BIOPHYSICS, PHYSIOLOGICAL ECOLOGY, AND CLIMATE CHANGE: Does Mechanism Matter?

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■ **Abstract**   Recent meta-analyses have shown that the effects of climate change are detectable and significant in their magnitude, but these studies have emphasized the utility of looking for large-scale patterns without necessarily understanding the mechanisms underlying these changes. Using a series of case studies, we explore the potential pitfalls when one fails to incorporate aspects of physiological performance when predicting the consequences of climate change on biotic communities. We argue that by considering the mechanistic details of physiological performance within the context of biophysical ecology (engineering methods of heat, mass and momentum exchange applied to biological systems), such approaches will be better poised to predict where and when the impacts of climate change will most likely occur.

INTRODUCTION

The earth's climate is changing at a rapid rate (1), but uncertainty is considerable about this perturbation's impact on the planet's biota and about how and where we should look for these effects. The task for biologists is to measure and anticipate the magnitude and rapidity of the effects of climate change on natural ecosystems and to explore any potential for mitigation or prevention (2–4).

Recent studies have documented climate-related mortality events (3–12), changes in population abundances (13–15), shifts in species range boundaries (15–19), and phenological shifts in the timing of reproductive and migratory events (18–20). In particular, meta-analyses of species distribution patterns have elucidated climate-driven effects, but these studies have emphasized discovery of large-scale patterns without necessarily understanding the mechanisms underlying them (18, 19, 21–23).

Concomitantly, however, new biochemical and molecular investigations of the effects of body temperature on organismal and subcellular physiology have

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flourished (24–28). These latter studies have not only better revealed the mechanisms underlying the physiological responses of organisms to thermal stress but have also provided metrics of stress levels under field conditions (24, 26–39). Meta-analyses of pattern in nature and studies conducted at biomolecular scales, however, have tended to operate independently of one another.

Here we advocate for the inclusion of physiological insight when predicting the effects of climate change on populations and ecosystems (40–43). We describe how the application of biophysical ecology techniques (engineering methods used to explore the exchange of heat, mass, and momentum between organisms and their environment) can explicitly link studies at physiological and biomolecular scales with those at the level of populations and ecosystems (20, 35, 40, 41, 43–47). Moreover, we exemplify how ignorance of the physiological response of individual organisms, or populations of organisms, to environmental parameters can sometimes confound predictions of the effects of climate change on organisms (42, 48, 49). We highlight the importance of studying physiological performance within the context of the organism's local microclimate using a series of examples taken from intertidal, shallow-water marine, and terrestrial environments.

First, the relative importance of environmental factors that may limit a species' geographic or local distribution can vary markedly in space and time (50–53). A clear understanding of how multiple climate-related environmental parameters may alternatively limit species distributions is essential for predicting how each parameter will affect populations. Moreover, even when a single variable (such as body temperature) is a causative factor, which aspect of the environmental signal (e.g., average, maximum, or minimum temperature, or time history of the thermal signal) is most relevant to the species' fitness is not always clear (26, 35, 36, 54–57).

Second, just as environmental stressors can vary over a range of scales, the physiological capacity of an organism to resist or recover from environmental stress can vary significantly in space and time. As a result, it is impossible to predict the level of mechanical or physiological risk to which an organism is likely to be subjected without first quantifying both the magnitude of the environmental stressor and the ability of the organism to resist the environmental condition in question. For example, simply recording the force that a crashing wave imparts on an organism has little meaning without first understanding how the ability of the organism to resist that force may vary (58–60). Thus without a detailed mechanistic understanding of environmental safety factors (58–64), it is possible that our current efforts to characterize environmental signals may be insufficient in many cases.

Third, climate change does not produce a simple increase in global average temperature; rather it involves a characteristic set of changes in diurnal, seasonal, and geographic patterns of temperature, precipitation, and other atmospheric conditions. Analysis of ecological responses to climate change during the past century reveals a diversity of responses (or lack of response) that varies widely among populations and species. We argue that understanding the physiological mechanisms

that underlie how specific components of climate affect key life cycle stages will be important for predicting the ecological responses of many species to climate change.

Species and Population Responses to Climate Change

Environmental conditions can influence the physiological performance of organisms through three general mechanisms that vary in response time and reversibility (after Reference 65). First, environmental change can lead to genetic adaptation, a change in allele frequencies in a population via natural selection. This process is typically slow (requiring at least a generation) and irreversible during an individual's lifespan. Second, individuals may exhibit phenotypic plasticity or variable expression of genetic traits in response to environmental conditions. Plasticity can be reversible or irreversible and requires relatively brief times (usually less than one generation). For example, multiple phenotypes can arise where environmental conditions induce alternative developmental programs. The differential activation of developmental switches (e.g., arrested development) can lead to discrete phenotypes, whereas variations in the rates and degrees of expression cause phenotypic modulation (65). Another form of phenotypic plasticity is acclimatization, which involves a short-term compensatory modification of physiological function and tolerance in response to environmental change. Third, organisms can rapidly if not acutely adjust physiological state in response to environmental change. Such adjustments require seconds to days and are generally reversible.

Thus climate change may have three different outcomes depending on the physiological response of the species or population in question, as described by Fields et al. (24). First, if environmental changes are sufficiently small, organisms may acclimatize to those conditions. Second, if environmental conditions exceed the ability of some, but not all, of the individuals to cope with environmental change, then natural selection may favor some genotypes already present in the population. Under this scenario, the species range may be unchanged, but allele frequencies may vary (66–68). Third, if conditions are sufficiently severe, all organisms in the population will die or emigrate and the entire species range will shift (69).

Most difficult to uncover is the first of these scenarios, where environmental conditions do not directly affect mortality but instead alter phenotypic expression of genetic traits. Although acclimatization may imply improved organismal performance, such phenotypic plasticity may not necessarily improve fitness. For example, plasticity often involves the re-allocation of resources to one trait at the expense of another (e.g., trade-off between growth and reproduction). Furthermore, phenotypic variation can strongly influence biological interactions within a community, often in complex and counterintuitive ways (70, 71). Phenotypic plasticity is common in a broad range of plant and animal taxa, yet the consequences of trait-mediated interactions (TMIs) on community dynamics have rarely been documented, largely because of experimental constraints (70, 71). Thus the current challenge for biologists is not only to characterize the plastic responses of

organisms to environmental change, but also to improve our understanding of how trait plasticity can affect community dynamics (72).

Here we explore these issues using a series of case studies to illustrate the potential pitfalls that can appear when aspects of physiological performance are not incorporated into the predicted consequences of climate change on biotic communities. It is not our intention to detract from the significant insights that have resulted from large-scale meta-analyses and monitoring studies, but rather to argue that by considering the mechanistic details of physiological performance within the context of biophysical ecology, such approaches will be better poised to predict where the impacts of climate change will most likely occur (40, 41, 46, 47, 73). Although our examples focus on invertebrate animals, we also draw from the plant and vertebrate literature. Our goal is to illustrate the role of physiological performance and biophysical ecology and to emphasize the importance of mechanism in predicting pattern in nature.

Few of the issues raised here are new to physiological ecology, although many have renewed urgency in the face of global climate change. However, the combination of new molecular techniques, coupled with biophysical methods of measuring and modeling environmental parameters, urges a reevaluation of the role of physiological mechanism in studies of climate change. The merger of these approaches presents an unprecedented opportunity to address explicit hypotheses regarding the effects of climate change on natural communities under field conditions (26, 39–41, 46).

HOW DO WE MEASURE THE ENVIRONMENT? THE ROLE OF BIOPHYSICS IN CLIMATE CHANGE BIOLOGY

The response of any individual organism to climate change can be viewed as a series of cascading scales, in which an organism's microclimatic conditions are transduced through the animal or plant's morphology to modify its cellular environment, ultimately eliciting a physiological response. Such measurements and models of climate and climate change are feasible only through large-scale approaches such as remote sensing and observatory networks. These technologies are not only incapable of directly providing information at smaller (microclimate) scales relevant to physiological performance, but they also fail to account for the effects of organism phenotype on physiological response. One promising approach for spanning this diverse range of scales lies in the application of biophysics, which accounts for heat, mass, and momentum exchange between organisms and their physical environment (40, 41, 46, 47).

For example, multiple interacting climatic factors, including short- and long-wave radiation, conduction, convection, and evaporation (43, 74–76), determine body temperature. Furthermore, many characteristics of the organism such as its color, morphology, and mass may modify heat exchange. Thus two ectothermic organisms exposed to identical climatic conditions can exhibit markedly different

body temperatures (47, 75). Morphological variation in coefficients of drag, lift, acceleration, and mass transfer (77) can similarly affect the exchange of mass (gas and nutrients) and momentum. For these reasons, the use of environmental temperature indices obtainable by satellite or global observatories [such as sea surface temperature (SST) and air temperature (T_a)] as proxies for body temperature (T_b) require explicit validation, even as relative indicators of thermal stress.

In a specific example, most predictions of coral bleaching are based on measurements of SST (3, 11, 12), even though this metric may indicate the temperature of only the uppermost few centimeters of the water column, and temperatures at depth can often change over much smaller spatial and temporal scales (78, 79). Whereas SST anomalies appear to be good predictors of bleaching over large scales (80), linking small-scale variation in coral physiology with these large-scale indicators of environmental stress is challenging. Indeed, spatial heterogeneity in coral bleaching may be related to concomitant variability in water temperature and flow (4, 81), but these patterns may be difficult to detect with satellite imagery without extrapolating such measurements to scales relevant to the organism.

Similarly, although SST is probably a good indicator of body temperature of intertidal organisms during submergence at high tide, it is not a good proxy for T_b during low tide (47, 82) when these organisms are known to be exposed to damaging thermal conditions (26, 83–85). Likewise, at least for some intertidal organisms, T_a is also a poor indicator of T_b (47, 82).

Biophysical methods, however, provide the critical link between large-scale measurements and individual organisms, and thus may enable large-scale prediction of climate change impact. Such methods explicitly model and measure rates of heat, mass, and momentum exchange between organisms and their environment and quantitatively provide an environmental context for controlled physiological studies (40, 41, 43–47, 59, 75, 85). A biophysical approach is a powerful means of predicting how environmental parameters, such as climate or wave height, are translated into physiologically relevant parameters, such as body temperature or force acting on organisms, and even more importantly of describing the temporal and spatial scales over which these processes occur. Such an understanding is a vital link in knowing where and when to anticipate the effects of climate change.

WHEN DOES CLIMATE SET SPECIES RANGE LIMITS? THE ROCKY INTERTIDAL ZONE AS A MODEL SYSTEM

The assumption that climate and, in particular, temperature set the local and geographic distributions of species is implicit to the idea that climate change will significantly alter natural ecosystems. Indeed, strong correlations exist between temperature and the distribution of species and populations over a range of spatial and temporal scales (14, 26, 86–102). However, several other studies spanning a range of ecosystems have found poor correlations between climate and species

range boundaries, challenging this assumption (49, 53, 103, 104). Here we exemplify this issue by considering attempts to understand limits to the distribution of intertidal organisms.

The rocky intertidal zone has been a primary natural laboratory for understanding the role of physical factors in setting range limits (105, 106). It is the interface of the terrestrial and marine environments and is one of the most physically harsh environments on earth. Forces acting on algae and animals from crashing waves in the intertidal zone can regularly exceed those generated by hurricane-force winds on land (58, 61, 107–112), and the body temperatures of intertidal organisms can fluctuate by 25°C or more in a matter of hours during aerial exposure at low tide (74, 82, 85, 86, 113–115). Because gas exchange during aerial exposure concomitantly leads to desiccation, many intertidal invertebrates rely partially or completely on anaerobiosis during low tide, which can lead to marked changes in body chemistry that have cascading influences on physiological performance even after resubmergence (31, 116–120). Temperature and desiccation also interact to influence the growth and survival of macroalgae (121–123). Salinity levels can fluctuate dramatically and, particularly for salt marsh plants, edaphic conditions can have extensive impacts on community structure (52, 124, 125).

Because rocky intertidal invertebrates and algae evolved under marine conditions, these species are generally assumed be exposed to the highest stress levels at the upper (vertical) edges of their intertidal distributions (105); where temperature and desiccation stresses are assumed to be maximal, periods of maximal aerobic metabolism are greatest (116, 126), and feeding is most limited. The lower distributional limits of these organisms, in contrast, are set by biotic factors such as competition (127) and predation (128). The result is often a striking pattern of zonation in which bands of species replace one another at regular intervals along vertical gradients of physiological stress (105).

Two logical extensions of this paradigm have relevance to the expected effects of climate change on rocky intertidal communities. First, if rocky intertidal species are already living at the absolute limits of their physiological tolerances, then any marked change in the physical environment should be reflected by shifts in upper zonation limits. Specifically, in the face of warming, the upper zonation limits of species should shift downward wherever these limits are set by some aspect of climatic stress (2). Second, if some aspect of physiological stress related to climate sets species range boundaries, then, as in other ecosystems, the distribution of warm- and cold-acclimated species should shift at extremes of range boundaries (13, 15, 129, 130). Several lines of evidence, however, suggest that these expectations are too simplistic.

First, how often upper zonation limits actually are set by climatic factors remains unresolved (104, 131), although some evidence suggests a relatively straightforward linkage. Wethey (50) experimentally transplanted barnacles (*Semibalanus*) above the level at which they naturally occur in New England (United States), and showed that high summer temperatures set the upper zonation limit of this species through post-settlement mortality. Chan & Williams (132) showed similarly that

heat stress appears to set the upper distributional limit of the barnacle *Tetraclita* on the rocky shores of Hong Kong. Tomanek & Somero (133) recently demonstrated that the production of heat shock proteins by two congeneric species of intertidal snails (*Tegula* spp.) appears to match their intertidal distributional limits, and Hofmann & Somero (30) have reported similar patterns for congeneric species of mussels (*Mytilus* spp.) over latitudinal scales. Southward (134) compared the thermal tolerances of several species of intertidal invertebrates in the United Kingdom with the climatic conditions to which they were normally exposed. Whereas he found that organisms at the upper limits of their intertidal distributional limits were seldom subjected to lethal thermal limits, his results did suggest that distributional limits were set by sublethal exposures to physiologically damaging temperatures or by the indirect effects of thermal stress on biotic factors such as competition for space.

In contrast, Wolcott (104) found little correspondence between maximum habitat temperature and the upper intertidal distribution of the limpet *Acmaea* and suggested instead that the distribution of these animals was set by biotic factors such as competition or food availability. Sanford (56, 57) presented evidence that the upper foraging limit of the sea star *Pisaster* was driven by seawater temperature and appeared to be unrelated to terrestrial conditions. Harley & Helmuth (53) compared microscale patterns of body temperature of barnacles and mussels in Puget Sound (United States) and found that upper zonation limits were tightly correlated with temperature at some sites, but at others the correlation was very weak, suggesting that temperature alternated with an additional limiting factor, such as feeding time, in setting upper zonation heights of these species in this region. Similar uncertainty exists when examining patterns over larger latitudinal scales.

If geographic range limits of intertidal species are set by temperature, as are upper zonation limits, then increased warming should bring about a relative increase in warm species at the more equatorial ends of species distributional limits (2, 13, 15, 16). Just such a pattern was observed over a 60-year period at a site in central California (13, 15), and Southward et al. (16) reported similar shifts in distributions of intertidal and planktonic species based on 70 years of climatic and faunal records from the western English Channel. Both studies related the observed shifts in abundance to increases in SST. However, as stated above, SST is not always an effective proxy for the body temperature of intertidal organisms (35, 47, 73, 82), and predicted patterns of thermal stress based on SST can vary significantly from those based on body temperature during aerial exposure at low tide (77). Specifically, Helmuth et al. (73) showed for intertidal mussels on the Pacific coast of North America that instead of a monotonic increase in thermal stress with latitude, a series of "hot spots" exist, where the timing of low tide coincides with hot terrestrial conditions and low wave splash (135). As a result, some sites in northern Washington State and Oregon are likely to become more thermally stressful than sites 2000 km to the south in central California (47, 73). Data collected at multiple intertidal sites (47) suggest that the site examined by

Barry et al. (15) and Sagarin et al. (13) in central California may in fact represent one of these hot spots, and thus it may not be possible to extrapolate results from studies conducted at a single site to the entire Pacific coast of the United States. Predictions of the effects of climate change on the geographic distributions of intertidal organisms, which are based on air temperature or SST alone, are therefore at variance with those based on predictions of the body temperature of the animals (47, 73). As described by Sagarin & Gaines (129, 130), one common model of species range distributions assumes that species peak in abundance near the center of their distributions, where environmental conditions are presumably near the species' physiological optimum, and that abundances taper off near the edges of the species distribution. Sagarin & Gaines measured the abundances of 12 species of intertidal invertebrates at 42 intertidal sites along the Pacific coast of North America, from Mexico to Alaska. Of the 12 species examined, only 2 showed evidence of the abundant center distribution (129, 130). Although these patterns have yet to be explicitly matched against predictions of organismal body temperature, these results are consistent with whatever factor is determining patterns of abundance in these intertidal species not increasing monotonically with latitude along the west coast of the United States.

Similarly, understanding patterns of selection in the field may be difficult without first explicitly quantifying the scales at which environmental stressors operate (35, 107, 136). For example, Schmidt & Rand (137, 138) showed for barnacles that high levels of spatial heterogeneity in the thermal environment were sufficient to maintain genetic polymorphism for alleles affected by thermal stress. Recent studies have suggested that small-scale heterogeneity in thermal niches over the scale of centimeters can often exceed those observed over the scale of thousands of kilometers on the west coast of the United States (35, 37, 47, 73). Clearly, even in a model ecosystem (114, 128, 139) understanding the relationship between climate and climate change in driving species distribution patterns is more challenging than previously assumed.

THE IMPORTANCE OF ENVIRONMENTAL SAFETY FACTORS: EFFECTS OF SHIFTING WAVE CLIMATE ON ROCKY SHORE COMMUNITIES

Vertical zonation in intertidal communities can be influenced by a variety of horizontal gradients in environmental conditions such as wave exposure, substrate orientation, salinity, or nutrient supply (99, 139–141). On rocky shore headlands, for example, increased wave splash and run-up expand and shift zones upward (53, 139). Water motion can also influence the strength of biological interactions, often altering the dominance of a species in a particular zone. One well-known example is the competitive dominance of mussels in the mid-intertidal zone of wave-exposed shores, where they find refuge from mobile predators such as crabs, snails, and sea stars (142–144). Predators are typically effective in reducing mussel abundance

in calmer habitats, allowing competitively inferior species, such as barnacles or macroalgae, to persist.

Accordingly, large-scale change in these other variables may affect intertidal communities and is foreseeable. Indeed, one predicted consequence of global warming is an increase in the severity of wave conditions in many parts of the world's oceans. For example, wave heights on the west coast of North America are linked to El Niño (ENSO) conditions, which have increased in frequency and severity over the past few decades (145–147). In the North Atlantic, wave heights have increased at the rate of 2% annually since 1950, and the severity of winter storms is associated with the phase of the North Atlantic Oscillation (NAO) (148–150). The intensity and frequency of hurricanes in the region has also increased in recent years (151).

How will rocky shore organisms respond to increased wave severity? Following the mechanistic approach developed by Denny and colleagues (65, 158, 159), increased wave height should generate increased hydrodynamic forces on organisms (lift, drag, etc.) that could potentially exceed an organism's attachment force and cause mechanical failure. Thus a general prediction is that more severe wave conditions should result in increased dislodgment, shifting species distributions to more wave-protected habitats. Alternatively, species capable of altering hydrodynamic properties (by streamlining morphology, reducing size, etc.) or increasing attachment strength could potentially maintain their distribution. Discerning which of these two scenarios is most likely for a given species has proven difficult for a number of reasons. First, the linkage between offshore wave height (the metric climatologists provide) and the hydrodynamic forces generated on rocky shore organisms has proven difficult to characterize. This is in part because waves are subject to local modification by factors such as seafloor topography, wind speed, and direction. Waves breaking on topographically complex rocky shores undergo further modification (funneling, constructive interference, etc.), yielding maximal flows that are spatially heterogeneous and, in some instances, only weakly correlated with offshore conditions (107, 111, 112, 136). Additionally, our understanding is limited of how a given flow generates hydrodynamic forces on organisms in situ. Despite much progress on the hydrodynamic roles of morphology, flexibility, and aggregation (63, 154–160), direct measures of flow forces on wave-swept organisms are scarce (110, 160).

Second, increasing evidence indicates that the attachment strength of a given organism is often not fixed but instead varies temporally and spatially along gradients of hydrodynamic stress. For example, macroalgae can increase holdfast strength in high-energy habitats (161, 162), and mussel attachment at a given site can vary twofold during the course of a year (58, 163). Therefore, predictions of mechanical failure must evaluate whether organismal attachment strength is sufficient in the context of environmentally and temporally relevant flow forces. Johnson & Koehl (63) conducted such an analysis of environmental safety factors for the subtidal kelp *Nereocystis leutkeana*, concluding that kelps compensate for increased flow in high-energy habitats by increasing strength and becoming

more streamlined. Similar observations for other large macroalgae (161, 164, 165) suggest that in many cases increased wave climate will affect algal size, morphology, and tissue mechanics rather than survivorship alone. Such trait plasticity may nonetheless have important fitness consequences by altering reproductive output or biotic interactions.

Not all phenotypic plasticity can be considered acclimatory, as is the case with the blue mussel, *Mytilus edulis*. Environmental safety factors for mussels in southern New England vary considerably during the course of the year owing to a mismatch in the phenology of attachment strength and wave climate (58). Mussels are most sensitive to dislodgement during August to November when large storms coincide with weak mussel attachment. Despite the difficulties in precisely characterizing hydrodynamic forces discussed above, measurements of wave disturbances to mussel beds largely validate these mechanistic predictions (E. Carrington, unpublished data). Thus generic changes in overall wave climate may not be relevant to all organisms; rather, only changes in those extreme events that coincide with periods of low safety factors may be ecologically important. Increases in storm activity during periods of high safety factors (e.g., late season Nor'easters in New England) would likely have little effect on survivorship. Note that these insights would not be possible without a mechanistic understanding of the biophysics of mussel attachment in the surf zone and how it varies seasonally.

The physiological response of mussels to environmental conditions defines the window of time where they are susceptible to dislodgment by severe wave conditions. This window of sensitivity is from late summer to fall for mussels in southern New England, but in spring for the same species on the other side of the Atlantic, in the United Kingdom (58, 59, 163, 166). The two populations therefore differ in their sensitivity to wave climate; mussels in New England will respond strongly to shifts in hurricane activity, whereas those in the United Kingdom will be more responsive to changes in storm activity that occur later in the storm season. This biophysical analysis therefore provides insight into which aspects of wave climate (seasonal storm patterns) may be most important for mussels in a given geographic location. Broad generalization beyond these two mussel populations, however, requires an understanding of the proximal environmental causes of plasticity in mussel attachment. It is likely that environmental parameters other than wave action are also involved (167), and synergistic effects are likely. For example, if low temperature is the proximal cue for increased attachment strength, then a gradual increase in water temperature would shift mussels to calmer habitats, even in the absence of a shift in wave climate.

Another potential synergism involves how changes in wave climate may influence biotic interactions, such as the ability of mussels to dominate space on high-energy intertidal shores. Mussel dominance depends not only on mortality but also on growth and recruitment (168, 169). That is, mussel beds can maintain 100% cover (excluding competitors) with substantial mortality rates as long as the vacated space is reoccupied by growth of the survivors or the arrival of new recruits. These latter two processes are largely driven by other aspects of the environment

(temperature, food supply, or currents), which in turn may be subject to climatic shifts. If the effect of climate change on wave height is highly seasonal (i.e., just increased hurricane activity in late summer/fall), then mussels in New England are predicted to shift into what are currently lower-energy habitats. But in such habitats mussels may no longer have a refuge from predation because foraging activities are most intense in summer. In this manner, seasonally dependent climatic change (more severe winters, increased hurricane activity) may shift the distributions of some organisms but not others. Although biophysical models provide an essential component in predicting range shifts, whether the organism of interest persists ultimately depends on the strength and direction of biotic interactions in the new community assemblage.

INSECT RESPONSES TO CLIMATE CHANGE: PATTERNS, PROCESSES, AND PREDICTIONS

The quantitative relationship of weather and climate to distribution and abundance of insects has been extensively explored for over half a century (170). Statistical and semi-mechanistic models relating climate to geographic distribution have been developed for many insects, in particular for agricultural pests and disease vectors. As a result, insects have provided some useful case studies for examining and predicting how climate change can alter insect distribution and abundance (171).

Butterflies are a particularly good example because data are abundant on their geographic ranges and the demographic, behavioral, and physiological mechanisms by which weather and climate affect their ecology (172). For example, seasonal aspects of environmental temperature, radiation, and moisture influence (*a*) larval growth and development rates and the number of generations per year; (*b*) overwintering mortality; (*c*) phenological shifts of the life cycle relative to host plants and natural enemies; and (*d*) thermoregulation, flight activity, and realized fecundity of females [see (172) for a detailed review]. This understanding has been used to predict two major qualitative ecological responses of butterflies to climatic warming: shifts in range and abundance at northern and southern range boundaries (173) and phenological shifts in the seasonal life cycle in spring and fall (174).

Several recent analyses have evaluated aspects of these predictions for butterflies in western Europe, where annual mean temperatures have increased by ∼0.8°C during the past century. Parmesan and colleagues (175) found that during the past 30–100 years, 22 (63%) of 35 nonmigratory species shifted their ranges northward; only 2 of 35 species shifted southward. Typically, northern range shifts were the result of northward shifts in the northern boundaries: Only 22% involved northern shifts in both northern and southern boundaries. The extent of boundary shifts was 35–240 km (along a single boundary), similar to the mean shift in climatic isotherms in Europe during the past century (120 km). As a result, the overall response of most of these species to climate warming has been an increase in geographic range to the north.

Roy & Sparks (176) used data from the British Butterfly Monitoring Scheme to explore phenological shifts in adult flight season during the past two decades. They found that 13 (37%) of 35 species had earlier average spring or summer adult appearance dates; none showed later average appearance dates. For species with multiple generations (flight seasons) per year, the duration of the flight season was also greater. Using regression analyses, Roy & Sparks (176) estimated that a 1°C increase in mean annual temperature would advance adult appearance by 2–10 days in most species.

These analyses clearly demonstrate the consequences of recent climate warming for European butterflies and suggest that predicted climate change during the next 50–100 years will cause range and phenological shifts in butterflies in northern temperate regions. However, there are some important limitations to these conclusions for understanding general responses of butterflies to climate change. For example, these analyses for European range shifts excluded many, perhaps the majority, of nonmigratory European butterfly species (migratory species were also excluded). Species were excluded if they were limited by host-plant distribution, were strongly habitat restricted, or had experienced severe habitat loss (175); thus the analyses naturally focused on those species anticipated to respond to climate. Even among this subset of species is considerable heterogeneity in whether response to climate was detected in northern or southern range boundaries or phenological appearance. As explored before, ecological and physiological differences among species likely contribute to this heterogeneity in response to recent climate change.

Several recently developed models predict how anticipated global climate warming in the coming decades will affect distributions and extinctions of assemblages of insects and other organisms (23, 177). These models combine two main elements. First, a model of the climatic niche or envelope of each species is developed. Although the statistical details and assumptions of different methods vary (178), the basic approach is to use information on geographic occurrences of a species and climatic variables to predict the probability of occurrence (or absence) as a function of climatic variables at different geographic locations. The model for the climatic envelope may use information on only mean annual temperature and precipitation (178) or more detailed information about seasonal or mean monthly temperatures and precipitation (179); none of the current models uses biophysical approaches to measure climate spaces that mechanistically connect environmental conditions to body temperature (75, 180). Second, predictions from general circulation models are used to develop climatic scenarios for future climate conditions. Because the grid size of most general circulation models is quite large, interpolation methods are used to predict local geographic conditions. With this approach, recent analyses predict widespread extinctions and/or distribution changes in the butterfly faunas of Mexico and of Australia (23, 177, 179).

There are several important issues to consider in interpreting these predictions regarding future climate change. First, different annual and seasonal aspects of climate are strongly spatially auto-correlated, making it difficult for climatic

envelope models to correctly identify which aspects of climate are associated with occurrence. Yet a diversity of studies illustrates how specific seasonal components of climate during key life stages can dominate the responses of most butterfly species to climate change (43, 172, 181, 182). This probably contributes to the heterogeneity of responses of butterflies to recent (past) climate warming (see above).

Importantly, climate change involves much more than simple increases in global mean temperatures. There is general consensus from predictions of global circulation models about the ways in which greenhouse gases will alter climate (20, 183). First, warming will be greater at higher than at lower latitudes, especially in the northern hemisphere. Second, warming will be greater in winter than in summer, especially at high latitudes. Third, warming will be greater for nocturnal (nighttime) than for diurnal (daytime) temperatures in most seasons and geographic regions, leading to a reduction a daily thermal variation. Indeed, nearly all of the climatic warming seen in north temperate regions in the past century is the result of increased nighttime temperatures. Fourth, the mean and perhaps the variability of global precipitation will increase, with greater winter precipitation at higher latitudes. The general pattern is that anticipated climate change will have greater effects on low temperatures than on high temperatures, and will tend to reduce daily, seasonal, and latitudinal variation in temperatures. As a result, predicted climate change will alter the correlations among different seasonal and spatial components of climate. This will alter the accuracy of predictions of responses to climate change based on statistically estimated climatic envelopes. One way to assess the accuracy of currently available predictions for responses to future climate change is to test the success of current climatic envelope models in predicting responses to past climate change or for range changes in introduced or invading species. Samways et al. (49) provide an interesting example of this approach, making use of data on 15 ladybird species that have been intentionally introduced as biocontrol agents in different areas around the world. They determined climatic envelopes for each species in their native range, using a widely used climatic envelope model (CLIMEX), then compared their introduced geographic range with model predictions. The match between predicted and observed ranges varied from 0 to 100%, and only 4 of 15 species ranges were predicted with high accuracy (49).

All these considerations suggest that a more mechanistic approach is needed to quantitatively predict changes in abundance, geographic range, or phenology of insects in response to climate change. To explore this further we consider several more-detailed case studies of recent responses of butterflies, mosquitoes, and other insects to climate change (20).

The White Admiral Butterfly (*Ladoga camilla* L.) experienced a large northern and western extension of its range in southern Britain during the first half of the last century (172). Detailed field studies at the species range boundary indicated two primary causes of this range extension. First, mean daily temperatures in June caused increased growth and developmental rates, thereby reducing larval and pupal mortality owing to predation. In addition, warm and sunny weather during

July increased the time available for flight because these butterflies behaviorally thermoregulate body temperatures to achieve the elevated temperatures required for active flight (43). This increased the number of eggs laid by females. These two seasonal components of climate are most strongly associated with the observed range extension in White Admirals (172). More generally, mean temperatures and insolation in June-July are the best predictors of butterfly population abundance for more than 80% of British butterfly species that have been studied (172).

Crozier (184, 185) used a more experimental approach to explore climatic determinants of the range expansion of a North American species, the Sachem Skipper (*Atalopedes campestris* L.). The Sachem is a generalist species that feeds a variety of grasses as a larva. During the past half century it has extended its northern range by nearly 500 km into the Pacific Northwest region of the United States. Over this time the mean minimum January temperature has increased by $3°C$ in this area; the boundary shift is correlated with the $-4°C$ mean January minimum isotherm. The Sachem species lacks a physiological diapause stage and overwinters in larval stages. Measurements of supercooling points and minimum lethal temperatures demonstrate that -5 to $-6°C$ is a critical thermal limit for the Sachem: this limit is not influenced by life stage, acclimation, or population of origin (184). In chronic cold stress experiments, mortality is high in diurnally fluctuating temperatures typical of winter conditions at the current range boundary. For example, larval survival over a 2–3-week period was greater than 70% under a 8 to $0°C$ thermal cycle, less than 10% at 4 to $-4°C$, and 0% at 0 to $-8°C$. Reciprocal field transplant experiments of larvae between the current range boundary and ~100 km inside the range showed significantly lower larval survival rates over the winter at the range boundary compared with that inside the range, with mean overwintering survival rates of 1% or less at the range boundary (185). In contrast, there were no significant differences in larval mortality in summer conditions inside and at the range boundary. Field population censuses of adults show that population sizes increase dramatically from spring to fall each year both inside and at the range boundary; in fact, the magnitude of population expansion is greater at the boundary than inside the range.

The picture that emerges from this case study of the Sachem is that summer population expansion alternates with high overwintering mortality at the range boundary. A demographic model that incorporates these climatic effects shows that winter warming was a prerequisite for this butterfly's range expansion (185). Because future climate change is expected to increase winter temperatures more than summer temperatures, especially at higher latitudes, this may be a major determinant of recent and future range extensions in insects that are freeze-intolerant or that lack a physiological diapause state.

It is well known that tolerance to extreme high and low temperatures varies among insect species. Addo-Bediako et al. (186) recently compiled the data available for supercooling points (SCP), lower lethal temperatures (LLT), upper lethal temperatures (ULT), and critical thermal maxima (CTmax) for 250 insect species representing 87 families and 10 orders. SCP and LLT were strongly correlated

for freeze-intolerant species but not for freeze-tolerant species. There was no significant relationship of latitude to either ULT or CTmax; most of the variation in ULT and CTmax was at the family or generic level. In contrast, mean LLT and SCP declined with increasing latitude. This pattern is largely because of the large increases in variation in LTT and SCP among species at higher latitudes, which reflects the fact that there are a variety of physiological and behavioral mechanisms, in addition to reduced SCP and LTT, by which insects may weather low winter temperatures at higher latitudes (187, 188). One crucial factor is the phenological timing and predictability of snow cover, which strongly moderates exposure to extreme low temperatures at higher latitudes and altitudes. There are two important implications of these studies for responses to future climate change. First, increasing minimum winter temperatures at higher latitudes owing to climate change may cause northern range extensions for insect species in which SCP and LTT are the major physiological determinants of overwintering mortality. Second, current global climate change models also predict increased winter precipitation at higher latitudes. However, it is unclear how the combination of increased winter temperature and precipitation will affect timing and extent of snowpack, which will determine temperatures of insects in their overwintering sites. This will likely increase the heterogeneity of the responses of different insects to future climate change and may be one cause of the heterogeneity of response of European butterflies to recent climate change (see above).

The seasonal life cycle of most insects is mediated by seasonal cues that initiate and terminate diapause, estivation, quiescence, or other states in which growth, development, and reproductive processes are suspended. For many temperate and higher latitude insects the transitions to and from diapause are mediated by daylength or photoperiod, and there is widespread geographic variation within and between insect species in the critical photoperiod (CP) that initiates or terminates diapause (189). Thus changes in photoperiodic responses may be an important mechanism by which insects respond to climate change. Bradshaw & Holzapfel (190) provide an elegant demonstration of this response for pitcher-plant mosquitoes, *Wyeomyia smithii*. The larvae of pitcher-plant mosquitoes are restricted to the water-filled leaves of purple pitcher plants, which occur in distinct geographic populations over a wide latitudinal gradient in eastern and central North America. The CP for initiating and terminating larval diapause increases with increasing latitude, such that northern populations terminate diapause later in the spring and initiate diapause earlier in the fall than southern populations. Studies of diapause responses in this species during the past three decades demonstrate genetic shifts in the CP initiating diapause during the past 25 years, coincident with increases in mean annual temperatures during this time period (190). This evolutionary shift has occurred primarily in northern populations, where climate change has been greatest, and corresponds to a nine-day advancement in the date of diapause initation in northern populations. This study illustrates that evolutionary changes may be an important component of biological responses to climate change for insects and other short-lived organisms (171, 191).

MECHANISTIC ECOLOGY IN THE FACE OF CLIMATE CHANGE: WHERE DO WE GO FROM HERE?

Physiological ecologists have long recognized the multitude of interactions between environmental factors in driving physiological stress in the field, and large-scale studies of the effects of climate on ecosystems have rightly pointed to the difficulties inherent in beginning with models at the level of the organism (16, 18, 48). Nevertheless, despite the difficulties in this approach, a failure to consider the mechanistic details of environmental heterogeneity, coupled with the physiological response of organisms to these variables, can lead to erroneous predictions regarding how and where we should look for the effects of climate change.

While the application of physiological techniques to questions of biogeography and ecology has a long history, the advent of new field-based techniques, coupled with biophysical/biomechanical approaches, offers an unprecedented opportunity in the form of hypothesis generation and testing. Specifically, through large-scale meta-analyses we are able to detect patterns and then correlate these patterns with environmental variables; indeed, it may be through these types of approaches that we are best able to determine where trouble spots are occurring on regional and global scales (18, 80). However, although these approaches may be good at detecting pattern, their predictive ability in terms of forecasting future changes may be poor. In contrast, biophysical methods may provide a means of generating explicit hypotheses regarding where and when we should or should not expect to observe physiological stress in the field. Previously, testing such predictions would have required the observation of range shifts or large-scale mortality events, but with the application of new field-based physiological techniques we are now able to precisely test these predictions on small temporal and spatial scales (26–28, 35, 37, 39). The combination of molecular physiology and biophysical ecology, coupled with the detection of large-scale patterns of change, thus presents our best chance of predicting what to expect in the face of global climate change in the coming decades.

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