, Higgins JK: **Complex life cycles and the responses of insects to climate change**. *Integr. Comp. Biol.* 2011, **51**:719–732.

32. Potter KA, Davidowitz G, Arthur Woods H: **Cross-stage consequences of egg temperature in the insect Manduca sexta**. *Funct. Ecol.* 2011, **25**:548–556.

33. Barton MG, Terblanche JS: **Predicting performance and survival across topographically heterogeneous landscapes: The global pest insect Helicoverpa armigera (Hubner, 1808) (Lepidoptera: Noctuidae)**. *Austral Entomol.* 2014, **53**:249–258.

34. Pincebourde S, Casas J: **Warming tolerance across insect ontogeny: Influence of joint shifts in microclimates and thermal limits**. *Ecology* 2015, **96**:986–997.

35. Rivero a, Giron D, Casas J: **Lifetime allocation of juvenile and adult nutritional resources to egg production in a holometabolous insect. [Internet]**. *Proc. Biol. Sci.* 2001, **268**:1231–7.

36. Boggs CL, Freeman KD: **Larval food limitation in butterflies: effects on adult resource allocation and fitness. [Internet]**. *Oecologia* 2005, **144**:353–61.

37. Focks DA, Haile DG, Daniels E, Mount GA: **Dynamic Life Table Model for Aedes aegypti (Diptera: Culicidae): Analysis of the Literature and Model Development**. *J. Med. Entomol.* 1993, **30**:1003–1017.

38. Focks DA, Haile DG, Daniels E, Mount GA: **Dynamic life table model for Aedes aegypti (Diptera: Culicidae): simulation results and validation**. *J. Med. Entomol.* 1993, **30**:1019–1028.

39. Sutherst RW, Maywald G: **A Climate Model of the Red Imported Fire Ant , Solenopsis invicta Buren ( Hymenoptera : Formicidae ): Implications for Invasion of New Regions , Particularly Oceania A Climate Model of the Red Imported Fire Ant , Solenopsis invicta Buren ( Hymenoptera : F**. *Popul. Ecol.* 2005, **34**:317–335.

40. Sutherst RW, Maywald GF: **Climate-matching for quarantine, using CLIMEX**. *Plant Prot. Q.* 1991, **6**:3–7.

41. Sutherst RW, Maywald GF: **A computerised system for matching climates in ecology**. *Agric. Ecosyst. Environ.* 1985, **13**:281–299.

42. Gutierrez AP, Ponti L: **Eradication of invasive species: why the biology matters. [Internet]**. *Environ. Entomol.* 2013, **42**:395–411.

43. Tobin PC, Nagarkatti S, Loeb G, Saunders MC: **Historical and projected interactions between climate change and insect voltinism in a multivoltine species**. *Glob. Chang. Biol.* 2008, **14**:951–957.

44. Régnière J, St-Amant R, Duval P: **Predicting insect distributions under climate change from physiological responses: Spruce budworm as an example**. *Biol. Invasions* 2012, **14**:1571–1586.

45. Kooijman SALM: *Dynamic energy budget theory for metabolic organisation [Internet]*. Cambridge University Press; 2010.

46. Maino JL, Pirtle EP, Kearney MR: **The effect of egg size on hatch time and metabolic rate: theoretical and empirical insights on developing insect embryos**. *Funct. Ecol. (Online Early View)* 2016, [no volume].

47. Kooijman SALM: **Waste to hurry: dynamic energy budgets explain the need of wasting to fully exploit blooming resources [Internet]**. *Oikos* 2013, **122**:348–357.

48. Sgrò CM, Terblanche JS, Hoffmann AA: **What Can Plasticity Contribute to Insect Responses to Climate Change? [Internet]**. *Annu. Rev. Entomol.* 2016, **61**:433–452.

49. Bradshaw WE, Holzapfel CM: **Genetic response to rapid climate change: it's seasonal timing that matters [Internet]**. *Mol. Ecol.* 2008, **17**:157–166.

50. Hoffmann AA, Sgro CM: **Climate change and evolutionary adaptation [Internet]**. *Nature* 2011, **470**:479–485.

51. Gienapp P, Reed TE, Visser ME: **Why climate change will invariably alter selection pressures on phenology [Internet]**. *Proc. R. Soc. B-Biological Sci.* 2014, **281**:8.

52. Kearney MR, Porter WP, Williams C, Ritchie S, Hoffmann AA: **Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: The dengue mosquito *Aedes aegypti* in Australia**. *Funct. Ecol.* 2009, **23**:528–538.

53. Erguler K, Smith-Unna SE, Waldock J, Proestos Y, Christophides GK, Lelieveld J, Parham PE: **Large-Scale Modelling of the Environmentally-Driven Population Dynamics of Temperate Aedes albopictus (Skuse) [Internet]**. *PLoS One* 2016, **11**:28.

54. van Asch M, Tienderen PH, Holleman LJM, Visser ME: **Predicting adaptation of phenology in response to climate change, an insect herbivore example [Internet]**. *Glob. Chang. Biol.* 2007, **13**:1596–1604.

55. van Asch M, Salis L, Holleman LJM, van Lith B, Visser ME: **Evolutionary response of the egg hatching date of a herbivorous insect under climate change [Internet]**. *Nat. Clim. Chang.* 2013, **3**:244–248.

56. Satake A, Kawagoe T, Saburi Y, Chiba Y, Sakurai G, Kudoh H: **Forecasting flowering phenology under climate warming by modelling the regulatory dynamics of flowering-time genes. [Internet]**. *Nat. Commun.* 2013, **4**:2303.

57. Hansen TF, Pelabon C, Houle D: **Heritability is not Evolvability [Internet]**. *Evol. Biol.* 2011, **38**:258–277.

58. Kellermann V, Loeschcke V, Hoffmann AA, Kristensen TN, Fløjgaard C, David JR, Svenning JC, Overgaard J: **Phylogenetic Constraints In Key Functional Traits Behind Species' Climate Niches: Patterns Of Desiccation And Cold Resistance Across 95 Drosophila Species [Internet]**. *Evolution (N. Y).* 2012, **66**:3377–3389.

59. Van Dyck H, Bonte D, Puls R, Gotthard K, Maes D: **The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? [Internet]**. *Oikos* 2015, **124**:54–61.

60. Buckley LB, Kingsolver JG: **Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change [Internet]**. In *Annual Review of Ecology, Evolution, and Systematics, Vol 43*. Edited by Futuyma DJ. Annual Reviews; 2012:205–226.

61. Maino JL, Kearney MR, Nisbet RMRMRM, Kooijman SALM: **Reconciling theories for metabolic scaling. [Internet]**. *J. Anim. Ecol.* 2014, **83**:20–9.

62. Briscoe NJ, Porter WP, Sunnucks P, Kearney MR: **Stage-dependent physiological responses in a butterfly cause non-additive effects on phenology [Internet]**. *Oikos* 2012, **121**:1464–1472.

63. Kearney MR, Briscoe NJ, Karoly DJ, Porter WP, Norgate M, Sunnucks P: **Early emergence in a butterfly causally linked to anthropogenic warming. [Internet]**. *Biol. Lett.* 2010, **6**:674–677.

64. Kong J, Axford J, Hoffmann A, Kearney MR: **Novel applications of thermocyclers for phenotyping invertebrate thermal responses**. *Methods Ecol. Evol. (Online Early View)* 2016, [no volume].

65. Kearney MR: **Activity restriction and the mechanistic basis for extinctions under climate warming**. *Ecol. Lett.* 2013, **16**:1470–1479.

## Highlighted references


4. Hill MP, Thomson LJ: **Species distribution modelling in predicting response to climate change**. In *Climate Change and Insect Pests*. Edited by Björkman C, Niemelä P. CABI (Centre for Agriculture and Biosciences International); 2015:16–37.

** A review of different current approaches in predicting species distribution data (correlative or 'environmental niche models' and mechanistic models).

15. Maino JL, Kearney MR: **Testing mechanistic models of growth in insects**. *Proc. R. Soc. B Biol. Sci.* 2015, **282**:20151973.

* A comparison of different mechanistic models for insect growth.

16. Llandres ALAL, Marques GMGM, Maino JL, Kooijman SALM, Kearney MR, Casas J: **A dynamic energy budget for the whole life-cycle of holometabolous insects**. *Ecol. Monogr.* 2015, **85**:353–371.

* 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.

23. Woods HA, Dillon ME, Pincebourde S: **The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change [Internet]**. *J. Therm. Biol.* 2015, **54**:86–97.

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

27. Duffy GA, Coetzee BWT, Janion-Scheepers C, Chown SL: **Microclimate-based macrophysiology: Implications for insects in a warming world**. *Curr. Opin. Insect Sci.* 2015, doi:10.1016/j.cois.2015.09.013.

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

29. Bonebrake TC, Boggs CL, Stamberger JA, Deutsch CA, Ehrlich PR: **From global change to a butterfly flapping: biophysics and behaviour affect tropical climate change impacts. [Internet]**. *Proc. Biol. Sci.* 2014, **281**.

* 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.

34. Pincebourde S, Casas J: **Warming tolerance across insect ontogeny: Influence of joint shifts in microclimates and thermal limits**. *Ecology* 2015, **96**:986–997.

* 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.

48. Sgrò CM, Terblanche JS, Hoffmann AA: **What Can Plasticity Contribute to Insect Responses to Climate Change? [Internet]**. *Annu. Rev. Entomol.* 2016, **61**:433–452.

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

53. Erguler K, Smith-Unna SE, Waldock J, Proestos Y, Christophides GK, Lelieveld J, Parham PE: **Large-Scale Modelling of the Environmentally-Driven Population Dynamics of Temperate Aedes albopictus (Skuse) [Internet]**. *PLoS One* 2016, **11**:28.

* 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.

64. Kong J, Axford J, Hoffmann A, Kearney MR: **Novel applications of thermocyclers for phenotyping invertebrate thermal responses**. *Methods Ecol. Evol. (Online Early View)* 2016, [no volume].

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

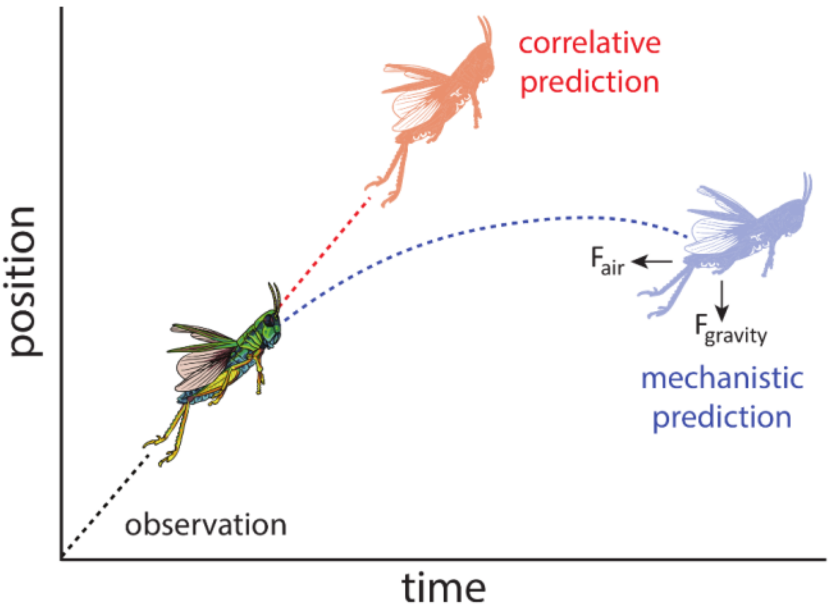
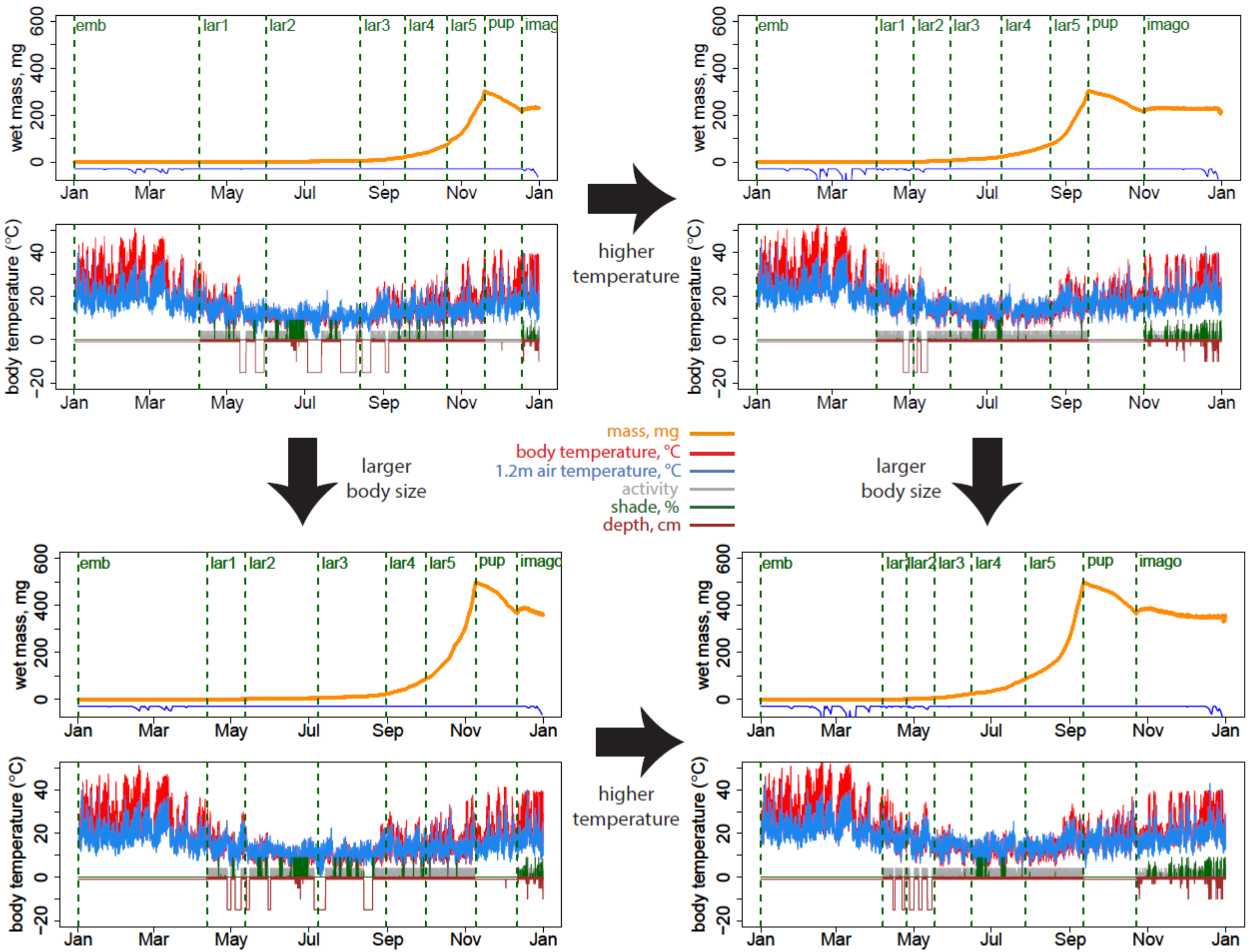



**Figure 1.** Mechanistic models can be particularly useful for prediction under novel circumstances. Using the observed trajectory of a grasshopper in flight, extrapolation by a correlative model makes an unrealistic prediction of the grasshopper's future position. Building the laws of motion into a mechanistic model, such as gravity and air resistance, improves the prediction and applies anywhere these physical rules operate, e.g. on a novel planet. Likewise, building in known biological processes into mechanistic models will improve predictions of species' responses to novel climatic circumstances.

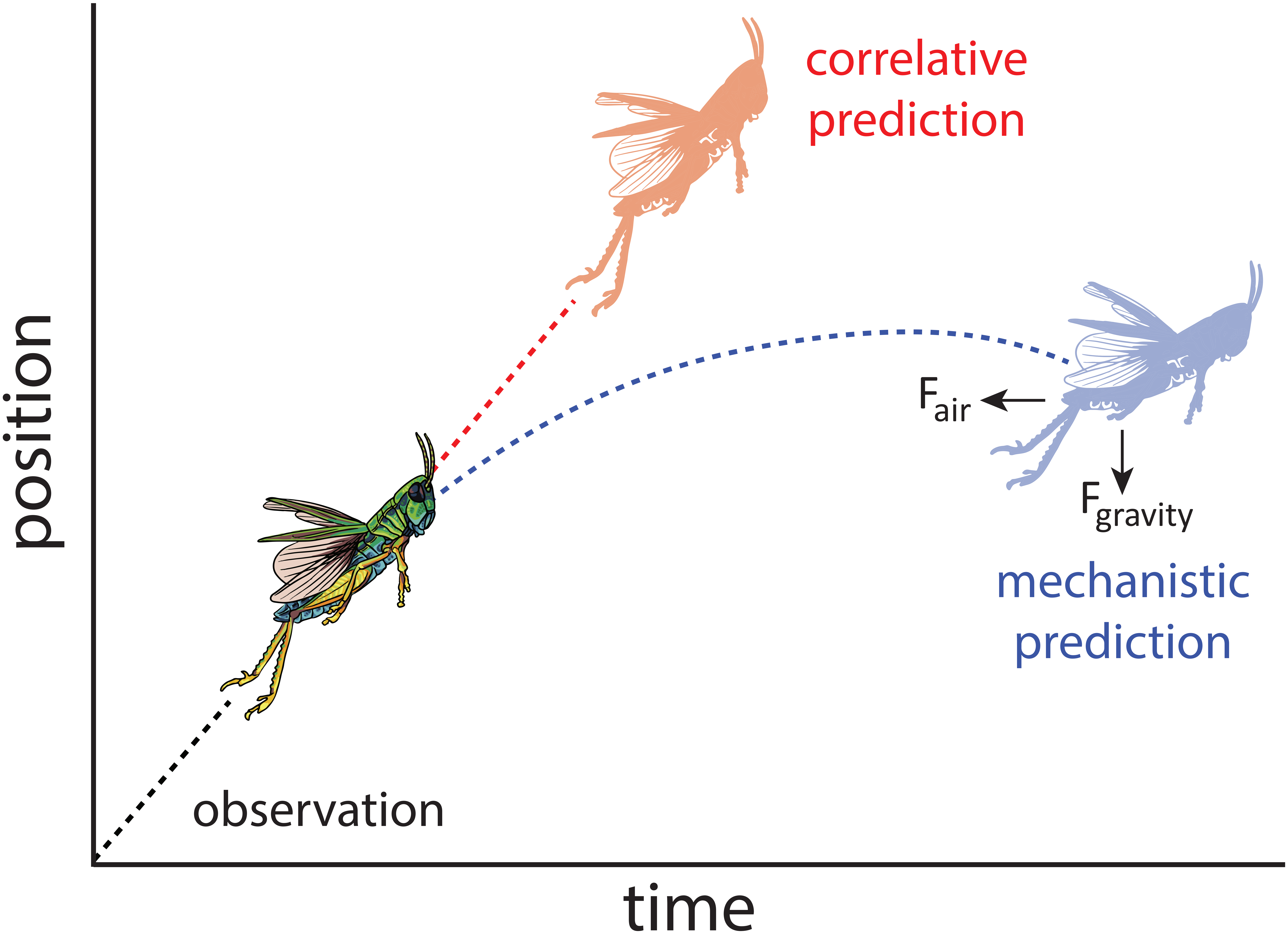


emb
lar1
lar2
lar3
lar4
lar5
pup
imago
wet mass, mg
body temperature (°C)
Jan
Mar
May
Jul
Sep
Nov
higher temperature
larger body size
mass, mg
body temperature, °C
1.2m air temperature, °C
activity
shade, %
depth, cm


419

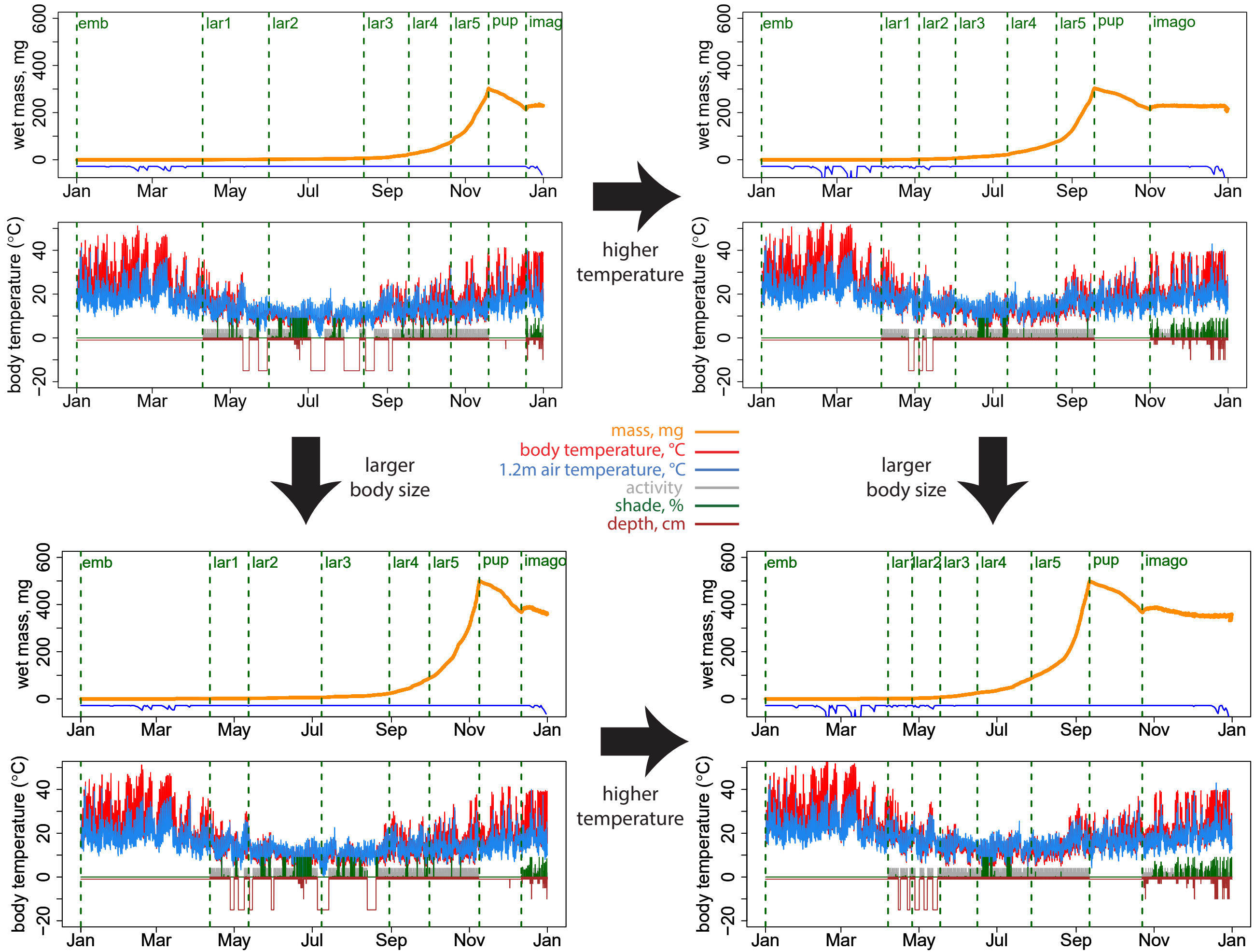
**Figure 2.** Model predictions for *Heteronympha merope* include growth trajectories and microclimate estimates under four simulation scenarios (top-left: baseline; top-right: warming; bottom-left: larger body-size; bottom-right: warming and larger body-size). The simulations were implemented in the 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.

Figure1



correlative
prediction
position
F
air
F
gravity
mechanistic
prediction
observation
time

**Figure2**



higher
temperature
larger
body size
mass, mg
body temperature, °C
1.2m air temperature, °C
activity
shade, %
depth, cm
emb
lar1
lar2
lar3
lar4
lar5
pup
imago
wet mass, mg
body temperature (°C)
Jan
Mar
May
Jul
Sep
Nov