A systems-modelling approach to predict biological responses to extreme heat

Daniel W.A. Noble[1] ‡, Margaret Mayfield[2] †, Ary Hoffmann[2] †, Zhong-Hua Chen[3,4] †, Steven J. Lade[5,6] †, Xuemei Bai[5] †, Danielle Way[7] †, Belinda Medlyn[3] †, Owen K. Atkin[7,8] †, Adrienne Nicotra[1,7] †, James M. Cook[3], Brajesh Singh[3], Alison Bentley[7], Ian Wright[3], Michael R. Kearney[2] ‡

Affiliations:

[1] Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra ACT 2601, Australia

[2] School of BioSciences, The University of Melbourne, Australia

[3] Hawkesbury Institute for the Environment, Western Sydney University, Australia

[4] School of Agriculture, Food and Wine, Waite Research Institute, University of Adelaide, Glen Osmond, SA 5064, Australia

[5] Fenner School of Environment and Society, The Australian National University, Canberra ACT 2602, Australia

[6] Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden

[7] Division of Plant Sciences, Research School of Biology, The Australian National University, Canberra ACT 2602, Australia

[8] Agrifood Innovation Institute, Australian National University, Canberra, ACT 2601, Australia

‡ Correspondence: daniel.noble@anu.edu.au & m.kearney@unimelb.edu.au

† These authors contributed equally to this work.

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Abstract

Anthropogenic climate change is leading to more frequent and extreme heat waves. These large-scale events are radically re-shaping interactions among organisms – impacting biodiversity, community composition and ecosystem services crucial to natural systems and food security. Predicting heat wave impacts on interacting species requires an understanding of the processes driving differential exposure and sensitivity of organisms to extreme heat events in a life-cycle context. To achieve this predictive capacity, we need to integrate models across scales while capturing species-specific responses at the individual level. We review and demonstrate how existing models in disparate fields can be linked to achieve an increased understanding of how individuals and communities will respond to extreme heat, now and into the future.

A systems-modelling approach to understand the biotic impacts of heatwaves

Climate change is leading to warmer and more variable thermal environments globally [1,2]. Greater thermal variability is resulting in organisms experiencing extreme heat waves that lead to thermal stress impacting organismal growth, survival and reproduction, with cascading effects on population dynamics, species interactions, community composition and ecosystem structure and function [3,4]. Climate variability has already been linked to dramatic global declines in pollinator abundance [5] and crop yields [6–8], but the causes underlying such declines, and their ramifications through communities and society, are not fully understood. The impacts of extreme heat on species and communities are driven by a combination of direct effects of heat stress on the physiology and fitness of organisms within a given species [9–11] and indirect effects on interactions (both positive and negative) among species [e.g., 12]. Understanding the dynamic interplay between direct and indirect effects of extreme heat, and how these are mediated by environmental factors (e.g., water and food availability, microbial community), has been hampered by inadequate coupling of models that predict short-term physiological damage on a given species' fitness with population and community dynamic models across species [11,13,14]. A systems-thinking approach is now needed to tackle the multifaceted nature with which extreme heat manifests within a community. This approach will require interdisciplinary collaboration to integrate biophysical, physiological, population and community ecology processes so that we can capture and model the dynamic feedbacks, nonlinearities and interactions between species that drive responses across scales [15,16].

Using plants and insects as examples, we review broad classes of models across subfields of ecology and evolution and discuss how they can be linked to effectively model the biotic impacts of heatwaves from individuals to communities (Figure 1). We focus on plant and insect communities given the strong interconnections between them, the ease with which they can and have been studied, and their importance to socioecological systems [17]. Physiological models can now be seamlessly integrated with biophysical models to characterize temperatures experienced by organisms and simulate the effects of extreme heat events on the entire life cycle of species within ecological communities [18–21] (Figure 1). Physiological models that incorporate estimates of thermal sensitivity across species can capture the delicate balance between damage and repair of physiological systems [10,11,13,22], yielding predictions of the immediate and cumulative impacts of extreme heat on growth, survival and reproduction. Importantly, mechanistic physiological models provide outputs at the individual level (e.g., energy and water requirements, waste production, activity constraints, vital rates) that can be integrated into population and community ecology models to capture how extreme heat events perturb interactions among species and across whole, complex communities [23,24]. We demonstrate how such a coupling can be made within and across species and highlight the opportunities it presents to develop a greater understanding of the ways in which extreme heat stress manifests across species. We discuss the challenges of coupling models across diverse species in communities, and of capturing the eco-evolutionary feedbacks that will be necessary for accurate predictions in the future.

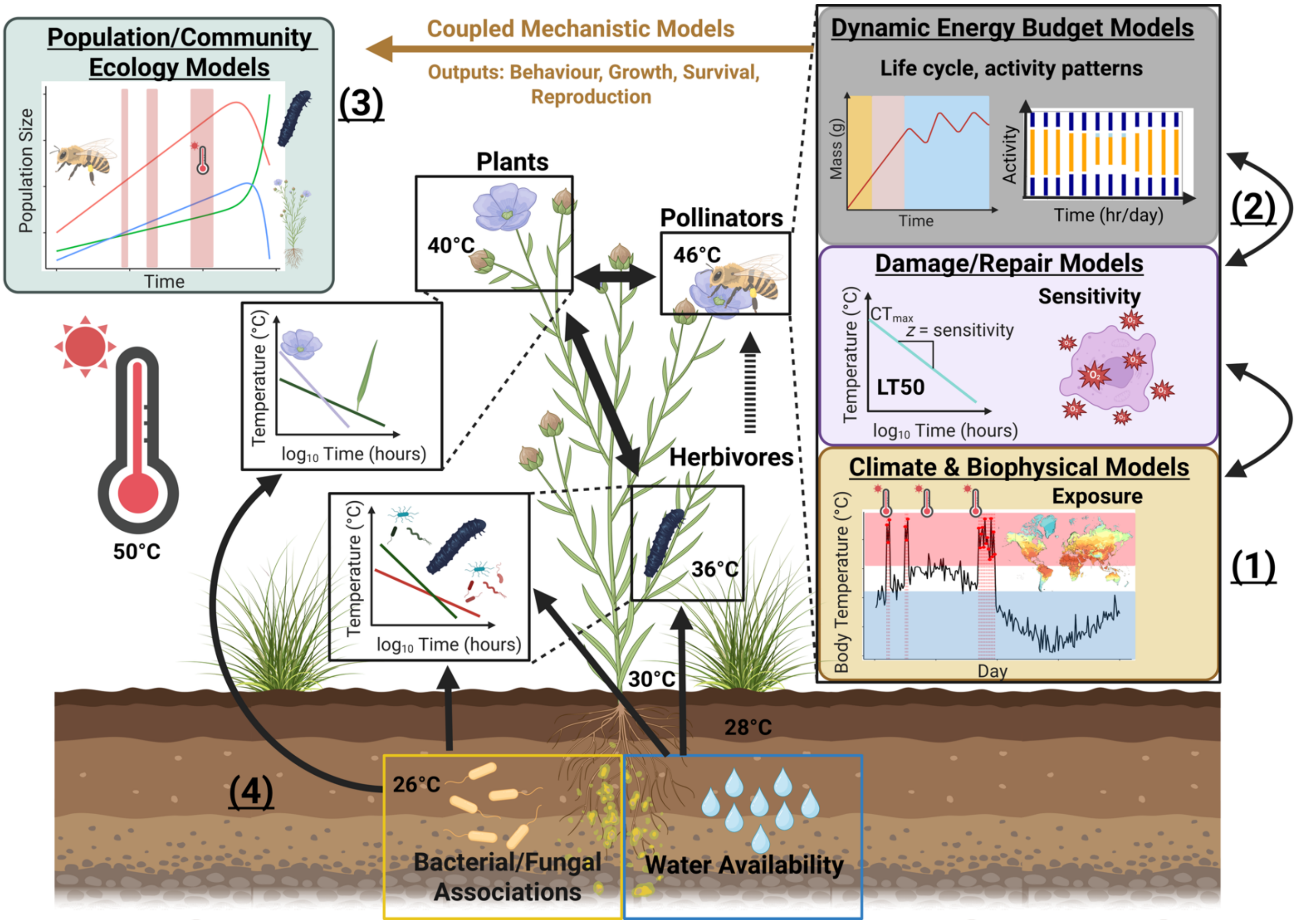

Figure 1- A coupled systems modelling framework for predicting the effects of extreme heat on ecological communities. A systems modelling approach first integrates (1) climate/biophysical models to predict the different microclimates species experience. (2) Microclimates experienced by organisms then provide inputs for physiological models that integrate temperature exposure with explicit physiological processes that simulate development, behaviour, survival (e.g., 50% survival thresholds, LT50) and reproduction in response to microclimate dynamics across life history stages. Physiological models can be built around the unique life cycles of the diverse species in communities, capturing lagged responses to extreme heat, phenological mismatches and mechanistically informed responses to extreme heat for species of the system in question. Outputs (behaviour, growth rate, biomass accumulation, survival and reproduction) from physiological models of individual organisms can then be integrated into (3) population and community ecology models (such as those developed with in the Modern Coexistence Theory Framework – see text) to predict population growth and community composition under a specific type of change (either to the environment or suite of interacting species). Environment-mediated feedback loops (4) influence organism thermal exposure and sensitivity, including water availability and microbial communities, which can vary across different life stages and organs depending on the microclimates occupied. Coupling existing models will allow for quantitative predictions to be made on how extreme heatwaves perturb biological systems and for the development and implementation of strategies to enhance biological system resilience to extreme heat. Created with BioRender.com.

From weather to microclimates: predicting community wide exposure to extreme heat

Extreme weather events such as heatwaves are predicted by Global Circulation Models (GCMs), typically at large spatial scales (e.g. 0.5°grid cells), and can be regionalized by downscaling to smaller spatial scales. However, species within communities experience heatwaves differently because of the varied microhabitats they occupy. For example, while air temperature may be 50°C, an organism a metre below the soil surface may be exposed to temperatures ~20°C cooler (Figure 1). Therefore, to understand how extreme heat affects a community of organisms, we must characterize the **microclimates** experienced by individuals of different species under a given atmospheric event. Microclimate predictions are made by taking the atmospheric conditions as independent forcing variables and combining them with detailed information on terrain (slope, aspect, hill shade), vegetation [plant-area index (PAI), stomatal behaviour, leaf reflectance] and soil hydrothermal properties to predict how radiation, wind speed, air temperature, humidity, soil temperature and soil moisture vary on small spatial scales [25–32]. Capturing the interaction between soil moisture and temperature in microclimate models is critical because the same atmospheric heat wave can have different implications for microclimatic conditions depending on the recent history of rainfall and temperature [33]. Downscaling to microclimate conditions requires the specification of key environmental properties (e.g. % shade, soil characteristics, surface albedo) at a fine scale (metres) for the local area of interest. Depending on the organism and question of interest, not all input variables are needed to parameterize a given microclimate calculation, as recent guides to microclimate modelling illustrate [e.g., 34,35,36].

Beyond parameterization, the benefit of a systems-thinking approach in the context of microclimate modelling is its ability to capture vegetation and soil dynamics which can dramatically shape microclimate conditions within and between species dynamically across time. While the large-scale feedbacks from plant and soil dynamics to heatwave development are captured in GCMs [e.g. 37], these dynamics are also important in determining thermal regimes at micro-scales. For example, plant water use dynamics can amplify or reduce within-canopy temperatures via effects on photosynthetic capacity, stomatal decoupling, cuticular conductance, leaf damage and plant mortality [20,38]. These impacts are important for the plants themselves and for thermal regimes available to other organisms. Forecasting future thermal regimes is challenging because it involves forecasting future vegetation dynamics, including changes in key vegetation properties such as leaf area index, as a function of plant growth, phenology, plant population dynamics and shifts in community composition. Despite the complexity and non-linearity of these interactions across the soil-plant-atmosphere continuum, there is existing capacity, and growing potential, to model them and determine individual-specific exposure to extreme heat. For example, a wide range of vegetation models is available for this purpose, from crop growth models that simulate growth and yield of crops over a season (e.g. Agricultural Production Systems sIMulator (APSIM); [39]) up to the dynamic global vegetation models (DGVMs) that simulate vegetation function and distribution at local to global scales [40].

Translating exposure to organism temperature: biophysics to the rescue!

Once microclimates are quantified, it is crucial to estimate the heat and water budgets of organisms to determine how microclimate variability within a system translates to realized organismal temperatures and hydration states. Heat and water budgets can be computed using a combination of species functional traits (e.g., body mass, metabolic rate, surface area, solar absorptivity) along with how heat energy and water are exchanged with the environment – dependent on the microclimate experienced. Such **biophysical models** have a long history [41,42] but have become more widely applied in ecology in the past 20 years, facilitated by developments in environmental datasets, microclimate modelling, and the emergence of high-level programming languages such as R [21]. Biophysical models of ectothermic animals make use of equations for energy and mass exchange between an organism and its environment and can account for complex radiative heat transfer and the role of evaporative water loss across surfaces [21,25,43]. Equivalent models of leaves incorporate the dynamic role of stomata [20, 44] (**Box 1**). Biophysical models are powerful because, by translating microclimate conditions to organism body temperature and hydric states, simple regulatory decision-making models can be used [45,46]. For example, given an understanding of an organism's thermal activity windows, thermal optima, and critical thermal limits we can determine what microclimates the organism should chose to get close to its target body temperature [e.g., 45,46]. Such behavioural thermoregulatory decision making is crucial for mitigating the negative impacts of extreme heat. Incorporating it into models can inherently capture the trade-offs such a strategy entails through reduced foraging time [21,45]. Similarly, changes in stomatal behaviour can mitigate or exacerbate the extreme temperatures leaf tissue experiences while simultaneously shaping the microclimate conditions for other organisms [20,47] (**Box 1**). Future developments in biophysical modelling of organismal temperature under extreme heat will involve understanding the nuances of plastic physiological and behavioral responses. For example, lizards may pant when exposed to high temperatures [48], birds may 'wind surf' or seek thermal micro-refugia [49], and stomata can enact emergency cooling, departing from the typical responses to vapor pressure and light intensity [38], though this response may depend on prior soil moisture conditions [50]. Although biophysical models require many traits for parameterization, the models and parameters can be tailored to the question and organism of interest [21]. In addition, many traits can be approximated based on traits of similar species, and then validated and updated as more species-specific data become available. The application of biophysical models in concert with microclimate models can thus be used to infer the thermal conditions to which members of the same ecological community are exposed with different degrees of detail. Realised thermal exposure can then be linked to physiological models.

Capturing both physiological damage and repair to predict multi-species thermal sensitivity

Translating how heat waves impact plants and animals not only depends on modelling temperature *exposure* but also the varying *sensitivity* of organisms to extreme heat [22,51]. Sensitivity to extreme heat can be captured by **thermal load sensitivity (TLS) / thermal death time (TDT)** models that explicitly account for how heat stress depends on both the body temperature experienced and its duration [13,22]. TLS models predict the relative accumulation of damage to cellular and sub-cellular systems that compromise physiological function. Without periods of recovery, where damage can be repaired, organisms accumulate damage over time, reducing growth and impacting survival and reproduction (**Box 2**). Typically, TLS models focus on endpoints that include survival (e.g., lethal temperatures, LT_{50} or LT_{80}) or some measure of reduced fertility, but this need not be the case [13]. Endpoints are predicted by assuming the effect of time at a given temperature decreases survival and/or fertility exponentially, and have been shown to have high predictive power [10,11,22,51]. For example, Ørsted *et al.* [11] show that both mortality and fecundity follow a clear exponential relationship with time in the Spotted Wing Drosophila (*Drosophila suzukii*), with survival and fecundity being compromised most for long thermal exposures at high temperatures. Importantly, they also show that reproductive sensitivity can be higher than mortality, with heat injury impacts accumulating faster for reproduction than survival [11]. TLS theory also applies well to photosynthetic function in plants [52,53], highlighting its generality. TLS models are crucial for predicting how heat waves affect organisms because accumulated damage to physiological systems can result in lagged responses to heat stress or exacerbate future stress (i.e., future heat waves / droughts) – a common feature of extreme heat events [13,54].

Environmental factors known to impact thermal sensitivity, such as water and drought stress [e.g., 55,56], along with nutritional and dietary changes [e.g., 57,58], can be incorporated into systems modelling approaches through their impacts on thermal sensitivity and tolerance [13] (Figure 1). Indeed, an exciting potential application of a systems-modelling approach is to explore how microclimatic conditions mediate changes to interactions between plant and animal microbial communities. Interactions between plants and microorganisms, such as plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), and bacterial or fungal endophytes, are known to enhance growth, defense, and heat tolerance in plants [59,60], and gut microbiota can improve heat tolerance in animals [61]. Additionally, modelling the intricate balance between damage and repair for a suite of different species can help identify susceptible species, life stages and tissues that are most at risk from extreme heat events due to direct sensitivity to extreme heat, allowing more accurate predictions of the varying levels of species sensitivity within a community [13].

Box 1: Building a systems modelling approach to capture multi-species exposure to extreme heat

Here we outline how a systems-modelling approach can be developed, illustrated with a simple hypothetical community (Figure IA). The focus is on how climate, microclimate, and biophysical models can predict the differential exposure to extreme heat events across species, how species can alter each other's microclimates, and the incorporation of 'behavioural' responses of species in response to temperature (e.g., stomatal behaviour, thermoregulation). Predicted organismal temperatures are used from these models to then predict life-cycles for species, incorporate differences in thermal sensitivity, and ultimately estimate vital rates for population and community ecology models (**Box 2**).

The context is a heatwave event in January 2018/19 at Renmark, South Australia (Calperum Station). The historical SILO climate dataset (0.05° resolution, 1889 to present) [62] was used as input to the `micro_silo` function in *NicheMapR* [20,63], in conjunction with *microclima* [26,27] in the R statistical language to compute microclimates. Microclimates are calculated at various heights above ground (20cm-1.2m, relevant to our plants and insects) and soil depths (for burrowers) with varying levels of shade (we use 40% and 80%). Simulating these varied conditions captured the diversity of microclimates that different species in a community might experience and provided opportunities to build in behavioural plasticity.

With available microclimates predicted, we can compute leaf and body temperatures using biophysical models. However, plant temperatures will impact the temperatures experienced by the grasshoppers because plant stomatal conductance changes in response to extreme heat events. Stomatal responses of leaves to their environment can be captured with the help of the *plantecophys* package [44] and used in conjunction with the `ectotherm` function in *NicheMapR* to compute realistic leaf temperatures as stomata open and close in response to temperature and vapor pressure deficit (Figure IB). The combination of microclimate, leaf traits (e.g., shape, leaf conductance, emissivity) and stomatal behaviour thereby produces realistic leaf temperature estimates during the heatwave event.

Calculated leaf temperature can then become part of the microclimate of the insects (Figure IC). The `ectotherm` function of *NicheMapR* can be used to compute insect body temperature, given the microclimate (including plant leaf temperature) and insect traits. The insect temperature calculations incorporate their capacity to thermoregulate behaviourally. For example, Species B moves to cooler parts of the plant to minimize thermal stress, when possible (Figure IA), given a range of available microclimates and using information on their thermal preferences. All code to demonstrate this process is available at: https://daniel1noble.github.io/thermal_tol_interactions/.

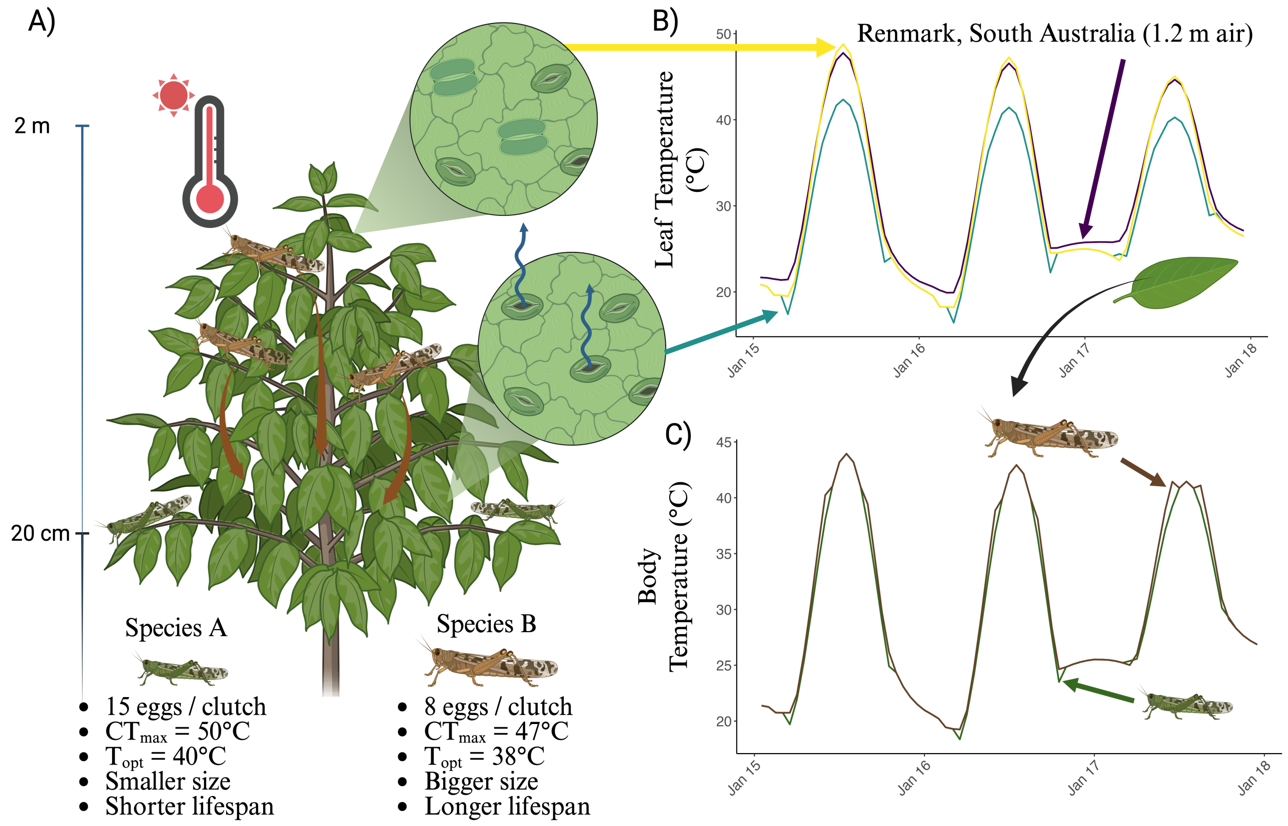

Figure I: Predicting and coupling microclimate and biophysical models of a plant and two grasshopper species that vary in their thermal tolerance and life history (A). Biophysical and thermoregulatory models use miroclimate data to predict leaf (B) and grasshopper (C) temperatures through time (coloured lines) incorporating changes in insect and stomatal behaviour. Created with BioRender.com.

Glossary

Biophysical models: Biophysical models capture the balances of heat, water, and other aspects of energy and mass exchange between organisms and their microclimatic environment to predict how organisms function, survive, and behave in varying environments.

Coexistence: Coexistence occurs when populations of two or more species are able to persist in each other's presence indefinitely at steady state under constant abiotic conditions.

Functional traits: Functional traits are the characteristics of organisms that influence their performance and fitness, such as body size, reproductive output, and metabolic rates. In the context of extreme heat, functional traits can be used to categorize species based on their responses to thermal stress.

Modern Coexistence Theory: A theoretical framework derived from population ecology describing the conditions under which species can coexist mathematically. It has resulted in the development of population growth models using criteria based on niche and fitness differences, mutual invasibility and feasibility domains.

Microclimate: Microclimates are the local conditions experienced by organisms, which can differ substantially from the broader atmospheric conditions. Microclimates are influenced by factors such as vegetation cover, soil properties, and topography, and can significantly affect the thermal and hydric environment experienced by organisms.

Thermal load sensitivity (TLS) / thermal death time (TDT) models: Models that calculate thermal stress load from a time series of body temperatures to quantify lethal and sublethal impacts on tissues, organs and whole organisms.

Vital rates: Demographic parameters that determine how populations change over time. They include measures of birth, death, growth, and reproduction.

Physiological models that capture the effects of extreme heat across life

Accumulated damage to an organism from experiencing extreme heat events will impact survival probability in the future and needs to be integrated with a full account of growth, development and reproduction through life to scale effects to populations and communities. Dynamic Energy Budget (DEB) models are physiologically-explicit life-cycle models of energy and mass uptake and conversion that predict key life-history transitions, growth, reproduction and survival (senescence) through time [18,64]. DEB models consider organisms as a thermodynamic system (fully obeying energy-mass conservation) capturing the exchange of food, water, respiratory gases and metabolic waste throughout the life cycle [21]. DEB models can translate short-term (hours) variation in factors such as temperature, toxins (e.g., toxicants, [65]) and resource availability (nutrients) [66,67] into long-term (days, months, years) effects on development, growth, reproduction and survival [19,21]. DEB theory, when combined with biophysical models more generally, allows the full water budget to be computed to account for heat stress impacts of a hydric nature [21]. Perhaps most importantly, DEB theory calculates the life cycle trajectory of an organism and so can account for the effects of timing of heat wave impacts relative to life stage. Applied to multi-species assemblages, DEB models can capture how different species' life cycles are affected by heat and interact with each other to predict how traits such as birth, age at maturity, reproductive events, energy flow and lifespan vary across species (**Box 2**). DEB models integrate many fundamental physiological processes and are parameter-sparse (one parameter per process). Moreover, the necessary parameters have already been estimated for > 7000 species already (although there are taxonomic biases) [68,69]. New analytical approaches using phylogenetic imputation methods show promise for calculating energy budgets for species without data. Such methods have, for instance, already been used to predict DEB parameters for over 1.3 million animal species [see, 70]. In addition, software packages such as *NicheMapR* [25,63] allow for simulations of life-cycles using parameters for diverse species. DEB model outputs, such as body mass and size, reproductive success and timing, and survival, can be used to parameterize vital rates needed for population and community models, with additional options to incorporate eco-evolutionary feedbacks (see **Box 3**).

Analogously, physiology-based vegetation models simulate plant growth over time as a function of carbon, water and nutrient uptake and use, following mass balance principles [71]. Model drivers typically include incident radiation, humidity, rainfall, and soil properties, as well as air temperature. The models capture the direct effects of temperature on key physiological processes, such as photosynthesis, respiration and phenology, as well as the indirect effects via feedbacks on vegetation water balance and soil nutrient availability. Short-term responses to temperature are captured well in these models through representations of enzyme kinetics, but representation of longer-term responses remains challenging because plants show high flexibility in their ability to acclimate to ambient temperatures [72]. Another area under active research is capturing plant damage and death from hot-dry weather extremes. Considerable progress has been made by representing the plant hydraulic system explicitly, enabling the risk of hydraulic failure to be predicted under conditions of low rainfall and high evaporative demand [73]. Direct damage to plant tissue from extreme heat has yet to be represented in such models, but the thermal death time framework outlined above offers a promising way forward.

Mechanistic approaches that ‘speak’ to population and community ecology under extreme heat

Modelling tools developed as part of **Modern Coexistence Theory** (MCT) [16] offer a promising suite of approaches for combining biophysical, physiological, and population ecology models to predict whole community responses to extreme heat events. Population growth models are core to predicting species **coexistence** within this framework. In their most recent applications, these simple pairwise population growth models have been used to underpin horizontal network models that allow one to examine how species in a community interact and create stable communities [15,74]. Other extensions of MCT tools have integrated environmental variation [24], traits [75] and cross-trophic dynamics [76,77] in predicting the outcomes of species interactions in community contexts. Fundamentally, this approach relies on simple two-species individual-based population growth models [78,79], but key extensions involve the use of whole communities as one “species” [80,81] or the grouping of species to simplify interaction matrices while accounting for a small number of dominant species [77].

Population dynamic models that are used as part of MCT can calculate the individual fitness effect of interactions in relation to environments experienced by organisms [23,77,82]. As these models use the same fitness measures as DEB models, they offer a population modelling framework to add thermal biology to community diversity predictions. This is because population dynamical models can be combined, for example as networks [15] and compared between microsites with different biophysical properties and harbouring species with different thermal responses to their microenvironment. For example, Bimler *et al* [15] used this approach to determine which species were keystone species under shady and sunny portions of the same plant communities.

Modified **vital rate** functions (which can incorporate any measure of fitness) can be used in population growth models to compare population dynamics for individuals in areas with different biophysical properties and/or thermal tolerances. Indeed, the predicted traits from DEB models could be used to directly parameterise growth rate models (**Box 2**) or to predict **functional traits** which, at a community scale, can be used to categorise species with different response and effect profiles. Horizontal interaction networks can then be used to determine how important microclimates with different biophysical properties are for species interactions (defined by their fitness responses to their thermal environment) within the context of whole communities. These networks can be made to target particular types of interaction effects or responses to extreme heat events, or used to compare how species interact in areas with different thermal landscapes. The main limitation of these methods is that they are data hungry, but even this can be handled by categorizing species by ‘traits’ or shared phylogenetic relationships, which are simplifications shown to be effective at reducing model complexity without sacrificing model accuracy [83].

Box 2: Scaling up extreme heat effects from impacts on individuals to populations and communities

We use predicted organismal temperatures (Figure I in Box 1) to take stock of how thermal heat stress accumulation impacts survival probability and simulate life cycles for two interacting grasshopper species under their respective microclimates.

To start, using existing parameters for a dynamic energy budget (DEB) model for grasshoppers [84], we can use the `ectotherm` function in *NicheMapR* to simulate life cycles for each of the two species. We assume that both species have similar DEB parameters but vary in their life-history, thermal physiology, size and reproduction.

DEB models incorporate a simple Gompertz mortality function to capture senescence, but do not integrate the effects of thermal load accumulation in response to extreme heat events into survival functions. We assume reproduction is not impacted by heat for simplicity, but thermal load on reproduction can also be incorporated in a similar way [11]. By using thermal sensitivity parameters for mortality endpoints from TLS models (i.e. z, slope and α = critical thermal limit), they can be used to predict the accumulation of damage through time during stressful temperatures (environmental temperatures T_e > critical temperatures T_c) experienced under realistic conditions for each species by calculating heat injury (HI) accumulated between time point t_i and t_{i+1} across the insect's life (using an LT_{50} threshold)(Equation 1) ('red lines' in Figure IIA) [10,11,13,51].

$$HI = \sum_{i=1}^{T_e > T_c} \frac{100 \cdot (t_{i+1} - t_i)}{10^{\left(-\frac{1}{z} \cdot max(T_i; T_{i+1}) + \alpha\right)}} \qquad (1)$$

After calculating HI accounting for repair [85], and converting to the probability of mortality through time, we can calculate the total probability of survival (i.e., from senescence, thermal stress, and activity-based mortality) for each age/stage class. In combination with the DEB model outputs on total reproduction across life, we can build a simple age/stage-structured population matrix (day of life or developmental stage) (Figure IIB) to estimate population growth rate [r_{max} = ln(λ)] for each species under their respective microclimates. r_{max} can then be included in a two-species, density dependent Ricker model (a model commonly used as the basis for coexistence modelling in the MCT framework) to predict their population growth under competition (Equation 2).

$$N_{t+1}^{i} = N_t^i \cdot exp\left[r_{max,i}\left(1 - \frac{N_t^i + \sum_{j \neq i} \alpha_{ij} N_t^j}{K_i}\right)\right] \qquad (2)$$

where N_t^i is the population size of species i at time t, r_{max_i} is the intrinsic growth rate of species i, K_i is the carrying capacity of species i, and α_{ij} is the competition coefficient that describes how much species j affects species i. Note that, because mechanistic physiological models are used, the population matrix can be updated each generation to reflect changes in vital rates (survival and reproduction) under different microclimates in the future.

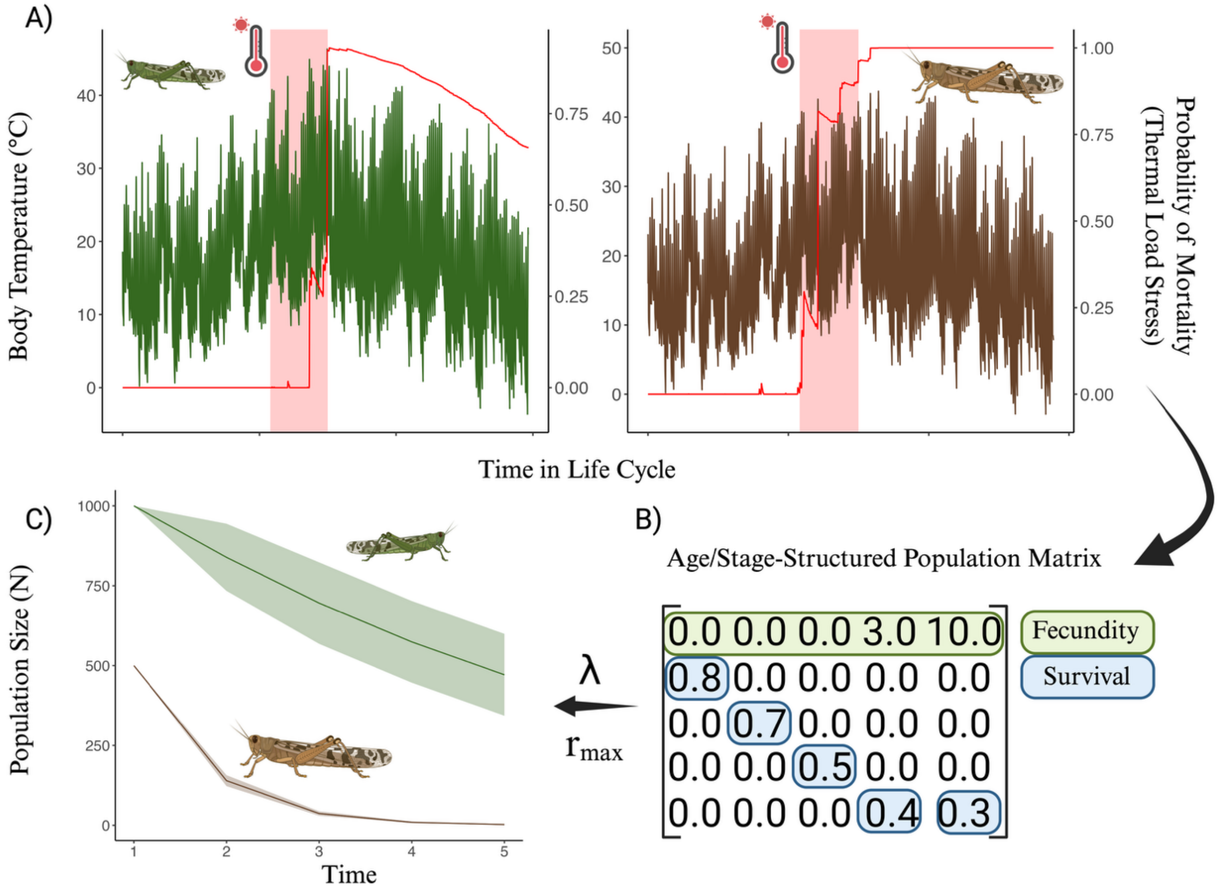

Figure II: A systems approach to using mechanistic physiological models to capture life-cycle vital rates and thermal load stress on survival to scale up to multi-species population dynamics. Created with BioRender.com.

‘Hot’ solutions for a changing world

Extreme heat will have dramatic and widespread effects on biological and socioecological systems that humans rely upon. For example, under current global climate change scenarios, each degree Celsius increase in global mean temperature is estimated to reduce the global yield of wheat by 6.0% and soybean by 3.1% [86], exacerbating food shortages.

A systems-modelling approach can help us develop suitable interventions, predict the varied consequences of such interventions, and allow for adjustments that can improve decision making for mitigating the impacts of extreme heat in real world situations. As a simple example (Figure 2A), a systems modelling approach can allow for informed predictions about how to mitigate heat stress to crops while also considering the potential for pest outbreaks. In essence, we want to add a minimal amount of water to a system to cool leaves while avoiding depleting limited water supplies and/or creating better microclimate conditions for pests. Making use of real weather data to predict microclimates and organism temperatures, we can assess how adding 2, 5, 10, or 20 mm d^{-1} of water to a system affects leaf temperatures and the life-cycle for a grasshopper species that is a known pest (Figure 2). We can see that adding 2-5 mm d^{-1} of water can decrease leaf temperature by up to 3.87°C (Figure 2B), but adding more water does not result in significant gains in cooling. In addition, 2-5 mm of water added each day results in the grasshopper population being suppressed over time, whereas not adding water at all results in grasshopper population growth, leading to potential heatwave-associated outbreaks. Here, the optimal solution is adding 2-5 mm d^{-1} of water to both cool plants and protect them from pests. Identifying and/or modifying the thermal suitability of landscapes, such as in our simple example, may dramatically benefit plants and animals under extreme heat and is a promising feature of a systems-thinking approach [21]. Additionally, as our understanding of the mechanisms associated with heat tolerance improve, genetic tools, environmental manipulations (e.g., promoting beneficial microbes) and targeted plant breeding can be used to enhance thermal tolerance, creating more resilience to extreme heat events [e.g., 60].

Systems modelling can also help understand how people's responses to the impacts of extreme heat could lead to accelerating changes in plants, animals and landscapes. Farmers or ecosystem managers may introduce new species, alter management practices or farm remaining unaffected areas more intensively. Thermal stress may ultimately result in people leaving areas, potentially making remaining communities more vulnerable through loss of resources and services [87]. Thermal risks to ecosystems may also precipitate declines in individual wellbeing, and these consequences may accrue differently across regions and peoples [88].

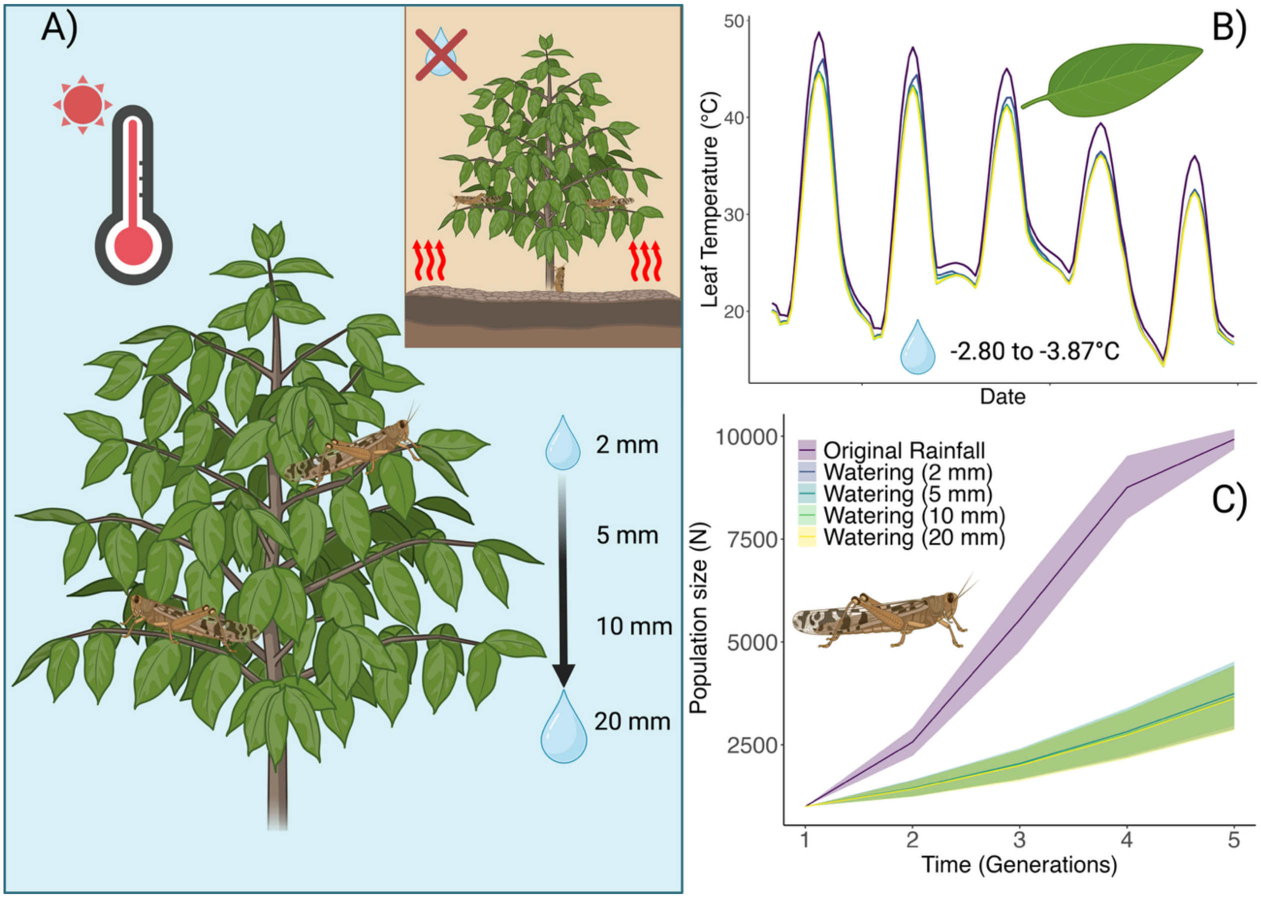

Figure 2 - How a systems modelling approach to extreme heat can be used to inform solutions. Heat stress to crops can result in foliage loss and crop failure, but also weaken crops to pests. Using a hypothetical case study of a crop and associated pest, we explore how different watering regimes affect plant temperatures and the flow on effects such regimes have for pest dynamics (A). Using a site near Renmark, South Australia, we use microclimate and biophysical models to estimate leaf temperatures (detailed in Boxes 1 & 2). We see that, compared to original rainfall conditions, certain watering regimes can significantly reduce leaf temperatures by nearly 4°C, providing protection to leaves (B). Modelling how these changed microclimate conditions translate to grasshopper body temperatures, we can then estimate changes to grasshopper life cycles and use the vital rates to predict population dynamics, showing, in this case, that even small amounts of water can indirectly suppress pest growth through lower body temperatures (C). Created with BioRender.com.

Box 3: An important frontier: integrating eco-evolutionary feedback within a systems-modelling framework

Extreme climactic events, such as heatwaves and droughts, can result in intense episodes of selection which can lead to rapid evolution of heritable traits [89]. Given the intensity of selection associated with extreme climatic events, these events have the potential to radically alter the phenotypic and genetic variability available to selection [90], potentially impacting population resilience to future events. Predicting evolutionary responses from extreme heat events is challenging because of their rarity and stochasticity which makes quantifying the strength of selection difficult as it often can only be opportunistically measured [89].

Predicting evolutionary responses also relies on our ability to predict heatwaves and how organisms experience them in the future – a task that is becoming more feasible with new climate models [e.g., 91,92]. Evolutionary consequences of extreme heat events will depend on the characteristics of these events (e.g., frequency, timing, exposure intensity and duration), the traits under selection and their levels of genetic (co)variation, as well as the demographic and ecological context in which the event occurs [93–95]. Considering various forms of plastic responses (e.g., behavioural, developmental, and physiological plasticity) as environments change through time is also crucial because plasticity can weaken selection and shelter genetic variation while also promoting persistence [96,97]. Many of these processes can now be incorporated into a systems modelling framework (e.g, behavioural plasticity), to capture environment-phenotype feedbacks.

A more complete systems modelling approach that captures eco-evolutionary dynamics needs to treat 'traits' more broadly than is typically done in evolutionary ecology (e.g., body mass). For example, 'traits' can include the parameters within models that establish functional traits within a population (e.g., DEB parameters)[98,99], which may provide predictions for suites of resulting traits that emerge from such parameters. Furthermore, it is important to consider the evolution of suites of traits as can be done using the multivariate breeders equation [100]:

$$\Delta\bar{\mathbf{z}} = \mathbf{G} \cdot \boldsymbol{\beta} \qquad (3)$$

where $\Delta\bar{\mathbf{z}}$ is the vector of changes in the mean trait values, $\mathbf{G}$ is the genetic covariance matrix and $\boldsymbol{\beta}$ is the vector of standardised selection gradients that regress each trait on relative fitness (i.e., $\boldsymbol{\omega} = \boldsymbol{\alpha} + \boldsymbol{\beta}^{\mathbf{T}} \cdot \mathbf{z} + \mathbf{e}$; [101]). Plasticity can be captured by mapping trait development to the environment and incorporating environmental variability into the breeders equation [see also, 102]. While the multivariate breeders equation can be useful for predicting short-term evolutionary responses (i.e., one or a few generations) it likely has limited predictive power over longer timespans because of changes in heritability and selection through time, which is a future challenge [95,101].

Concluding Remarks

Implementing a systems-modelling approach will no doubt be challenging, particularly for complex communities, and knowledge gaps remain (see **Outstanding Questions**). But, more than ever, we need mechanistic approaches that can capture key biological processes (physiology, behaviour, phenology, species interactions and eco-evolutionary dynamics - **Box 3**) to better predict biological responses to extreme heat [54,103]. Coupled mechanistic models within and across species are expected to have improved predictive power when projected to new environmental conditions and will better capture interacting processes [21,103]. Nonetheless, application of a systems modelling approach will require a solid foundation of species natural history, diverse modelling expertise, and a concerted effort to collect and collate trait and environmental data for model building and validation.

There are exciting new tools and data that are helping to overcome these challenges [26], and careful consideration of the key processes important to a system can help alleviate these challenges [21]. For example, large databases of physiological traits for both plants and animals now exist [e.g., 104,105] and advanced missing data approaches can help estimate likely parameters for data deficient species [70,74,106]. Ever more sophisticated and powerful computational pipelines (e.g. *NicheMapR*, *TrenchR*, *mcera5*, *terra* in R) make it easier to implement and connect models. Model selection and validation are important steps in any modelling process and will be more complicated when applied to entire systems; however, starting with a simple model, validating predictions with empirical data, and then adding complexity as needed can make building systems models more tractable [21]. Even simple models that compare counterfactual scenarios may provide important quantitative insights into the impacts of extreme heat on organisms, populations and communities [107–109]. Such insights can form the basis for prediction-driven solutions to mitigate the impacts of extreme heat on biodiversity. By working collaboratively we can develop a more quantitative and predictive understanding of the impacts that extreme heat will have on organisms, populations, and communities, and decide how to mitigate these impacts to preserve diverse systems now and into the future.

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