



## INVITED PERSPECTIVES

# Leveraging Organismal Biology to Forecast the Effects of Climate Change

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**Synopsis** Despite the pressing need for accurate forecasts of ecological and evolutionary responses to environmental change, commonly used modeling approaches exhibit mixed performance because they omit many important aspects of how organisms respond to spatially and temporally variable environments. Integrating models based on organismal phenotypes at the physiological, performance, and fitness levels can improve model performance. We summarize current limitations of environmental data and models and discuss potential remedies. The paper reviews emerging techniques for sensing environments at fine spatial and temporal scales, accounting for environmental extremes, and capturing how organisms experience the environment. Intertidal mussel data illustrate biologically important aspects of environmental variability. We then discuss key challenges in translating environmental conditions into organismal performance including accounting for the varied timescales of physiological processes, for responses to environmental fluctuations including the onset of stress and other thresholds, and for how environmental sensitivities vary across lifecycles. We call for the creation of phenotypic databases to parameterize forecasting models and advocate for improved sharing of model code and data for model testing. We conclude with challenges in organismal biology that must be solved to improve forecasts over the next decade.

## Introduction

Many organisms have responded to recent climate change by shifting their distribution or phenology, experiencing population shifts, acclimating, or evolving (Scheffers et al. 2016). Yet, we have little ability to predict how particular species will respond based on their traits (Buckley and Kingsolver 2012; MacLean and Beissinger 2017). Considering the complexities of how organisms respond to their environments and to other organisms, our poor predictive ability is not particularly surprising. Prediction is particularly challenging because organisms will increasingly experience environments that are novel with regard to their evolutionary histories (Veloz et al. 2012; Maguire et al. 2015). A core challenge is to identify which aspects of organismal biology are essential to consider and which can be omitted from predictive models.

Predicting responses to environmental change offers an opportunity to test our understanding of organismal biology. Indeed, making accurate predictions requires addressing most of the grand challenges in organismal animal biology identified by

the Society for Integrative and Comparative Biology (SICB) (Schwenk et al. 2009). In particular, physiological insight is needed to integrate across levels of biological organization (Mykles et al. 2010), whether organisms use behavior to buffer their environment must be considered (Sih et al. 2010), and appropriately characterizing organism–environment interactions requires an interplay between theory and empirical research (Angilletta and Sears 2011). Robust forecasts require operationalizing knowledge gained from the grand challenges (Denny and Helmuth 2009).

Statistical environmental niche models (ENMs) remain the most common forecasting tool, but their performance is mixed (Maguire et al. 2015). For example, using ENMs to prioritize reserve design for mammals during a past period of rapid climate change yielded performance that was little better than random prioritization (Williams et al. 2013). One point of ENMs failure is poor extrapolation into novel environments (Veloz et al. 2012). Mechanistic modeling approaches that incorporate environmental data and phenotypes to estimate

physiology, performance, and ultimately fitness (rather than relying on statistical associations between environmental conditions and organism presence as do ENMs) should extrapolate better into novel environments (Buckley et al. 2010; Urban et al. 2016).

Effective forecasts must address how organisms respond to spatially and temporally variable environments. Many distribution models such as ENMs can readily incorporate finer spatial data but generally require temporally averaged environmental data. They thus omit many important aspects of organismal responses including thresholds, non-linearities, and thermal histories. Mechanistic models are well suited to handle time series of environmental data, but their application is limited by the availability of biophysical models and organismal data (Helmuth et al. 2005; Buckley et al. 2010; Urban et al. 2016).

Here we summarize data and modeling limitations for ecological and evolutionary forecasting and highlight promising directions. Limitations to environmental data, and to associated climatic, biophysical, and niche models, undermine our ability to accurately forecast responses to climate change (Dillon and Woods 2016; Nadeau et al. 2017). The availability of environmental data is increasing rapidly, but they generally are not provided at the fine spatial and temporal scales relevant to the physiology, energetics, and demography of organisms (Potter et al. 2013). Limited data on morphological and physiological phenotypes (and their inter-individual and interpopulation variation) hinder modeling organismal responses to environmental conditions (Urban et al. 2016). Existing knowledge is largely inadequate to predict how organisms evade (through behavior or other forms of plasticity) or cope with environmental stresses, particularly given that the incidence and magnitude of environmental stress varies temporally.

Most of these limitations have been reviewed elsewhere (e.g., Helmuth et al. 2005; Kearney and Porter 2009; Buckley et al. 2010; Huey et al. 2012; Dillon and Woods 2016; Sinclair et al. 2016; Urban et al. 2016; Dietze et al. 2018), but we see value in a synthetic assessment of challenges for ecological and evolutionary forecasting and a roadmap for their potential remedies. We highlight recent progress toward addressing the limitations, which combined substantially enhance our forecasting capacity. We consider better leveraging organismal biology as central to meeting the remaining challenges. Our assessment concentrates on ectothermic animals for tractability, but many of the limitations are general across taxa.

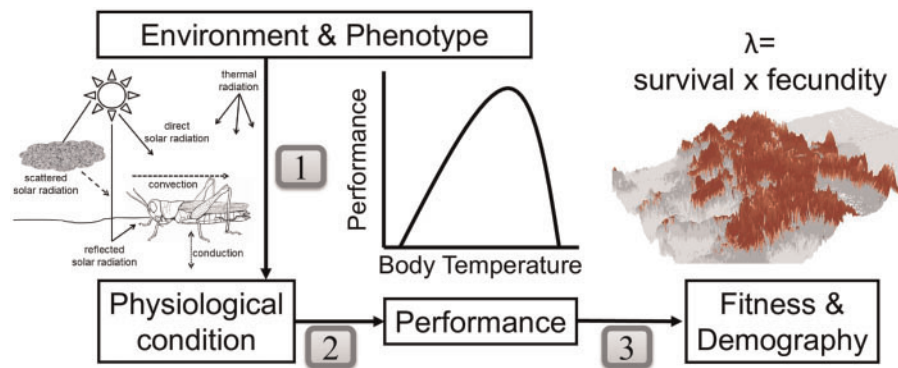
We advocate integrating models at the physiological, performance, and fitness levels to connect environmental conditions, phenotypes, and the ecological and evolutionary consequences of climate change (Buckley and Kingsolver 2012). We divide our review into three sections corresponding to components of the modeling approach (Fig. 1). First, the environment must be sensed at scales relevant to organismal physiology. Second, these microclimatic conditions must be filtered through organismal phenotypes to estimate body temperature and organismal energy and water balances (Porter and Tracy 1983). These patterns can be integrated with organismal performance data to predict consequences for survival, development, and reproduction. Third, these different fitness components can be combined to predict population demography and fitness.

### **Sensing the environment at scales relevant to organismal physiology**

Online databases and dissemination tools are rapidly expanding access to environmental data. However, few tools are equipped to deliver data with sufficiently fine spatial and temporal resolution to be immediately biologically relevant (but see our group's efforts at [trenchproject.github.io](https://trenchproject.github.io)). Fine scale data are also limited. Air temperature data are widely available, but estimating the body temperatures of terrestrial organisms minimally requires data on surface temperature, radiation, and wind speed and energy budget models for integrating those data. Unfortunately, temperature data tend to be available at spatial resolutions 10,000-fold coarser than the size of focal animals and 1000-fold coarser than the size of focal plants (Potter et al. 2013). Most point or interpolated data are derived from weather stations with a height of 2 m, where temperatures can be drastically different from those close to the ground, where organisms often occupy surface boundary layers (see also microclimate model section below).

### **Dataloggers and sensors**

Many researchers try to circumvent these problems by using data loggers to collect their own microclimate data (Bramer et al. 2018). iButtons and similar sensors are relatively inexpensive and easily used to record air or water temperature. Their utility can be enhanced by embedding them in physical models of organisms or live organisms so that they indicate body temperatures (Bakken 1992; Dzialowski 2005; Helmuth et al. 2016). However, many organisms are too small to make iButtons practical.



**Fig. 1** An ecological forecasting framework using (1) environmental conditions and an organism's phenotype to predict its physiological condition such as heat and water balance. (2) Estimates of organismal performance as a function of physiological condition can be used to (3) predict fitness components such as survival and fecundity and ultimately demography and distributions. The numbers correspond to sections of our review.

The thermocouples or thermistors compatible with many data loggers are likewise too bulky for many small organisms. Small thermocouples or thermistors generally require channels that measure voltage or resistance levels, which can be prohibitively expensive. Single loggers with a sufficient number of channels can cost thousands of dollars, resulting in complex tangles of thermocouple or thermistor wires connecting to single data loggers. Data loggers suitable for the fine-scale measurements needed by organismal biologists remain difficult to obtain and deploy and lag far behind the technological innovations available for other applications (e.g., industrial).

Low-cost microcontrollers (e.g., the Arduino open-source electronic prototyping platform) built onto single circuit boards are rapidly expanding sensor and data logging options, but biologists often lack the electronics skills required to deploy the microcontrollers. Communities of electronic hackers (create.arduino.cc, hackster.io, instructables.com) assist aspiring creators, but easy to implement plans for environmental data loggers are needed (but see [github.com/millerlp/Thermocouple\\_datalogger](https://github.com/millerlp/Thermocouple_datalogger)). Although low-cost solutions have improved considerably, investment of time and energy is required to make them reliable (Barnard et al. 2014). Deployment (e.g., cabling and waterproofing) and long-term viability in the field remains a challenge (Lockridge et al. 2016). Approaches for creating wireless networks of data loggers are also needed.

### Sensing spatial variation: IR cameras, drones, and satellites

Low-cost, versatile data loggers promise improved spatial and temporal resolution for environmental data, but complementing dataloggers with spatial sensing tools can improve characterizations of microclimate

variability across landscapes. Information on how animals use microclimate variability is also needed. As animals move through landscapes, particularly for behavioral thermoregulation, their experience of the environment can differ drastically from mean conditions (Huey et al. 2012; Potter et al. 2013; Woods et al. 2015). The spatial distribution of microclimates influences the efficacy of thermoregulation (Sears et al. 2016). Lightweight tracking devices offer information on how organisms are moving through and using microclimates (Kays et al. 2015).

Remote sensing can effectively characterize microclimate landscapes in some habitats (Anderson and Gaston 2013) but is sensitive to methodological issues such as sensing distance and differences in emissivity among organisms and surfaces (Faye et al. 2016). Remote sensing is thus particularly powerful when validated using on the ground sensors (Sutton and Lakshmi 2017). Promising technologies for assessing surface temperatures and other environmental variables include thermal cameras mounted on drones and satellites (Faye et al. 2016). Thermal cameras are becoming more affordable and accessible. Options include inexpensive cameras that attach to smartphones (e.g., FLiR one, SEEK), but they offer limited resolution and accuracy relative to more traditional thermal cameras. Additionally, few inexpensive options offer the ability to expediently extract temperatures for each pixel or to collect time series. Reduced restrictions on flying drones are expanding their use in assessing microclimate landscapes (Allan et al. 2015). Although satellite data are proliferating, many satellites do not collect appropriate thermal IR data for estimating land surface temperature. Hopefully the situation will improve as new initiatives and private companies expand data availability (Boyle et al. 2014; Turner et al. 2015).

### Microclimate and biophysical models

Once fine-scale data are obtained, the challenge remains to estimate how organisms filter the microclimates into body temperatures. The challenge consists of two components: (1) estimating the microclimate experienced by organisms and (2) estimating body temperatures based on microclimate. Both empirical (sensors) and modeling tools exist to address each challenge. Sensors mimicking the physical properties of organisms (e.g., see “robomussel” section below) indicate body temperatures in particular microclimates, but have limited utility for estimating body temperatures in other sites, for other organisms, or at other times. Alternatively, models of energy fluxes within the environment (e.g., soil) or between organisms and the environment provide a general approach to predict temperatures (Kearney et al. 2014; Levy et al. 2016), but errors can be generated due to both the quality of the input environmental data and the models' approximations. We describe modeling approaches below with the hope of encouraging further development and application.

Biophysical equations have long been available to predict the microclimates and body temperatures available to organisms based on environmental data (Porter and Gates 1969; Gates 1980; Campbell and Norman 2000). Porter and colleagues have pioneered the development of biophysical models in ecology, but adoption has been limited due to model inaccessibility. Their release of the NicheMapR R package has recently expanded access to these tools (Kearney and Porter 2017), but the source code is only available for a subset of functions at this stage. Other functions are released only as Fortran executables, which limits their utility because they cannot be modified and one must rely on documentation to understand their performance. Others, including our research group (trenchproject.github.io), are working to increase the transparency and adaptability of microclimate models by releasing open-source versions.

For the first challenge component, microclimate modeling tools can simulate diurnal variation and estimate temperature and wind speed profiles, which can scale data from the measurement height (usually ~2 m) to the height relevant to organisms (Porter et al. 1973; Campbell and Norman 2000). Microclimate models can also be used to estimate unmeasured variables. For example, soil energy balances can be modeled to estimating surface and soil temperatures based on air temperature, wind speed, and radiation (Kearney and Porter 2017). Solar

radiation responsible for heating organisms can be modeled, but cloudiness is an important determinant of heating and difficult to estimate (Porter and Gates 1969; Porter et al. 1973; Campbell and Norman 2000; Kearney et al. 2014; Norris et al. 2016).

For the second challenge component, energy budget models balance heat losses and gains from thermal and solar radiation, conduction with the ground, and convection with the surrounding air or water to estimate organismal body temperatures (Porter and Gates 1969; Gilman et al. 2006; Kearney and Porter 2017). The models require phenotypic data (e.g., solar and thermal absorptivity, morphology, and physical properties) in addition to environmental data. Air temperature is often used as a proxy for body temperature in climate change studies, but body temperatures can differ substantially from air temperatures for organisms that absorb solar radiation or evaporatively cool (Sunday et al. 2014). Increasing availability of biophysical modeling tools should improve estimates of how organisms experience microclimates.

### Accounting for environmental variability and extremes

Most techniques for measuring and analyzing environmental variability and organismal responses have focused on mean or constant environmental conditions. Failing to consider environmental variability and extremes may compromise forecasts. The non-linearity of biological rates, with rate increases in warm temperatures occurring faster than linear, leads mean biological rates in variable environments to differ from, and generally exceed, biological rates at mean temperatures (i.e., Jensen's inequality [Martin and Huey 2008; Denny 2017]). The asymmetry of the temperature dependence of organismal performance additionally makes accounting for environmental variability essential (Martin and Huey 2008; Huey et al. 2012; Vasseur et al. 2014; Sinclair et al. 2016).

Extreme climatic events are a biologically important component of climate variability, but their inherent rarity poses a challenge for assessing their biological relevance. Environmental statistics offers techniques for describing the incidence and magnitude of environmental extremes, but the approaches have been only sparsely applied to biology (Denny and Gaines 2002; Denny et al. 2009). Statistical distributions that depart from normality (e.g., extreme value distributions) can accurately characterize the tails of temperature distributions and improve forecasts of future extremes (Kingsolver and Buckley 2017).



Translating time series of environmental data into frequencies can aid understanding time scales of environmental variation and biological responses (Dillon et al. 2016). In addition to the challenge of quantifying environmental extremes, relatively few measurements of biological responses and rates (other than critical thermal and survival limits) are made at temperatures corresponding to the tails of distributions (Kingsolver and Buckley 2017). Quantifying responses in variable and extreme environments will be central to accurate ecological and evolutionary forecasts.

### Case study: assessing environmental variability and extremes for intertidal mussels

Helmuth and colleagues have deployed an extensive network of robomussels-thermal data loggers with physical properties similar to mussels and thus with similar body temperatures. The data demonstrate the ubiquity of body temperature variation both within and among sites (Helmuth 2002; Helmuth et al. 2010, 2016). Here we leverage their published database (Helmuth et al. 2016) to illustrate the environmental variation within and among sites on the US west coast. Quantifying environmental variability and extremes can inform forecasting tools and enables generating realistic environmental data for incorporation in ecological and evolutionary forecasts.

We downloaded data for all sites in Washington, Oregon, and California from <http://datadryad.org/resource/doi:10.5061/dryad.6n8kf>. We analyzed all years of available data and all tidal elevations. We conducted a frequency analysis (employing the `spec_lomb_phase` R function available at [github.com/georgebiogeekwang/tempcycles/](https://github.com/georgebiogeekwang/tempcycles/)) to analyze the amplitude of environmental variation as a function of frequency (Wang and Dillon 2014; Dillon et al. 2016). We consider a sequence of 400 frequencies ranging from 0.001 to 1 days<sup>-1</sup>. Finally, we apply generalized extreme value (GEV) statistics (as in Kingsolver and Buckley 2017) to characterize the incidence of extreme thermal stress events. We fit GEV distributions to maximum daily robomussel temperatures using maximum likelihood and the `gev.fit` function in the `ismev` R package. We fit stationary distributions, but note that non-stationary fits can be used to account for shifts in the distribution due to climate change. We use the generalized Pareto distribution to characterize the tails of the distribution. We fit the distribution using maximum likelihood with the `fplot` function from the R package `evd`.

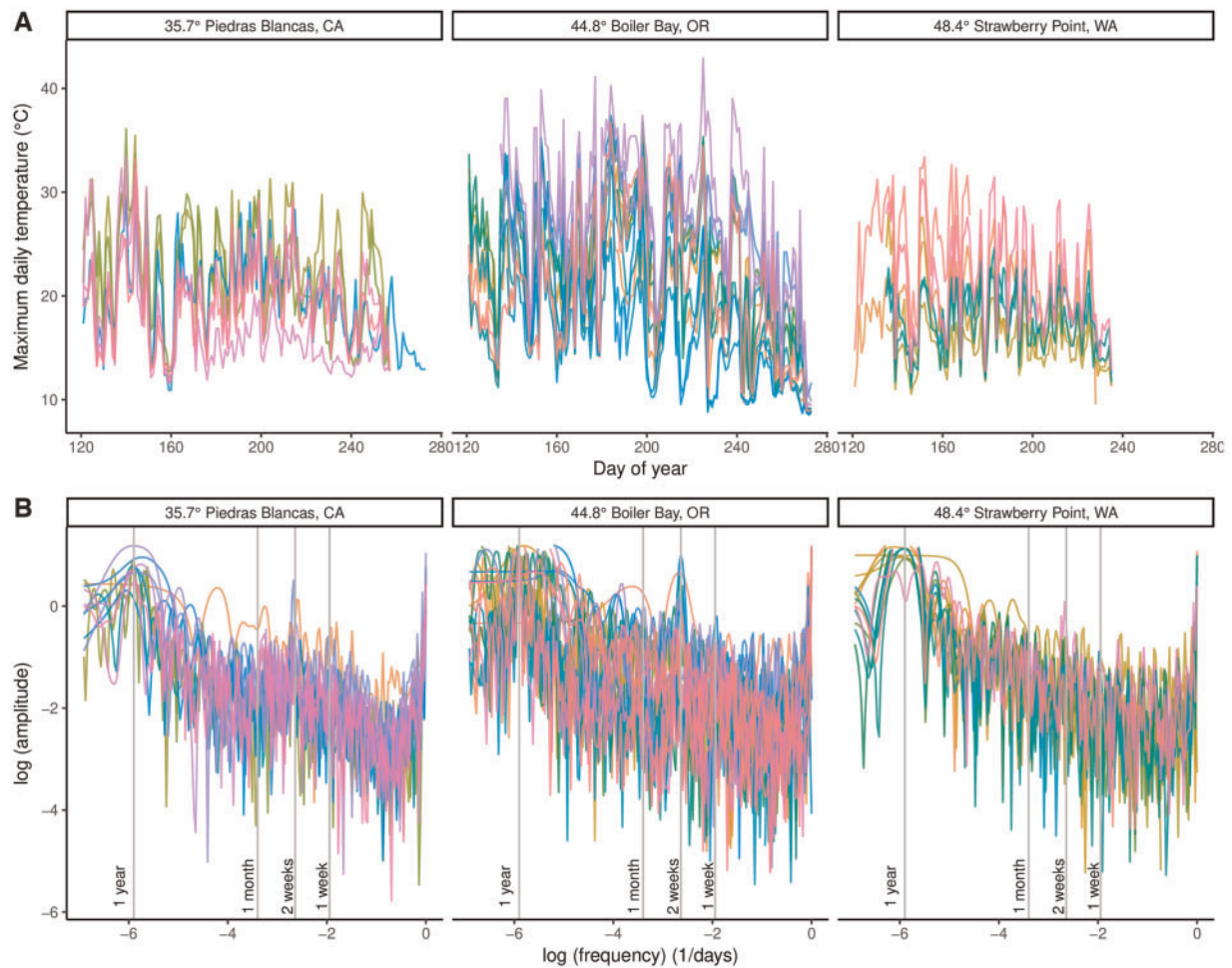
Our R code is available at [github.com/lbuckley/ClimateBiology](https://github.com/lbuckley/ClimateBiology).

The maximum daily temperatures of robomussels vary considerably within sites across the summer season due to microclimate differences (Fig. 2a). Local microclimates are particularly variable for intertidal mussels because heat extremes are experienced when the mussels are exposed to solar radiation during low tide. Thermal extremes depart from a typical latitudinal pattern, dramatically so because low tides tend to occur at midday in summer at the northern sites (Helmuth 2002; Helmuth et al. 2016). For example, the mid latitude site in Oregon reaches more extreme daily maxima than the southern California site (Fig. 2a). Microclimate variation is particularly pronounced for mussels due to their occupying different tidal elevations, but we note that similar vertical microclimate gradients occur in other habitats such as forests (Scheffers et al. 2014; Kaspari et al. 2015).

Employing a Fourier transform to partition the environmental variability into a sum of sine waves with different phases allows examining how the amplitude of environmental variation varies as a function of time interval (Wang and Dillon 2014; Dillon et al. 2016). Applying the analysis to robomussel data from three exemplar sites reveals that intervals of temporal variation are fairly characteristic within sites (Fig. 2b). We highlight the amplitude of variation at intervals of 1 week, 2 weeks, 1 month, and 1 year. Each of the sites exhibits extensive variation at the 2-week interval, corresponding to tidal cycles (Fig. 2b). Diurnal variation is substantial. The sites also experience pronounced interannual variation, likely reflecting regional climate oscillations.

Expanding the analysis to additional sites confirms that patterns of thermal stress depart from smooth latitudinal clines (Fig. 3). Northern sites tend to experience the most pronounced seasonal variation. While summers are generally cooler, the northern sites exhibit the warmest summer extremes due to large tidal fluctuations (Helmuth 2002; Helmuth et al. 2016).

GEV statistics can quantify the latitudinal patterns of variation (Kingsolver and Buckley 2017). GEV distributions are appropriate for distributions that depart from normality due to thick tails corresponding to a high prevalence of thermal extremes. Although GEV analyses have more frequently been applied to rare extreme events, they are increasingly being applied to daily maximum or minimum temperature data (Kingsolver and Buckley 2017). GEV distributions are described by three parameters: location indicates the position along the  $x$  axis, scale indicates the breadth, and shape indicates the



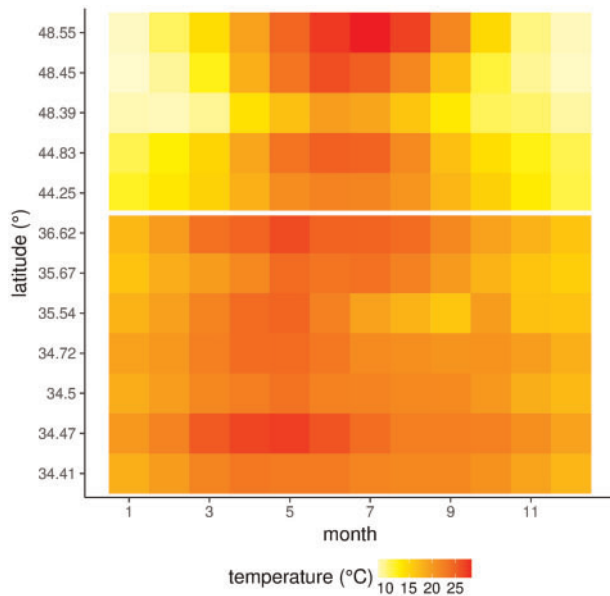
**Fig. 2** (A) Seasonal patterns of robomussel maximum daily temperature are variable both among (column labels: site names and latitudes) and within (colors: subsites, which vary in tidal height and habitat within sites). We depict data from 2002. Thermal extremes do not follow latitudinal gradients. See [huckleylab.shinyapps.io/ClimateBiology/](https://huckleylab.shinyapps.io/ClimateBiology/) for an interactive version. (B) Patterns of temporal variability can be characterized by analyzing the amplitude of variation as a function of frequency. Vertical lines indicate intervals of (from right to left) 1 week, 2 weeks, 1 month, and 1 year.

heaviness of the tail (illustrated in Kingsolver and Buckley 2017). Fitting GEV distributions to robomussel data reveals that most subsites have heavy tails (shape parameters  $> 0$  corresponding to a Frechet [type II] distribution). A minority of sites have shape parameters near zero (Gumbel [type I] distribution with a light tail) or less than zero (Weibull [type III] distribution with a bounded tail).

Although the mean robomussel data depart from a latitudinal cline, GEV analyses reveal latitudinal patterns of environmental variation. The southern sites exhibit warmer conditions on average (in part reflecting water temperatures), indicated by the GEV distribution being centered at higher temperatures (Fig. 4 location parameter). However, the northern sites tend to have fatter tails reflecting a higher incidence of thermal extremes (Fig. 4 shape parameter). The breadth of the temperature distribution does not

exhibit a latitudinal cline (Fig. 4 scale parameter). There is considerable variation in GEV parameters within sites corresponding to microclimate variation. GEV distributions—centered at warmer temperatures at the southern sites but possessing a heavier tail at northern sites—produce similar magnitudes of temperatures that are potentially stressful for organisms such as mussels. Consequently, neither the percent of days with temperatures above a 35°C threshold nor the maximum daily temperatures expected to be reached within 100 year intervals (100 year return interval) exhibit pronounced latitudinal patterns (Fig. 4).

Quantitative tools such as Fourier transforms and extreme value statistics are well suited to make sense of complex patterns of environmental variation. Both frameworks can be used to generate future environmental data for incorporation in ecological and evolutionary forecasts (Dillon et al. 2016). Applying



**Fig. 3** The mean (across years) of monthly maxima of robomussel daily temperatures departs from smooth latitudinal clines in summer months. Northern sites tend to experience the greatest seasonal fluctuations and the warmest summer extremes. The latitudinal axis is non-linear and the white line delineates northern and southern sites.

the tools highlights the importance of considering spatial variation within sites as well as variation in body temperatures rather than simply environmental temperatures, particularly for sessile organisms such as mussels.

### Translating environmental conditions into organismal performance

Laboratory and field measurements of the temperature dependence of organismal performance (e.g., thermal performance curves, TPCs) allow estimating responses to the environment. However, the methodology, conditions, and metrics of physiological and performance measurements often poorly reflect the spatially and temporally variable environments that organisms occupy (Sinclair et al. 2016). We summarize three key pitfalls in applying TPCs to estimate responses to the environment and propose future research needed to address the pitfalls: (1) timescales of measurements are often misaligned with the timescales of organismal response; (2) organismal responses often exhibit threshold temperatures, which are poorly captured in measurements; and (3) organisms respond differentially to temperature across their lifecycle, but measurements are generally restricted to a single life stage (Williams et al. 2016). We additionally advocate for

compilations of laboratory and field measurements to facilitate their incorporation in forecasts.

### Timescales of responses

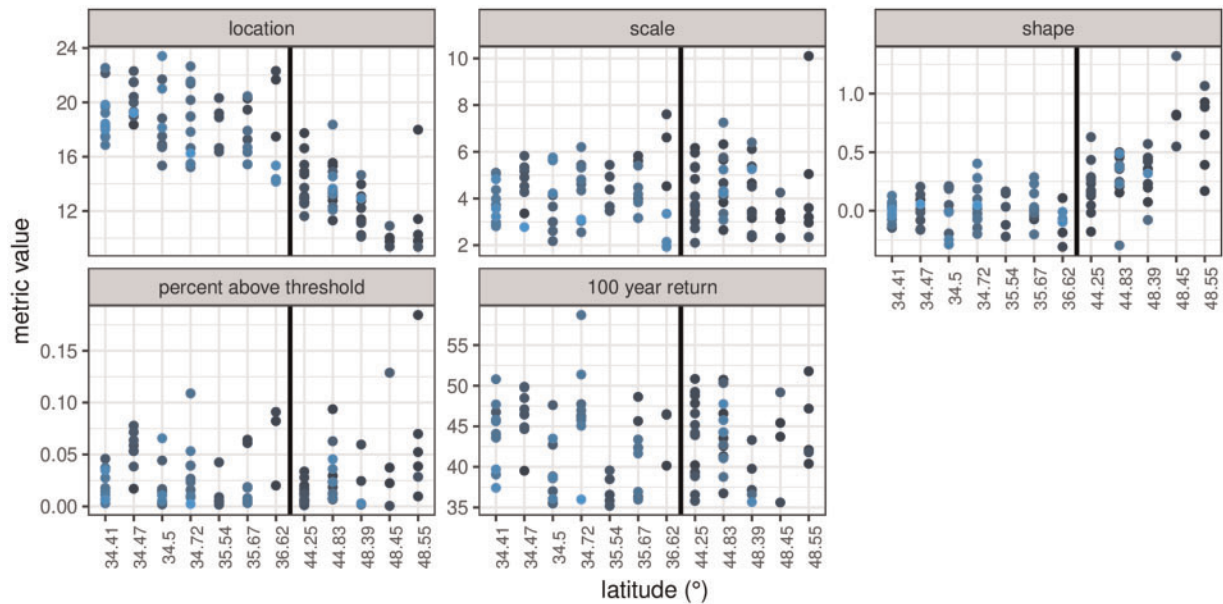
Data are increasingly showing that environmental variability and extremes strongly influence organismal responses. For acute thermal stress responses, assessment methods, particularly the rate at which temperature ramps, can bias estimates of critical thermal limits (Terblanche et al. 2007; Rezende et al. 2011). Over longer times scales, growth and development rates vary with whether they are measured at a series of constant temperatures, as is generally done, or in fluctuating temperatures (Kingsolver and Woods 2016). Translating between the timescale of measurement and of organismal responses to environmental variation is an important future objective.

Environmental history also shapes how organisms respond to their environments. The duration, severity, and frequency of past environmental stress determines whether organisms are less sensitive to the stress due to acclimation or more sensitive due to incurred damage or energetic costs (Williams et al. 2016). For example, organisms from variable, stressful environments tend to continuously express heat shock proteins, but have less capacity to induce additional expression in response to an acute thermal stress (Cavicchi et al. 1995; Hofmann and Todgham 2010). Environmental history also influences whether organisms respond to multiple stressors synergistically, additively, or antagonistically (Gunderson et al. 2016). We note that our review focuses on forecasting approaches based on temperature because physiological responses to temperature are better quantified than responses to other environmental conditions. Ignoring other stressors could invalidate forecasts, but we feel it is most tractable for general forecasting approaches to start with forecasting responses to temperature and subsequently build in responses to other, potentially interacting, stressors. Forecasts of responses to multiple stressors for particular organisms will inform future, general forecasts. Resource availability additionally interacts with temperature to determine organismal performance (reviewed by Sinclair et al. 2016).

### Thresholds

Organismal responses to environments are generally non-linear and dependent on whether thresholds are crossed. These thresholds include temperatures at which mortality or reproductive failure occurs, activity is limited, or energy or metabolic expenditure





**Fig. 4** Generalized extreme value (GEV) statistics provide insight into the likelihood of extreme thermal stress events for intertidal mussels. Within each panel corresponding to a GEV metric, sites are presented along a latitudinal cline on the US West Coast. The vertical line delineates northern and southern sites. The GEV distribution is centered at higher values at southern sites (location parameter) but has a longer tail of extremes at the northern sites (shape parameter). The breadth (scale parameter) is similar across sites. Consequently, the percent of days above a 35°C threshold and the highest temperature estimated to be reached over a 100 year return interval (100 year return) does not exhibit a latitudinal cline.

exceeds supply (Williams et al. 2016). Characterizing thresholds for an organism is a challenge for integrative biologists, particularly because the thresholds are sensitive to timescales of environmental variability and environmental history. For example, dividing a period of cold exposure into shorter, repeated exposures reduced the mortality and also the fitness of flies relative to a single exposure (Marshall and Sinclair 2009). Variation in thresholds also occurs across factors including seasonality, life stage, habitat, and oxygen levels (reviewed by Sinclair et al. 2016).

### Integrated consideration of the life cycle

Life stages differ in exposure and sensitivity to their environment (Kingsolver et al. 2011). They vary in microhabitat, coloration, and mobility. Differences can be as dramatic as marine organisms inhabiting pelagic environments as juveniles but intertidal environments as adults (Helmuth et al. 2005). Yet, measurements of thermal sensitivity tend to simplify life cycles or to be restricted to a single life stage (Levy et al. 2015). A comprehensive understanding of the impact of the environment on fitness requires an integrated consideration of environmental exposure and sensitivity across the life cycle that additionally considers environmental seasonality (Williams et al. 2015).

### Databases of phenotypes, physiology, and performance measurements

Generalizing to numerous species will require databases compiling physiology and performance measurements. Those measurements that are currently available are often difficult to compare and buried in papers, unpublished theses, and gray literature. Initial traits to include in a database of animals might include critical and lethal thermal limits, preferred body temperatures, physiologically optimum temperatures, and TPCs for key performance measures. Thermal tolerance databases are available (Bennett et al. 2018), but broad databases for animal physiology largely are not (Urban et al. 2016). Morphological and life history data are increasingly available (Jones et al. 2009; Wilman et al. 2014; Myhrvold et al. 2015). Researchers, including those attending a SICB Macrophysiology workshop (<http://www.sicb.org/meetings/2013/macrophysiology.php>), have called for a comprehensive database for animal phenotypes, physiology, and performance measurements, but progress has been limited.

Databases for animals have lagged behind those for plants (Kattge et al. 2011) in part because plant ecologists and physiologists have agreed upon standard measurements and measurement techniques (Cornelissen et al. 2003). Agreement on protocols was eased by most plants having an important and



restricted unit of focus (leaves) and appropriate and widely available tools (e.g., Licor 6400 photosynthesis system) to quantify relevant traits. Although consensus protocols may be more elusive for animals, they are essential. A recent paper compiles protocols for functionally-relevant traits of terrestrial invertebrates (Moretti et al. 2017) and may provide an initial step toward a comprehensive database. Machine learning initiatives (e.g., the opensource *DeepDive* and *Snorkel* initiatives) designed to extract data from publications have succeeded in constructing paleontology databases and may aid construction of an animal phenotype database (Peters et al. 2014). However, vetting and hand curating are often required to extract data from unstructured content.

The Global Biotraits Database (Dell et al. 2013) primarily compiles the thermal responses of ecological rather than physiological traits, but it illustrates the database challenges. Measurements tend to span a restricted range of temperatures relative to those organisms experience and to omit stressful or extreme temperatures (Fig. 5a). Measurements are often taken at a low number of constant temperatures (Fig. 5b), which makes it challenging to understand responses to variable environments (Kingsolver and Woods 2016; Williams et al. 2016). These characteristics reduce accuracy and often lead to extrapolation when describing thermal responses.

### Ecological and evolutionary consequences of climate change

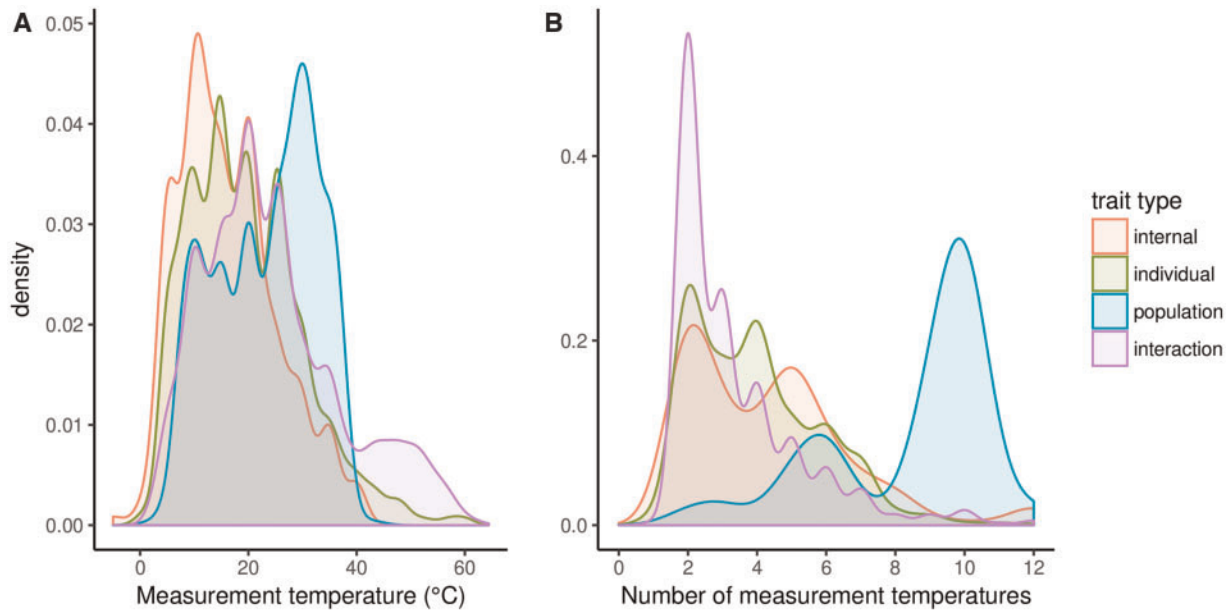
A particularly challenging component of forecasts is estimating fitness components from performance. Environmental variation and subsequent performance variation makes the estimation especially challenging (Martin and Huey 2008; Vasseur et al. 2014; Denny 2017). A viable approach is to translate performance into fecundity via the currencies of energy or time (Dunham 1993). Periods of low performance or conditions that preclude performance may reduce survival. One problem with fitness estimates is that most modeling is based on assuming linear (proportional and unidirectional) responses to mean environmental conditions. Yet, almost all organismal responses are non-linear and variable over short time periods.

As environmental and biological data increase in availability, techniques for temporal aggregation that reflect how organisms integrate climatic histories over their lives are needed (Huey et al. 2012). The sequence of environmental conditions, particularly time for recovery, determines the incidence of thermal stress. An appropriate aggregation would reflect

non-linearities in biological responses (such as rapidly increasing biological rates with increasing temperatures) and thresholds (such as temperature cutoffs for activity). Translating environmental conditions into metrics such as body temperatures, performance, or energetics at temporal intervals matching that of biological responses enables appropriate aggregation. These aggregation approaches would complement many ecological forecasting models, such as ENMs that are generally based on mean environmental conditions (Buckley et al. 2010).

Forecasting approaches that estimate fitness associated with phenotypes can be used to predict evolution. They allow estimating selection as well as considering the fitness consequences of acclimation and plasticity (defined to include all forms of phenotypic change, from long-term irreversible to short-term reversible). The interplay of plasticity and selection will be central to responses to climate change. Plasticity can slow evolution by buffering selection. For example, behavioral thermoregulation by lizards can initially buffer thermal stress associated with climate change, but can ultimately confer sensitivity to climate change by reducing selection (Huey et al. 2012; Buckley et al. 2015). Conversely, plasticity can facilitate evolution by enabling persistence or reducing variability in the direction and magnitude of selection associated with environmental variability (Chevin et al. 2010; Hendry 2015). Linking phenotypes to fitness suggests that the latter is the case for *Colias* butterflies: phenotypic plasticity can reduce variation in selection in response to both seasonality and interannual temperature variability and ultimately facilitate evolution in response to climate warming (Kingsolver and Buckley 2017).

Much additional research is needed to develop robust and general approaches to estimating fitness based on information about phenotypes and environments. For example, field experiments assessing selection in variable natural environments are needed to confirm predicted linkages between phenotypes, performance, and fitness. Emerging “omic” approaches (such as using genomics to infer the genetic basis of adaptation, using epigenetics to assess plasticity, and using metabolomics to assess the energetic implications of environments) offer promise in uncovering the genetic basis of responses to the environment as well as plasticity and selection in response to environmental variability and change (Bay et al. 2017). This information from omics will enable forecasts to better translate from environmental conditions to performance to fitness and evolution. Omic approaches will be particularly valuable



**Fig. 5** The Global Biotraits Database (Dell et al. 2013) illustrates limitations in thermal response measurements. Measurements tend to be (A) focused on a restricted range of temperatures relative to those that organisms experience and (B) include a low number of constant temperatures. Traits are divided according to whether they are internal (internal to the organism); individual (at the level of individual organisms that include mechanical interactions with the external environment); population (processes for a group of conspecific individuals); or interaction (involving interaction between two or more species).

for ecological forecasting when coupled with controlled laboratory or field environmental manipulations, common gardens, or reciprocal transplants (Hoffmann and Sgrò 2011). Many evolutionary forecasts will likely need to rely on quantitative genetic models because many traits involved in temperature dependence are determined by complex genetic mechanisms (Reusch and Wood 2007; Gienapp et al. 2008; Shaw and Etterson 2012). Finally, experiments are needed to assess heritability of such traits for use in evolutionary forecasts.

Models translating from environmental conditions and phenotypes to performance and ultimately fitness may be considered null models for forecasting. Other factors including species interactions and dispersal limitations that we omit here may strongly impact fitness and population dynamics and should subsequently be incorporated (Buckley et al. 2010; Urban et al. 2016). Although we have focused on estimating fitness from performance, the approach is complementary to other approaches being developed (Dietze 2017).

### Forecasting challenges

Progress toward meeting these challenges has been occurring steadily since previous reviews (e.g., Helmuth et al. 2005; Kearney and Porter 2009; Buckley et al. 2010; Huey et al. 2012), but many challenges persist (Sinclair et al. 2016; Urban et al. 2016;

Dietze et al. 2018). Improving our capacity for ecological and evolutionary forecasting depends on adequately characterizing organismal responses to spatially and temporally variable environments. Physiological, performance, and fitness responses to environmental fluctuations and extremes are characterized by nonlinearities and thresholds. Responses and whether they are modified by stress, acclimation, or plasticity are contingent on the environmental histories organisms have experienced. Environmental sensitivities vary across organisms' lifecycles. Microclimate selection and other forms of behavioral buffering alter how organisms experience environmental fluctuations. Accounting for all these complications of organism–environment interactions can be daunting, but emerging data and models promise to improve forecasts (Urban et al. 2016).

Much progress toward meeting these challenges has come in the form of delving into the empirical details of how the environment influences organismal performance and fitness and building forecasting approaches for particular organisms. The accumulation of these studies has positioned the research community to meet the challenges by generalizing understanding and approaches. Meeting the challenges is likewise aided by nearly 10 years of effort toward meeting the SICB grand challenges in organismal biology (Schwenk et al. 2009).

Over the next decade, we hope to see substantial progress toward solving the following challenges:

1. Sensing the environment at scales relevant to organismal physiology:
    - a. We need low-cost dataloggers with probes capable of collecting data on multiple environmental variables at scales appropriate to organisms. This goal will be facilitated by developing simple manuals and knowledge sharing initiatives for building data loggers from low-cost, simple-to-use microcontrollers and other technologies.
    - b. We require descriptions of spatial microclimates that can be obtained by environmental sensing technology including drones and satellites. Citizen science projects and private initiatives (e.g., [www.planet.com](http://www.planet.com)) have the potential to rapidly augment data availability and enhance data accuracy and spatiotemporal resolution.
    - c. We need microclimate and biophysical models capable of integrating data to accurately predict the body temperatures and conditions of organisms in their microclimates. The NicheMapR package is increasing awareness and usability of these tools but we encourage the release of source code to increase transparency. We invite anyone interested to contribute to our open-source initiative ([trenchproject.github.io](https://github.com/trenchproject)) or others.
- Assessment: Emerging technologies and a push toward open computing should enable meeting this challenge within the decade.
2. Translating environmental conditions into organismal performance:
    - a. We need more and better biological data if our forecasts are to improve. We hope to see the development of a database compiling animal phenotypic, physiological, and performance measurements relevant to forecasting. Design of the database should be done by consensus of a group willing to struggle with the methodological issues outlined above. What methodologies will be tractable while retaining the essential details of organisms' non-linear responses to their environments? Are there standard kinds of microclimatic, physiological, and environmental data that should be collected? Large scale initiatives to collect data for numerous species in a systematic manner will be required to fill and maintain the database ([Urban et al. 2016](#)).

Assessment: We see the development of databases, particularly those containing phenotypes, as the most

urgent forecasting challenge, which we hope funders will help meet.

3. Ecological and evolutionary consequences of climate change:
  - a. Publishing well-documented code ([Mislán et al. 2016](#)), release of software packages, and ideally developing common standards for model parameterization and data formats (e.g., Zoon R package, [github.com/zoonproject/zoon](https://github.com/zoonproject/zoon)) will speed modeling progress. Models and data collection efforts need to proceed in concert.
  - b. Although forecasting techniques are proliferating, many remain poorly tested ([Maguire et al. 2015](#)). Historical data, including environmental data, phenotypes, and ecological survey data, are necessary to test models. Necessary ecological data include phenology, distribution, and abundance data. Focusing on a select but diverse set of organisms (e.g., initially several ectothermic [insect and lizard] species, but eventually endotherms) would aid tractability. We need to assemble and disseminate both recent and paleo datasets for testing models. Historical data for model testing are currently limited, but we must collect data in a manner such that it can be used for future model testing.
  - c. The development of forecasting approaches should be forward-thinking and harness the potential of new types of data (e.g., omics) that may be readily available in the near future.

Assessment: General forecasting models are likely a distant reality, but practicing open-source science aimed at increasing reproducibility ([Parker et al. 2016](#)) and prioritizing model testing and adaptability will accelerate progress.

These and other challenges have led to continued predominance of statistical forecasting techniques that ignore important aspects of organism–environment interactions and perform poorly at predicting responses to past environmental changes ([Maguire et al. 2015](#)). Forecasting approaches that better account for temporal and spatial environmental variation and its influence on organismal physiology, performance, and fitness are overdue. Despite the difficulty, it is time to dedicate substantial effort and resources to improving forecasting models and collecting necessary data for parameterization. We need to accelerate the search for a middle ground to forecasting-models that are sufficiently simple to be generalized to numerous species but that include the complexities of how organisms respond to their temporally and spatially variable environments

necessary for robust forecasts. And we need the help of diverse organismal biologists from within SICB and beyond.

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