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REVIEW

Characterizing biological responses to climate variability and extremes to improve biodiversity projections

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Abstract

Projecting ecological and evolutionary responses to variable and changing environments is central to anticipating and managing impacts to biodiversity and ecosystems. Current modeling approaches are largely phenomenological and often fail to accurately project responses due to numerous biological processes at multiple levels of biological organization responding to environmental variation at varied spatial and temporal scales. Limited mechanistic understanding of organismal responses to environmental variability and extremes also restricts predictive capacity. We outline a strategy for identifying and modeling the key organismal mechanisms across levels of biological organization that mediate ecological and evolutionary responses to environmental variation. A central component of this strategy is quantifying timescales and magnitudes of climatic variability and how organisms experience them. We highlight recent empirical research that builds this information and suggest how to design future experiments that can produce more generalizable principles. We discuss how to create biologically informed projections in a feasible way by combining statistical and mechanistic approaches. Predictions will inform both fundamental and practical questions at the interface of ecology, evolution, and Earth science such as how organisms experience, adapt to, and respond to environmental variation at multiple hierarchical spatial and temporal scales.

Introduction

The problem: Unpredictability in climate change biology

Biological responses to climate change vary dramatically among populations and species to the degree to which some have argued that they are inherently unpredictable [1,2]. Simple approaches to predicting the responses of individual populations or species exhibit mixed performance. Shifts in species' distributions are often poorly predicted by statistical models correlating either species occurrences to their environment [3] or traits to the magnitude of species' response [4]. Some species predicted to become extinct from climate change have persisted through adaptation [5], whereas other species became extinct before their threat was known [6]. Further, biologists are just beginning to understand how genetic and epigenetic variation alters adaptation and resilience [7].

Although the responses of well-studied organisms to average conditions are generally known, the role of environmental variability in shaping organismal performance and fitness is still poorly understood [8,9]. Organisms integrate variability in different ways and apply strategies including microhabitat choice or plastic changes in physiology to avoid low-fitness conditions [10]. Along with variability, organisms must also contend with an increasing incidence of climate extremes, which are when variability crosses a threshold [11]. However, responses to variability and extremes are not often understood, tested properly, nor incorporated into predictive modeling [12]. Improving projections of biological responses is imperative for policy and management since the biodiversity and ecosystem impacts of increases in variability and extremes are accelerating [13,14]. Accurately predicting climate change impacts is essential to maximize the effectiveness of limited conservation and management resources [15].

The limited understanding of biological responses to extremes also stems from constraints in quantifying the incidence of climate extremes. For example, approaches to quantifying marine heat waves have only recently been developed and have uncovered increases in frequency and duration over recent decades [16] with implications for species, communities, and ecosystems [17]. Coupling the recent advances in threat quantification with information on organismal sensitivity offers a path forward in predicting biological responses to thermal extremes and variability [18].

Here we propose an approach to tackle the problem of unpredictability in climate change biology that focuses on characterizing and generalizing the mechanisms by which organisms respond and adapt to environmental variability. We aim to engage and inspire synergies among physical scientists quantifying environmental variability and extremes, molecular and organismal biologists probing the biological mechanisms underlying responses to environmental variability, and computational researchers working to improve biodiversity projections. We first overview existing biodiversity projection approaches and challenges that limited their performance. We then present and illustrate a strategy for characterizing key organismal mechanisms and incorporating them in predictive models. We address questions essential to improving projections of biodiversity responses to climate change: How can we tractably identify the key organismal mechanisms across levels of biological organization that mediate ecological and evolutionary responses to environmental variation? How can we feasibly and generally include these mechanisms in predictive models?

Biodiversity projection approaches and challenges

The ongoing and looming biodiversity impacts of climate change are well established. However, the definitive proportions of species estimated to face extinction in the IPCC (Intergovernmental Panel on Climate Change) WGII and the IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) reports are based on coarse modeling approaches with high uncertainty. For example, one study that informed the IPCC report projects that with emissions pledges corresponding to ~3.2˚C warming, ~49% of insects, 44% of plants, and 26% of vertebrates will lose >50% of their ranges and thus face a high risk of extinction [19]. In contrast, overall rates of extinction are estimated at 9% for a similar rise in temperature when aggregated over 131 studies implementing a spectrum of modeling approaches and a more conservative ~95% range loss threshold for extinction risk [13].

These and other biodiversity projections which inform policy recommendations are mostly generated by correlative niche models [14]. In this approach, species' locality data are correlated with underlying environmental data to estimate an environmental response surface, often termed a "climate envelope" [20]. Correlative niche models can be readily implemented using limited data and perform well on some tasks such as describing existing species distributions [21]. However, they often perform poorly in extrapolation, due to issues such as novel climates, changing species interactions, complex relationships between environmental variables, or interactions between environment and genotype/epigenotype [3]. Yet, alternative modeling approaches are not sufficiently general or parameterized well enough to make biodiversity projections at the scales desired to inform policy. Thus, we are ill-prepared to understand which species are under the greatest threats from climate change and design mitigation strategies to prevent their loss.

One way to improve our ability to predict climate change responses is to create models that incorporate the links between environmental variation, evolutionary history, genetic and epigenetic variation, functional traits, and subsequent demographic responses [14,22,23]. Functional traits are organismal properties that affect individual performance, including survival, development, growth, and reproduction [24]. This functional approach builds from a growing body of research that suggests that linking physiological traits to realistic environmental variation is often central to understanding ecological and evolutionary dynamics [11,25]. Moreover, an understanding of realistic genetic and epigenetic contributions to the phenotype is needed to predict changes to functional traits [7,26–28]. Lastly, because traits link multiple biological levels, functional trait models can reveal how responses to environmental variability integrate across multiple levels of biological organization, including ecosystem properties.

Two classes of models leverage functional traits to better predict responses to novel and variable environments. Mechanistic niche models scale up from functional traits and their environmental interactions to performance and ultimately fitness and are often discussed as a means of improving predictions of climate change responses (Fig 1). Researchers have developed mechanistic niche models that provide proof-of-principle for a variety of species [22]. However, these models are seldom applied widely because we usually lack the high-quality data to parameterize them for most species on Earth [14]. Moreover, the lack of a flexible, general modeling framework creates a roadblock for those without the time or resources to develop a model crafted for an individual species or ecosystem [15].

Hybrid niche models offer a practical alternative to purely mechanistic niche models. They incorporate key biological mechanisms, but use computational pattern-based approaches to inform uncertain or unknown parameters or relationships. Despite the benefits of this more flexible, mechanistic approach, these models have seldom been implemented [14,29–32]. Consequently, a potentially important process-based tool for predicting biological responses to climate change remains underdeveloped and under-used.

Here, we seek to define a middle ground by developing models that are feasible to parameterize and implement computationally but capture the key biological mechanisms needed to predict responses to climate variability and change [14,30,32–35]. We follow the recommendations for creating interoperable biodiversity projection models that are developed with open, reproducible, flexible, and integrative design principles [15]. Resultant models should account for uncertainties in data sources, model structure, and outputs [36].

Environmental variability

Organismal and ecosystem processes respond to multiple climatic conditions at numerous spatial and temporal scales ranging from minutes to millennia and meters to miles [8,37–39]. Yet, most ecological predictions rely on environmental variables, such as air temperatures, measured at unrealistically large spatial and temporal resolutions relative to organismal

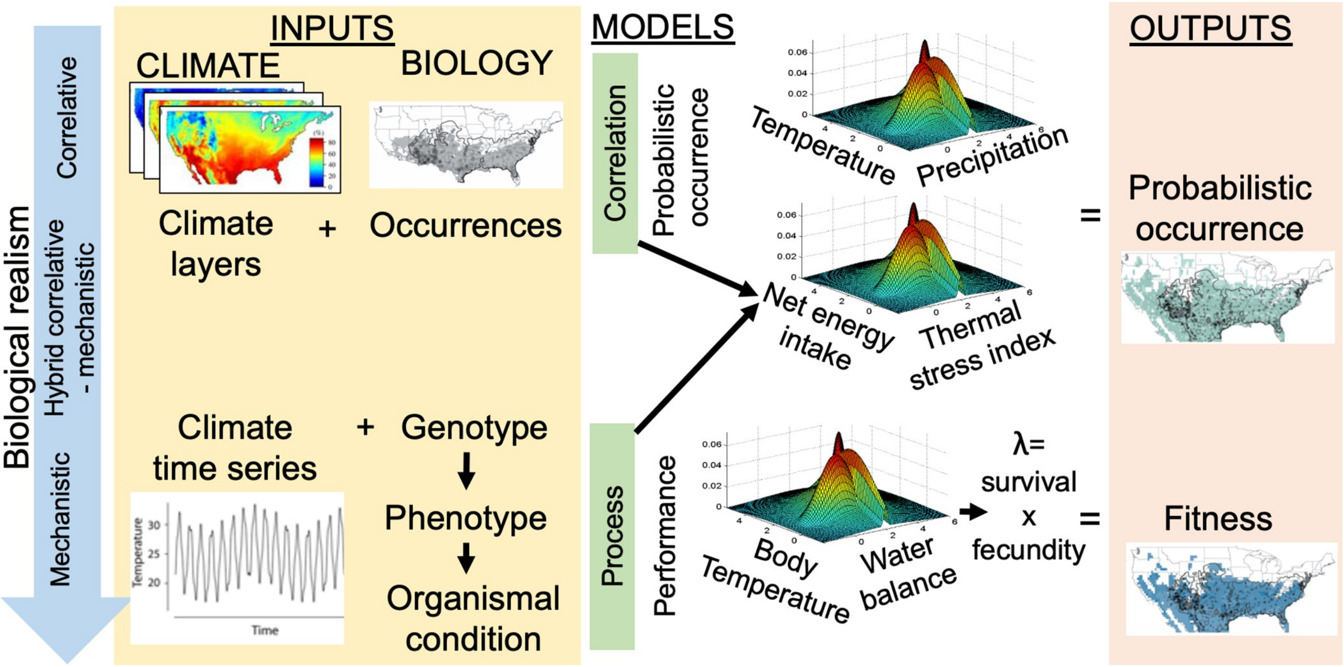

Fig 1. Correlative, hybrid, and mechanistic niche models for predicting distributions differ in their input, modeling approach, and output. Climate inputs are usually several temporally-aggregated (e.g., quarterly, annually) gridded datasets for correlative models versus climate time series for mechanistic models. Occurrence coordinates are input into correlative models whereas mechanistic models are parameterized with genotypes or phenotypes and other biological information. Correlative models predict the probability of occurrence based on statistically relating the climate data to occurrences and then spatially projecting the relationship. Mechanistic models explicitly model the processes by which organisms respond to the climate conditions. Often, empirically measured performance curves are used to estimate survival and fecundity (bottom row). Fitness estimates as a function of genotype or phenotype are estimated for each grid cell. Hybrid models meld correlative and mechanistic approaches. The most common strategy is to input biologically-informed layers into correlative models (middle row), but other strategies include using biological information to inform statistical relationships or statistically estimating parameters in process models.

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processes as well as body sizes, movement distances, and generation lengths [38–41]. This mismatch in scales reduces predictive accuracy by omitting variation at the scale of an organism's exposure [42,43] (Fig 2). Moreover, the non-linear responses of many biological processes to environmental variation cause performance at average conditions to depart dramatically from average performance over time [44,45]. Hence, we have yet to resolve the basic links between organismal fitness and environmental heterogeneity and their scaling and incorporate these insights into predictive models.

Examples are rapidly accumulating showing that variability and extremes can shape organismal and ecological responses to climate, with implications for distributions and diversity [46]. An assessment of responses to climate and weather extremes across taxa found that the majority of responses (including changes in body condition, fitness components, abundance, and distribution) were negative, followed by many ambiguous responses [47]. Most cases of neutral or positive responses were for species that benefit from disturbance. Short-term weather was found to better predict bird distributions than long term climate averages [48]. Tolerance to thermal extremes better predicts *Drosophila* distributions than does the thermal sensitivity of population growth [49].

The interaction of gradual climate warming and increasing extreme events is likely to exacerbate biodiversity impacts. Gradual warming can cumulatively stress organisms or elevate environmental variability and extremes into a thermal range that severely impacts organisms, which has been termed the press and pulse, respectively, of climate change impacts [50].

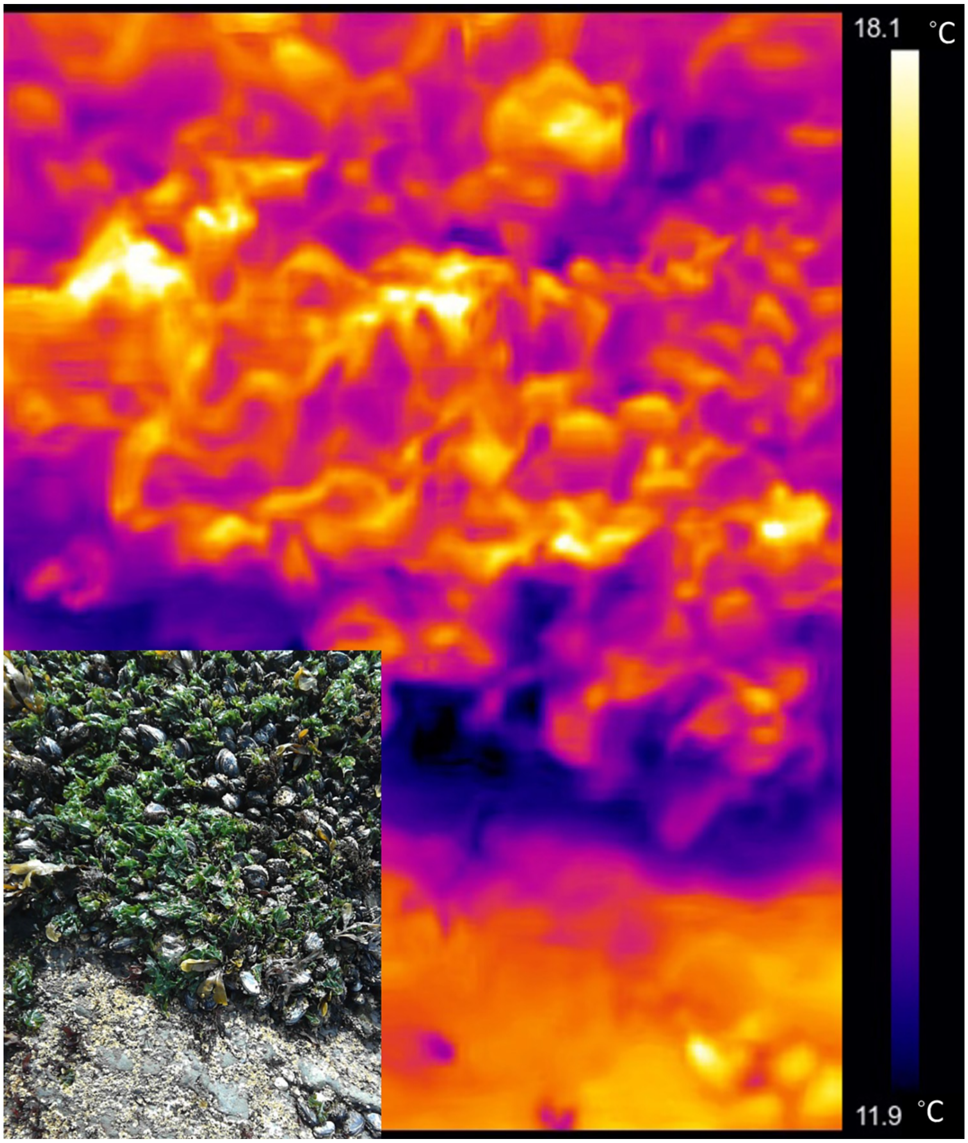

Fig 2. A thermal image of an intertidal mussel bed reveals substantial thermal variation over fine spatial scales (~1m, see visual image inset) as well as temperatures that exceed cool air temperatures due to solar heating.

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Thermal extremes, rather than gradual warming, appear to be driving insect responses to climate change, with implications for agriculture and biodiversity [51,52]. Heat extremes of the early 21st century are projected to become routine during the late 21st century and will interact with other weather extremes including drought and intense precipitation [53]. Organisms that can capitalize on these increasingly common extremes will be the winners of climate change, while those that cannot will be the losers. Yet, we still cannot predict which species are winners or losers or when current winners will become losers [12, but see 54].

Organisms in many regions will experience combinations of environmental conditions that are novel across their evolutionary history due to climate change [55,56]. However, linkages between organisms and their environments that are estimated statistically without attention to biological mechanisms are likely to extrapolate poorly across spatial and temporal scales and to novel environments [3]. Extrapolation requires a more holistic understanding of the numerous physiological processes responding to multiple environmental cues at disparate spatial and temporal scales. Additionally, the reshuffling of communities and other human-induced changes is also exposing organisms to novel species interactions [57], but phenomenological approaches tend to implicitly assume species interactions remain fixed [14]. Empirical and theoretical work has largely focused on thermal and moisture sensitivity, but research is increasingly highlighting the importance of considering how multiple environmental factors interact to influence physiology and performance.

Thermal variability tends to increase overall performance, via the increase in biological rates with temperature, until variability results in stressful temperatures [58]. Carryover effects including plasticity and damage can influence what temperatures are stressful [59]. Timescales of environmental variability relative to generation times and the duration of sensitive life stages are known to influence whether organisms can respond to the variability via plasticity or genetic adaptation [60]. In particular, high levels of unpredictable environmental variation often will be associated with constitutive molecular stress responses and potential tradeoffs with the strength of induced responses. The frequency and intensity of short term environmental variation relative to seasonal variation can determine the extent of temporal fluctuations in selection, the role of plasticity in altering selection, and resultant rates of evolution [61,62]. Spatial and temporal behavioral shifts can substantially buffer organisms from exposure to climate variability and change, which can slow thermal adaptation [41,43,59].

Comparisons of tropical and temperate elevation gradients have highlighted how organismal sensitivity shifts in response to environmental variability. Tropical organisms are thought to be particularly sensitive to climate change due to the evolution of thermal specialization to relatively constant, warm climates [63]. However, finer-scaled analyses indicate that high temporal environmental variability also can produce impacts of a similar or greater magnitude in temperate areas [64,65]. The survival of tropical organisms may be particularly affected by increasing variability. Increasing temperatures increase ectotherm energetic costs and decrease activity times at tropical or low-elevation sites [66]. Conversely, increasing temperatures may increase energy balance (and thus fecundity) at high-elevation sites [67].

Biological variability

Heterogeneous responses result from both differences in how much climate change organisms experience and how sensitive they are to it [60]. Many efforts to forecast responses to climate change focus on species, but within- and across-population variability can be pronounced and drive heterogeneous responses. Recent methodological advances facilitate linking genotype to phenotype and examining interactions with the environment, but generalizing these linkages in a manner that accounts for environmental and biological variability has been a challenge [26].

Organisms are also differentially sensitive to environmental variation in a variety of ways that can alter responses [68]. For example, plasticity is a common means by which organisms respond to predictable environmental variation in ways that enhance their fitness [69]. Phenotypic plasticity can facilitate evolution under certain circumstances by enabling persistence or reducing variation in selection across time or space, but it can alternatively slow evolution by buffering selection [69]. Epigenetics, the change in phenotypes without a change in genotype due to the environment, is a primary mechanism contributing to phenotypic plasticity [7,70].

Genetic variation also could provide the means for populations to evolve changed traits or different forms of plasticity to deal with environmental heterogeneity [26]. In particular, additive genetic variation in functional traits can provide the fuel for evolutionary responses that can rescue declining populations assuming large enough initial population sizes [61].

Evolutionary responses will occur proportional to this additive genetic variation, and this variation can be augmented especially by gene flow from populations already experiencing the local conditions [61]. Populations often differ across climate gradients in their adaptations to local conditions [28], and therefore species might harbor many of the important genetic variants necessary to survive future climates. The degree to which future responses to climate change will involve genetic, epigenetic, or some combination of both often remains unknown, yet is one of the most critical questions in climate change biology. The important point is to research these forms of biological variability further and incorporate what we do know into tractable models.

Making progress toward characterizing organismal responses to environmental variability

Characterizing and modeling how organisms experience environmental variability can reduce unpredictability in climate change biology. Identifying key timescales of environmental variation can inform the design of experiments investigating phenotypic and performance responses [8]. The characterizations can aid in simulating and parsing responses to realistic environmental variability. They can also be used to create variable environments without current analogs, which can be simulated to robustly test organismal mechanisms thought to mediate responses to variability.

Much of our understanding of organism-environment linkages currently derives from unrealistic or poorly planned empirical measurements. Many organismal thermal responses can be approximated by estimating thermal performance curves (TPCs) relating performance to body temperature [71] (Fig 4A). TPCs, or more simply thermal tolerances [72], have gained prominence as a tool for understanding physiological responses to variable temperatures [63,64]. However, TPCs are usually derived from experiments conducted at constant temperatures. Although some studies indicate that non-linear averaging techniques can use TPCs measured under stable conditions to accurately estimate responses to variable environments [73], others find substantial deviations due to carryover effects such as acclimation and damage [58,74]. Determining how TPCs can be measured, constructed, and applied to predict responses to variability is an important objective [71].

Two primary strategies for constructing TPCs relevant to variable environments are 1) devising statistical approaches to integrate across responses to environmental variability to estimate TPCs and 2) conducting performance measurements in environmental conditions with equivalent means but distinct patterns of environmental variation. Knowledge of response times can inform how to temporally integrate physiological responses measured in constant conditions to variable environments [25]. Promising statistical approaches for estimating performance in variable environments include scale-transition theory, a form of non-linear averaging [25,44,64]; an analytic framework [75] for distinguishing time-dependent effects including stress, acclimation, and compensation; alternative TPC descriptors including time-dependent shifts in response to acute stress [76]; and thermal death time models that unify estimates of thermal tolerance limits [77].

Time series measurements using -omics or physiological markers are increasingly feasible and can be used to assess the timescales of responses to environmental variation and clarify why non-linear averaging sometimes fails [78,79]. A promising approach is linking assays across levels of organization from genotype (SNP variation) to epigenome (whole genome methylation) to transcriptome (RNA abundance) to biologically relevant small molecules (metabolomics) to (energy and survival related) phenotypes [26]. Physiological (e.g., lipids) and genomic markers (e.g., heat shock proteins) can expediently capture responses to environmental variation. For example, bees exhibit parallel geographic clines in thermal tolerance and gene expression [28], and metabolomic profiling revealed that butterflies exposed to chronic warming shifted biochemical pathways involved in metabolism [80].

Case studies

We highlight cases where mechanistic or hybrid niche models have captured crucial biological dynamics in response to environmental variability that would otherwise have led to inaccurate results with correlative models (Table 1). We illustrate the process of quantifying exposure and sensitivity to environmental variability for intertidal mussels (*Mytilus spp*.) (Fig 2). Intertidal gradients are notable for dramatic shifts in environmental conditions at fine spatial (cm) and temporal scales (min). Tidal cycles transfer organisms from cool, relatively constant aquatic environments to more variable aerial environments often marked by pronounced solar heating and desiccation [25,37]. Small differences in tidal height can dramatically alter the duration and timing of aerial exposure, and complex interactions with other stressors (e.g., low salinity, pH, oxygen) are common.

Techniques to quantify environmental variability at scales relevant to organisms ("organismal climatology", [37]) are increasingly feasible [40]. "Robomussel" physical models, which have been extensively deployed [87], reveal body temperature clines that depart dramatically from smooth latitudinal gradients. Indeed, thermal extremes are most pronounced at northern latitude sites where long midday low tides often occur in summer [87]. Mussel body temperatures at 3 tidal heights at a site in Oregon, USA revealed substantial variation, and deviations from air temperatures (Fig 3A), that can be difficult to interpret. Fortunately, approaches including frequency analyses [8] and extreme value statistics [88] can be used to characterize key timescales and magnitudes of environmental variation relevant to organisms. Fourier transforms can decompose variation into sine waves of different frequencies and the

Table 1. Examples of mechanistic or hybrid niche models that project different responses to climate change than correlative niche models by accounting for biological responses to environmental variability. We focus on animal examples since plant studies more commonly incorporate mechanistic approaches.

Mechanistic Niche Models
Insects: Fitness estimates show that beetle populations along a tropical mountain will shift from growth to decline with a temperature increase of 2–3˚C [23]. Beetle populations lack the genetic variation to adapt to global warming [27].
Insects: Temporal expansions of montane butterfly thermal opportunity in response to recent climate change have generally offset survival impacts of thermal extremes. Phenotypic plasticity buffers fitness responses to environmental variation to promote the evolution of wing solar absorptivity [62].
Reptiles: Fitness advantages of longer lizard reproductive seasons associated with climate change will be offset by decreased summer survival of early life stages in response to thermal extremes [81].
Birds and mammals: Desert mammals have fared better through recent climate change than birds due to a greater capacity to buffer thermal extremes [82].
Mammals: Koala distributions are limited by water stress associated with heat waves and rainfall timing. Mechanistic and correlative projections of climate change responses diverged due to weather extremes and the breakdown of correlations among climate variables [83].
Hybrid Niche Models
Corals: Correlative SDMs that account for thermal extremes exceeding a coral's physiological tolerance project greater habitat contractions in response to climate change [84].
Amphibians: Hybrid and mechanistic SDMs projected different current and future energetically suitable habitat for salamanders than correlative models due to changes in resistance to water loss in response to thermal variability [85].
Mammals: Correlative SDMs incorporating mechanistic predictors of pika surface activity times, which account for behavioral buffering of environmental variability, predicted less habitat loss in response to climate change than those incorporating only climate predictors [86].

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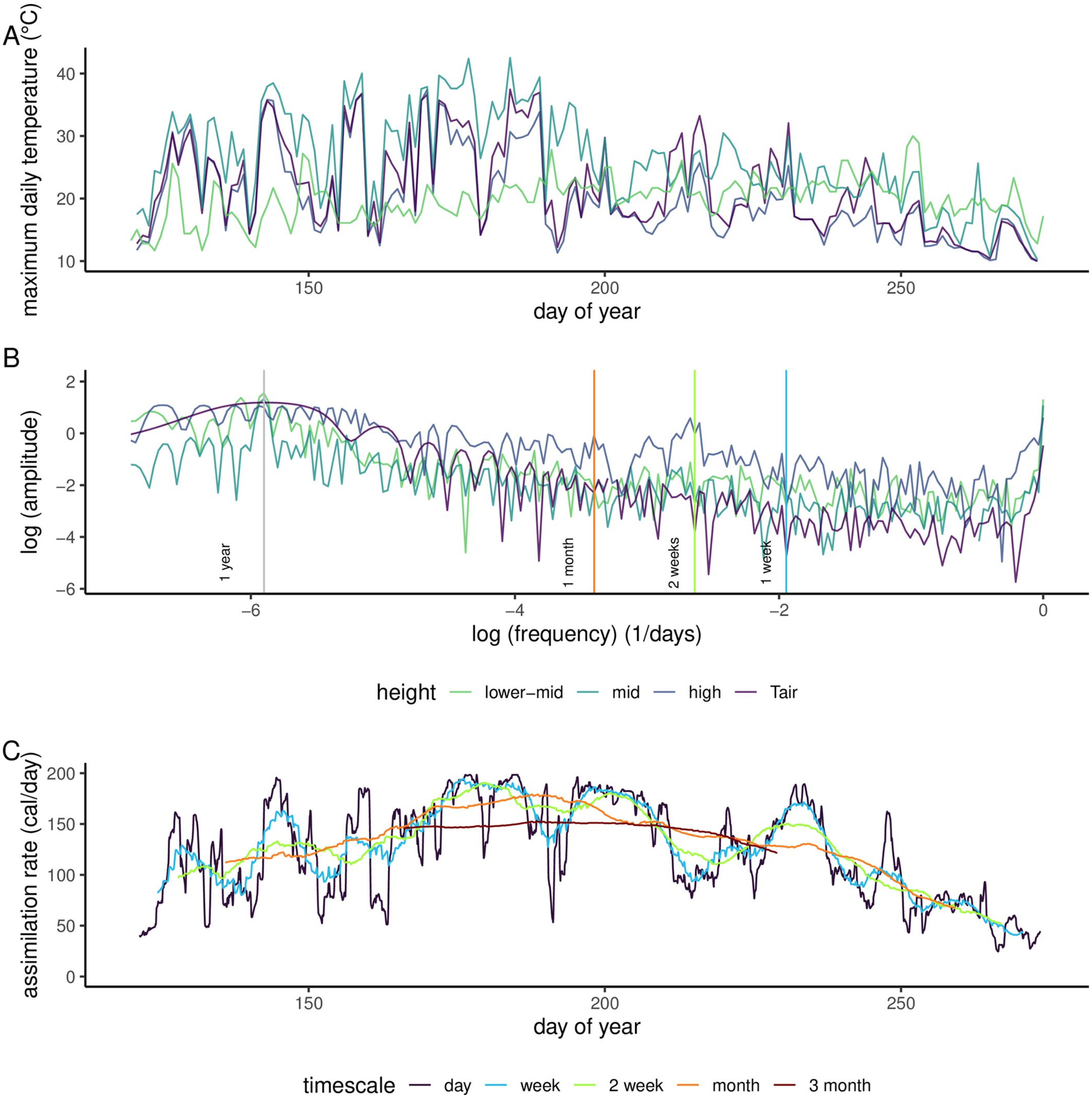

Fig 3. A) Robomussel physical logger daily maximum temperatures depart substantially from air temperatures (purple) during 2007 in Boiler Bay, Oregon, USA (Data from [87]). Temporal variability is substantial and increases higher in the intertidal (color). B) A frequency analysis of the daily maximum temperature data reveals that body temperature variation is pronounced at daily or circatidal [log(frequency) = 0], 2 week (tidal cycle apparent at the high site), and annual time scales. C) We then apply a TPC for assimilation rate to 10 minute body temperatures at the lower-mid intertidal site and rolling averages at coarser timescales (S1 Text). We omit the 10 minute data because estimated performance on many days ranges from 0 to the maximum. Even the coarser temporal scale data demonstrate the importance of accounting for fine temporal scale variation when considering performance implications. Code and data for analysis are available at https://github.com/lbuckley/VariabilityExtremesMussels.

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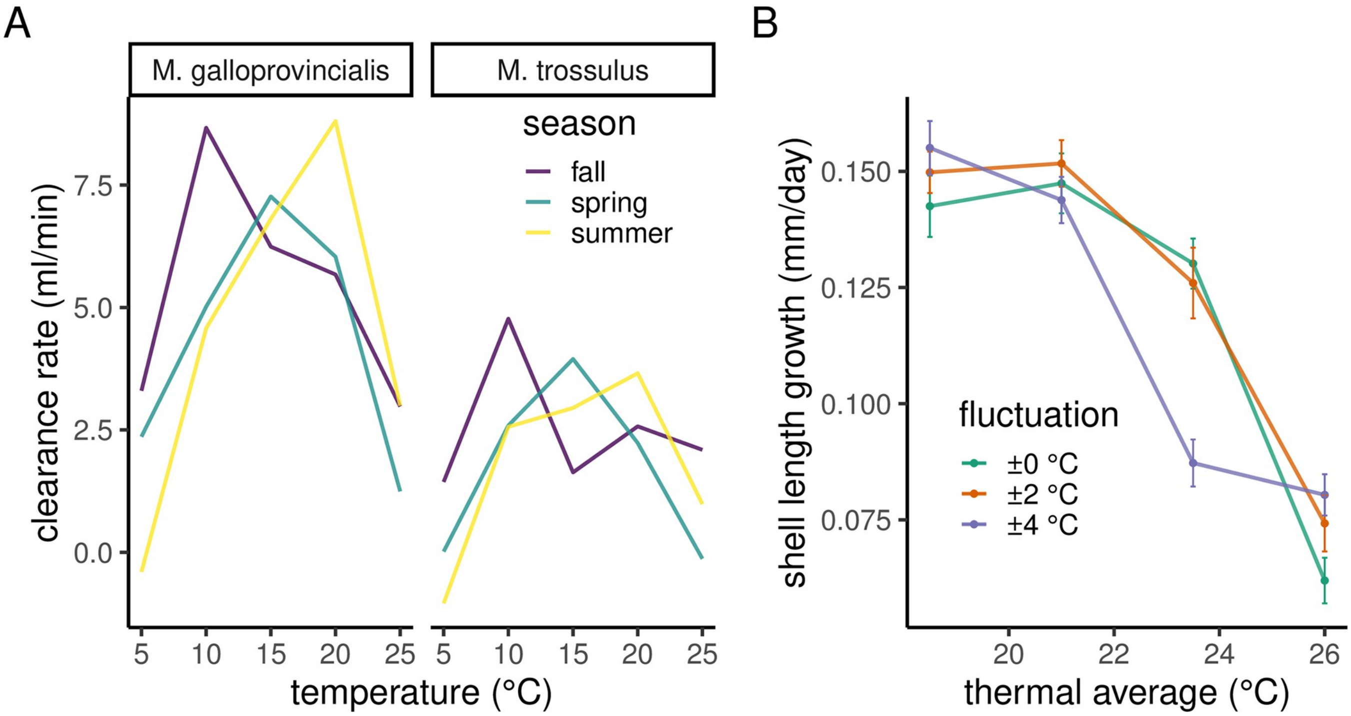

Fig 4. A) Clearance rate TPCs exhibit seasonal acclimation for mussel species (Data from [90]). B) Thermal fluctuations shift from augmenting to detrimenting long-term *M. edulis* shell length growth as average temperatures increase to approximate future marine heat waves (Data from [91]).

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corresponding magnitudes indicate how timescales contribute to overall variation. Our focal site reveals strong variation at intervals corresponding to short-term variability (diel, circatidal), tidal cycles (2 weeks), and annual variation (Fig 3B).

Experiments with intertidal mussels exemplify the need for caution when using performance responses to constant conditions to predict responses to environmental variability. TPCs vary both among organismal performances and with the magnitude of environmental variation [89]. Short-term performance is generally measured without thorough consideration of acclimation or thermal history [10,71]. Yet, feeding (clearance) rate TPCs for two *Mytilus* species shift to warmer water temperatures in warmer seasons (Fig 4A). An experiment with Pacific *M. trossulus* found that neither short-term (feeding rate, byssal thread production) nor long-term (growth, survival) responses to fluctuating water temperatures were well predicted by nonlinear averages of performance in constant environments [74].

However, feeding responses to short-term (1-day) thermal fluctuations were used successfully to predict Mediterranean *Mytilus* growth responses to constant and diurnally fluctuating thermal regimes [91] (Fig 4B). Whether experimental temperature fluctuations were beneficial or detrimental depended on the thermal environment. At the coolest mean temperatures, fluctuations resulted in warm temperatures that accelerate growth without inducing thermal stress (Fig 4B). When mean temperature approximated near-future heatwaves (23.5˚C), thermal fluctuations resulted in stressfully warm temperatures that were detrimental to growth. However, when the mean temperature approximated end-of-century heat waves (26˚C), thermal fluctuations provided relief from stressful temperatures that enhanced growth.

To roughly gauge the performance implications of temporal variation (assuming no carryover effects), we apply a TPC for assimilation rate [92, in 93] to 10-minute resolution body temperature data at the lower-mid intertidal site. Assimilation is a key performance metric, and we assume its temperature-dependency is maintained when the mussel emerges from water. Estimates often vary within days from poor performance to maximum performance as mussels experience fine temporal scale environmental variation as they move in and out of the water. We use rolling averages to portray how averaging body temperatures from daily to weekly to monthly masks variation in performance, particularly stressful periods that fall outside the critical thermal limits of the TPC (Fig 3C). The temporal aggregation highlights that mean performance does not equal performance at a mean temperature due to non-linear responses, which is a well-known mathematical outcome called Jensen's inequality [25,44]. Indeed, assimilation estimates increase from 92 to 122 to 137 cal/day as performance is estimated using ten-minute, daily, or monthly averaged body temperature data.

Experiments reveal mechanisms that drive deviations from our rough estimates. Both reversible and irreversible (developmental) plasticity altered the thermal tolerance of California mussels (*M. californianus*) and the energetic cost of plasticity reduced growth [94]. Exposure to a single heat extreme rapidly and persistently improved *M. californianus* thermal tolerance and survival of subsequent heat extremes [95]. Mussels from higher in the intertidal (high variability) acclimated more [96]. Environmental histories (including parental exposure) result in carry-over effects that alter bivalve phenotypes [97]. Both genetic and epigenetic variation determine the extent of environmental memory [70]. Environmental variability can either mask or unmask *M. californianus* physiological variation across levels of organization by reducing or accentuating fitness differences, respectively [79]. Further characterizing time series responses to environmental variation across levels of organization will be important to characterizing biological responses.

Mechanistic models have clarified how environmental variability shapes mussel fitness and demography, including by altering energy allocation. For example, allocation to energetically costly byssus fibers, that can improve attachment and thus survivorship, trades off with energy available for growth and reproduction [98]. Constraints on *M. edulis* distributions differ among regions between acute thermal survival and cumulative energetics [99]. This study suggests mechanistic models are likely needed when the thermal gap between performance failure and mortality is large relative to environmental fluctuations, indicating distinct thermal limits at acute and longer timescales [99]. Mechanistic models can also aid accounting for biotic interactions. TPCs have been applied to assess the relative thermal sensitivities of performance and energetics of mussels and their predators [93], but thermal history alters interaction rates and thus also needs to be incorporated [100].

Overall, this case study illustrates how an in-depth understanding of the spatial and temporal scales of environmental variability and biological responses can be integrated into mechanistic models that provide more realistic and accurate predictions for the future. Our case study suggests that SDM projections could be improved by using daily or sub-daily gridded environmental data to estimate body temperatures, which can depart substantially from air temperatures averaged over longer periods or not accounting for microhabitat effects (see approach below). Seasonal assimilation rates or other performance or fitness metrics thought to limit distributions could be input into correlative SDMs to create a hybrid SDM. Correlative SDMs and mechanistic calculations of mussel growth rates were integrated to identify thermal limits on distributions used to forecast future distributions [101].

Toward models better accounting for organismal mechanisms

So how can we feasibly and generally include these organismal mechanisms, such as genetics and plasticity, mediating responses to environmental variability in predictive models? Responses to environmental variability are inherently difficult to incorporate in correlative niche models because their climate input is static climate layers that are un-linked to the manner in which organisms experience the environment (Fig 1). In such cases, mechanistic models can be used to provide biologically-informed input layers for correlative models that translate environmental variability into performance measures via response functions, such as the activity time available to the organisms [102] (yielding hybrid models). Incorporating estimates of extremes relevant to particular organisms (heatwaves and droughts) can be used to refine correlative SDM output [103]. Another approach is to exclude areas identified as unsuitable by mechanistic approaches (e.g., those subject to environmental extremes) from correlative SDM output.

The climate inputs to these models should also be developed at the spatial and temporal scales that are relevant to focal organisms. While most correlative models assume body temperatures are equal to air or water temperatures, mechanistic models often include microclimate models, which can scale conditions from sensor to organism height and estimate unavailable variables such as surface temperature, and biophysical models for predicting body temperatures and water balance [22,38,40]. Using the finest temporal scale of weather data at a spatial scale consistent with home range or dispersal distance provides one starting point. Aggregating organismal responses in an appropriate manner temporally will require decisions about what time scale is most important for determining biological responses in a particular species, depending on the degree to which behavior, acclimation, demography, or evolution determine fitness.

An advantage of mechanistic models is that they can account for how genotypes and phenotypes mediate responses to climate time series to determine organismal conditions and performance (Fig 1). These linkages can account for phenotypic plasticity and behavior [10,41]. Experimentally identified determinants of fitness components (survival and fecundity) also can be incorporated. Survival is often governed by acute stress events whereas growth and reproduction are often determined by chronic environmental conditions (e.g., energy balance across a season) [67]. Estimates of natural selection and genetic variation can be used to incorporate evolution in the models [24,62].

Mechanistic models have been developed and tested for particular taxa, but a concerted effort is needed to develop modeling approaches that can be applied more generally [22]. Comparing responses to environmental variability across taxa, levels of organization, and locations based on genotypes, phenotypes, and life histories in mechanistic models will likely suggest common principles that can support more general conclusions for similar species. Nevertheless, a complete mechanistic understanding of the processes linking environments to organismal fitness is likely to remain logistically and scientifically prohibitive for many non-model species and systems [14]. Also, parameterizing these data-hungry models is likely to be difficult and often will need to rely on assumptions or values taken from distant species. Hybrid models offer an efficient way to build semi-mechanistic models that include key biological constraints to inform computational pattern-based models. However, these models remain under-used and under-developed, with most hybrid models consisting of including mechanistic predictors (e.g., activity times, water of energy balances, incidences or durations of stressful environmental conditions) in correlative models [104].

Emerging biologically-informed data science approaches offer great potential to develop new forms of hybrid SDMs. Such approaches can leverage accumulated biological and environmental knowledge to generate projections to account for biological (e.g., energetic, functional, evolutionary) constraints and processes [105,106]. For example, experimental data on salinity and thermal tolerance was incorporated into a Gaussian Process Model to inform statistical modeling of seaweed distribution limits [107]. Bayesian hierarchical joint species distribution modeling can be used to account for traits, phylogenies, and species interactions in estimating environmental responses [108]. New trait and range shift databases offer opportunities to further develop machine learning approaches to improve the ability of traits to predict climate change responses by accounting for thresholds, non-linearities, and interactions [4,109]. Machine learning classification or regression tree approaches can account for the influence of traits on distributions, for example of marine species [110]. Another promising hybrid modeling approach is inverse modeling whereby model parameters can be inferred from model endpoints such as species' occurrences [30,32]. For example, Approximate Bayesian Computation, or ABC, was used to estimate salamander overwintering survival based on lake ice dynamics [111].

In our experience, few species, systems, or questions can be answered with a purely mechanistic model given knowledge gaps of important parameters or functions. However, hybrid models that leverage new machine learning and Bayesian techniques to estimate unknown model features offer an efficient way to incorporate mechanisms in advance of empirical work that fills in these gaps. Such work could eventually lead to more mechanistic approaches, and thus all of this modeling should be viewed along a continuum and as a process. Moreover, we advocate for ensemble forecasts that incorporate multiple predictions, ranging from correlative to mechanistic, which often have higher accuracy than single models and allow for estimating structural uncertainties (uncertainties due to model choice).

Conclusions

The current unpredictability in climate biology might often derive from (physiologically and ecologically) diverse organisms responding to environmental variation at fine spatial and temporal scales. These responses are not well characterized by correlative models, which do not extrapolate well beyond mean conditions to variable or extreme biotic or abiotic environments. We argue that characterizing biological responses to environmental variability provides a path toward improving predictions of biodiversity responses to climate change. Central to the characterization is identifying key timescales and magnitudes of environmental variability, experimentally probing responses to the variability across levels of biological organization, and identifying general principles that allow tractable incorporation of the biological mechanisms into predictive models.

Crucial to using organismal mechanisms to improve biodiversity projections is improving datasets for parameterization and validation. There is great potential to leverage datasets including phenology, abundance, trait, and distribution data at multiple temporal (months to decades to paleo) and spatial (local to global) scales to better test niche models. There is also potential to innovate approaches to utilize natural history collections to assess genetic, physiological, and phenotypic responses to climate change [112]. Efforts to measure and catalog phenotypes along with life history and habitat information are rapidly advancing (e.g., TraitNet, TraitBank, ButterflyNet), but the available traits are often not those needed for mechanistic models. Organismal mechanisms of responses to environmental variability and mechanistic models should be used for prioritizing functional trait collection and assembly [24]. Methods to characterize environmental sensitivity such as thermal performance curves (TPCs) should be revisited to better account for environmental variability in future models. We also advocate for the inclusion of TPCs in existing trait databases or the creation of a database specific to these important traits. Cyberinfrastructure is needed to work toward the vision of integrating numerous existing mechanistic model components to create a unified, modular model [15]. A commitment to and investment in characterizing biological responses to environmental variability, rather than relying on models that necessarily omit environmental variability, is needed to improve predictability in climate change biology.

Supporting information

S1 Text. Supplementary methods for fitting data on the temperature dependence of mussel assimilation rate.
(DOCX)

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