

Physiological Correlates of Geographic Range in Animals

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Abstract

We evaluate the extent to which physiological tolerances and capacities can be considered as factors that impact the geographic range of animals. We also discuss the importance of understanding how environmental variability interacts with physiological function, concluding with a consideration of how our understanding of physiology in a macroecological context may contribute to our ability to predict the effects of climate change. The extent to which advances have occurred in predicting geographic range through constructing and testing hypotheses involving tolerances, physiological capacities, and plasticity (namely pervasive plasticity, climatic variability, and the Brattstrom hypothesis) is evaluated. Finally, we attempt to integrate our understanding of the interaction between physiology and distribution within current global warming scenarios. We suggest that it may be necessary to evaluate patterns of physiological diversity as a function of different ecological regions oriented to produce mechanistic explanations regarding the likely new (or lack of) physiological responses of animals to altered climatic conditions along geographic ranges.

Macrophysiology:
the conceptual
convergence between
the fields of ecology
and physiology in the
study of large spatial
and temporal-scale
patterns to explain
how high levels of
environmental
variability affect
physiological traits

INTRODUCTION

“As an ecological problem, the question of why a species has a restricted distribution, given its present physiological and other features, can be answered, even if with difficulty. But range limits pose an evolutionary problem that has not been solved” (Futuyma 1998, p. 535).

Levels of ecological organization, or hierarchies, provide one of the central themes around which ecologists attempt to understand patterns of distribution (Lawton 1991). Central to our understanding of the physiological responses of organisms to different environments is the analysis of the mechanisms that underpin within- and between-species variation in physiological traits as well as the ecological consequences of this variation at different hierarchical levels (McNab 2002, Spicer & Gaston 1999). Investigation of patterns, processes, and implications of such physiological diversity combines analysis of the mechanistic basis of trait expression with analysis of variation of these traits at higher levels of organization over broad geographic and temporal scales. For example, analysis of phenotypic trait variation along a geographic and temporal scale is considered a powerful approach for evaluating how physiological traits evolve at both intra- and interspecific levels (Chown et al. 2004).

Mechanistic explanations for these patterns link adjacent steps in the ecological hierarchy, as an understanding of the processes underlying patterns of distribution can be best achieved by the integration of physiology, ecology, behavior, and evolutionary biology (Gaston et al. 2009, Kearney & Porter 2009, Kearney et al. 2009, Spicer & Gaston 1999). Our knowledge of speciation, physiological adaptation, plasticity, and ecological interactions contributes to our understanding of the distribution and function of biodiversity along geographic gradients and the factors that determine the geographic range limits of species. These limits must be the (by-)product of complex interactions between species-specific physiological, phenological, and ecological traits; dispersal ability; and biotic interactions. In addition, many of the underlying traits may be phylogenetically conserved among related species. Thus, the phylogenetic history of species and clades must be incorporated into any understanding of range limits (Gaston et al. 2009). An understanding of the factors that determine the geographic range limits of species is essential to address fundamental questions in ecology and evolutionary ecology and is particularly pressing because of ongoing environmental global change (Gaston et al. 2009).

Historically, the importance of physiological mechanisms to our understanding of the ecology and evolution of taxa has been at best underestimated and at worst ignored; variation in physiological traits has been dismissed either as irrelevant or else as random noise/error. And yet, there has never been a time when our understanding of the physiological responses of animals to environmental changes is more urgent, given the current biodiversity crisis and in particular global warming, which provides an opportunity to examine how increased regional temperatures may affect animal well-being, distribution, abundance, and local (and global) extinction risks. For instance, although global trends in temperature are well established, regional changes are more difficult to predict, and as a result so too will be population responses to these changes. We suggest that a more integrative approach to ecology and evolution generally will require a comprehensive understanding of physiology.

A relatively new approach to investigation of physiological function in the context of exploring and understanding Earth ecosystems and biodiversity has emerged with the integration (or reunification) of physiological ecology and macroecology, termed macrophysiology (Chown et al. 2004, Gaston et al. 2009). Macrophysiology seeks to explain how physiological traits are affected by high levels of environmental variability encountered over large geographic distances as well as over large temporal scales (from seasonal comparisons, e.g., Stillman & Tagmount 2009). In general, this interdisciplinary convergence compares physiological features between individuals

CLIMATE-BASED HYPOTHESES FOR VARIATION IN GEOGRAPHIC RANGE AND PHYSIOLOGICAL RESPONSES

Climate-based hypotheses for variation in the geographic range of species—the CVH, the CEH, and the optimal climate hypothesis—establish that climatic variables account for much of the variation in range size. These hypotheses require information on physiological traits and assume that species have evolved differing optima and ranges of tolerances. Knowledge of physiological responses to climatic variables is inherent to predicting how climate may affect the geographic range of species and populations. Among these hypotheses, the CVH explains why range sizes are generally larger at higher latitudes, positing that as the range of climatic variability experienced by terrestrial animals increases with latitude, to survive individuals need a broader range of physiological tolerance, which consequently allows these species to become more extensively distributed. The mechanism behind this is phenotypic flexibility, which allows individuals to adjust to changing biotic and abiotic conditions through increases in performance and likely fitness.

possessing different (in some allopatric populations) geographic distributions. Such an approach to biodiversity seeks to elucidate patterns of geographic physiological variability (physiographic patterns) within the framework of the hierarchical structure of biodiversity and to understand the mechanisms that underlie these patterns.

Over the past decade many climate-based hypotheses regarding variation in distribution range of species have emerged (see Pither 2003) such as the climate variability hypothesis (CVH), the climate extreme hypothesis (CEH), and the optimal climate hypothesis (OCH). These use data on physiological traits of the species, focusing mainly on variation in latitude and altitude (Spicer & Gaston 1999) and using principally the intrinsic physiological properties of species to predict their responses to climatic variables and how these properties may affect the geographic ranges of assemblages, species, and populations (e.g., Addo-Bediako et al. 2000; Bernardo et al. 2007; Calosi et al. 2007, 2010; Compton et al. 2007; Gaston & Spicer 2001; Gibert & Huey 2001; Lee et al. 2009; Sgrò et al. 2010; Stillman 2002; Somero 2005) (see also sidebar on Climate-Based Hypotheses for Variation in Geographic Range and Physiological Responses). Consequently, in this review, we critically evaluate what is known of how physiological tolerances, physiological capacities, and physiological plasticity affect the range size and limits of organisms. We also consider the importance of understanding how environmental variability interacts with physiological function, concluding with a discussion of how our understanding of physiology in a macroecological context can contribute to our knowledge of the effects of climate change (and their mitigation).

PHYSIOLOGICAL TOLERANCES

Advances in Predicting Geographic Ranges and Limits

Environmental conditions vary over space and time, and thus populations and species are continually challenged to maintain homeostasis. Individuals are expected to evolve physiological adaptations, physiological tolerances, and capacity physiological acclimatization to local conditions in different and likely heterogeneous environments along geographic ranges.

Terrestrial organisms. Using spatially explicit biophysical models (incorporating physical principles from heat and mass transfer, physiology, morphology, behavior, and climatic and geographic information systems), Warren Porter and colleagues (2002) pioneered the principles for

Climate variability hypothesis (CVH):

for terrestrial animals, a positive relationship may exist between breadth of thermal tolerance range and level of climatic variability experienced by taxa with increased latitude

Climate extreme hypothesis (CEH):

extreme climatic variables located within the species distributional range may relate to range size

Physiological

acclimatization: a form of plasticity that allows an individual to express a broader capacity and tolerance windows, in the face of changing environmental conditions

determining physiology on a landscape scale, showing, for example, how temporal and spatial changes in microclimate resulting from differences in topography and vegetation cover alter animal physiology and distribution. Porter and coworkers also showed how different scales of observation provide data that can help elucidate different aspects of the actual distributions of a species, all of which contribute to defining fundamental aspects of taxa biogeography. Indeed, Kearney et al. (2009) integrated such biophysical models with evolutionary theory to predict climatic impacts on the dengue mosquito distribution range in Australia.

Kearney & Porter (2009) call for mechanistic niche modeling through a combination of physiological and spatial data to predict species' ranges. As they pointed out, these multidisciplinary approaches allow modeling of species distributions without using species distributions. Indeed, precise predictions of the potential distribution of range-shifting species are required for assessments of the impact of climate change on species. Range-shifting species pose a challenge for traditional correlative approaches to range prediction. Thus, mechanistically linking key organismal traits with spatial data using biophysical models may allow explanation and prediction of the current range as well as the potential for animals to expand or reduce their range under different climate scenarios. In other words, by quantifying spatial variation in physiological constraints, these trait-based approaches can be used to predict the range limits of any species and may also provide a mechanistic basis for understanding animals' potential to evolve at range edges. Other models have attempted the integration of physiological traits by focusing on the effect of their responses to environmental changes on species biogeography, which further highlights the importance of integration of species physiological abilities when attempting to predict their distribution and possible response to global climate change.

Now, it is possible to quantify physiological and behavioral variations at local scales and so quantify the requisite spatial and temporal distribution and resources that affect species' Darwinian fitness and distribution. As we will see, extinction of species may be a major impact of global climate change. Thus, physiology on a landscape scale with spatially explicit models, mechanisms of physiological performance, and biophysical ecology (heat, mass, and momentum exchange methods applied to biological systems) may be able to quantify and predict the consequences to animal behavioral energetics on real landscapes of future climate scenarios as well as how potential global changes might play out in terms of intra- and interspecific interactions, fitness-related traits, and shifts in distribution range on a landscape scale (Helmuth 2002, Kearney & Porter 2009).

Intertidal and marine organisms. Intertidal species spend a substantial amount of time exposed to air during low tides, and as such, seawater temperature is not an adequate predictor of body temperature during periods of emersion (Stillman & Somero 2000). As with terrestrial organisms, during periods of aerial exposure the actual body temperature of intertidal organisms will be determined largely by various meteorological conditions, habitat characteristics, and thermal properties of the organism (Helmuth 1998, Porter & Gates 1969).

Changes in body temperature, driven by changes in ambient temperature, have been shown to affect various attributes of intertidal invertebrates including physiological and reproductive performance, vertical zonation, and global distribution and survival. The investigation of the physiological basis of the zonation of marine organisms in the intertidal zone has deep historical roots (e.g., Davenport & MacAlister 1996, Newell 1979). More recently, Stillman & Somero (2000) showed, in sites separated by several thousands of kilometers, that the zonation of congeneric porcelain crabs of the genus *Petrolisthes* is related to the thermotolerance of the species and the maximum habitat temperatures that occur over a few meters. Functional analyses of the related effects of thermal acclimation on both heat and cold tolerance have been reported infrequently in multiple species adapted to different thermal habitats. Overall, the data reflect limited capability

to shift thermal limits when close to ambient thermal maxima in warm-adapted taxa and minima in cold-adapted taxa, although the former possess the ability to maintain broader thermal windows as a result of their great critical temperature acclimatory ability (Stillman & Somero 2000). This suggests an evolutionary and/or functional trade-off between the acquisition of extreme tolerance limits and the retention of high levels of plasticity of tolerance limits. Evolutionary trade-offs between extreme tolerance and plasticity have been demonstrated in *Drosophila* (Hoffmann et al. 2005), and thus evolutionary trade-offs are a reasonable hypothesis in the thermal adaptation of porcelain crabs. As Pörtner et al. (2006) pointed out, it will be challenging to determine whether further limitations to species scope for adaptation will constrain a species to narrower thermo-tolerance windows and whether these are close to as yet unidentified physiological limits on distribution (although see Calosi et al. 2010). The application of molecular and genomic tools promises to contribute greatly to understanding the links between physiological adaptation and geographic distribution. More specifically, these tools may provide a mechanistic understanding of such adaptations at the molecular level, thus producing more sensitive end points compared with some of the classical whole-organism traits used historically in this area (e.g., Dong & Somero 2008, Osovitz & Hoffmann 2005, Stillman & Tagmount 2009). For example, Fangue et al. (2006) showed that shifts in thermal tolerance (both CT_{max} and CT_{min}) of northern and southern populations of the common killifish *Fundulus heteroclitus* were underpinned by differences in the expression of specific heat shock protein (hsp) genes (e.g., *hsp70-2* and *hsc70*). Furthermore, Tomanek & Zuzow (2010) reported that in the western United States the invasive warm-adapted mussel *Mytilus galloprovincialis* exhibits lower sensitivity to high-temperature damage when compared with the indigenous *Mytilus trossulus*, which is consistent with the recent history of expansion in warmer waters of *M. galloprovincialis*.

It seems clear that variations in environmental thermal regime are relevant for ectothermic intertidal animals because temperature has both direct and indirect effects on physiological and ecological processes. Again, thermal constraints are particularly important for the activity of marine invertebrates inhabiting intertidal environments, where the animals are exposed periodically to terrestrial conditions with the cyclic rise and fall of the tides. During periods of low tides, intertidal organisms are exposed to terrestrial or semiterrestrial conditions that impose physiological challenges on them that approach their limits of physiological tolerance (Stillman & Somero 2000). Microclimatic variation in the intertidal is large even over the scale of a few meters; this is largely dependent on solar radiation. Thus, thermal variation in the intertidal habitat may have a major impact on the distribution of invertebrates. Consequently, it is perhaps surprising to find a strong correlation between level of environmental variability experienced by taxa along the bathymetric gradient they occupy and the size of their latitudinal range of distribution (Harley et al. 2003).

Unfortunately, the relationships between species' tolerance and the size, position, and limits of their bathymetric range of distribution are poorly understood. Historically, for deep-sea species the focus has been on the organism's ability to cope with changes in pressure, temperature, and oxygen saturation (reviewed in Spicer & Gaston 1999). Furthermore, future environmental challenges, namely a reduction in ocean alkalinity (known as ocean acidification; see Caldeira & Wickett 2003) and the increased occurrence of hypoxic events (Rabalais et al. 2010), may greatly reduce the aerobic scope of many marine organisms. As this is thought to underlie marine organisms' ability to tolerate elevated temperatures, some species will likely experience a compression of the range of habitable depths and, as a result, alterations in their global distribution. Arguably, the factors limiting the geographic range of subtidal (and deep-sea) organisms are less well understood than those for organisms operating in the intertidal zone, notwithstanding the difficulties of describing accurately the geographic distribution of deep-water forms in the first place.

Rapoport's rule:
proposes that the
geographic range size
of an organism
decreases as one goes
from high to low
latitudes

Hypotheses Involving Tolerance

The CEH states that extreme climatic variables located within a species distributional range may relate to range size. For example, species that can tolerate the crystallization of their body fluids (i.e., freezing tolerance) may be able to use a larger geographic area in comparison with those that are intolerant to extreme cold events that cause freezing (Pörtner et al. 2006). Several other hypotheses that link physiological properties, tolerance in particular, to species biogeography (range extent, position, and limits) have been proposed, although formal tests for some of these hypotheses (at least for some specific levels of biological complexity) are lacking (see Gaston et al. 2009).

Discussion of the importance of environmental temperatures in determining geographic limits of distribution has a long history (Merriam 1894) and is still a key question in biology. Physiological constraints determine the relationship between abiotic variables and the distributional limits of species, but the processes explaining such patterns remain poorly understood. As Spicer & Gaston (1999) pointed out, reported variations between species in physiological traits may arise from methodological differences, allometric problems, species-specific or phylogenetic differences, and specific environmental conditions experienced by species and populations.

Rapoport's rule states that "when the latitudinal extent of the geographic range of organisms at a given latitude is plotted against latitude, a simple positive correlation is found" (Stevens 1989). Stevens (1989) suggested variation among species' physiological tolerance level as the possible explanation for this pattern, which later became the CVH (see Gaston 2003, Gaston & Spicer 2001, Spicer & Gaston 1999). This hypothesis posits that for terrestrial animals a match exists between levels of climatic variability experienced by taxa and increased latitude, altitude, and thermal tolerance range width (Compton et al. 2007, Calosi et al. 2008b, 2010; Osovitz & Hoffmann 2005; Snyder & Weathers 1975). Such patterns should also be found on the population level when comparing thermal tolerance responses of individuals from populations living at different latitudinal positions along a thermal gradient (see Hoffmann & Watson 1993, Hoffmann et al. 2005, Klok & Chown 2003, Sgrò et al. 2010).

Altitudinal gradients are environmental and evolutionary analogs to latitudinal gradients, although they are exclusive to terrestrial and freshwater organisms and are probably characterized by some of the steepest environmental clines. Janzen (1967) proposed that high- and low-elevation species in the tropics experience a larger difference in climate compared with species in temperate zones; in other words, "mountain passes are higher in the tropics" (p. 234). In addition, as an extension to his previous work on latitudinal clines (Stevens 1989), Stevens (1992) reported a positive relationship between species' altitudinal range and their elevation of occurrence; species living at higher altitude showed broader altitude distribution range than species living at lower elevations. An assumption of both hypotheses is that differences in physiological tolerances between species maintain range boundaries. Indeed, when empirical tests were carried out, support was found at both the species (see Spicer & Gaston 1999) and the population level (Brown 1996, for Stevens' hypothesis only). Most importantly, it is difficult to determine whether physiological ranges are the by-product of local adaptation or the driving force of species distribution (Gaston 2003). Physiological evidence needs to be supported with information on species dispersal ability, life history, phylogenetic history among taxa, and phylogeographic relationships among populations of the same species, in an attempt to reduce (ideally to one) the number of viable alternative hypotheses (Calosi et al. 2010). In addition, we need to know if thermal tolerances are genetically variable in geographically marginal populations and if these populations could adapt quickly to more extreme temperatures. If so, physiological range might be a consequence of local adaptation.

PHYSIOLOGICAL CAPACITY

Endotherm Metabolism and Distribution

Thermoregulatory and energetic constraints often have been invoked to explain animal distribution. However, few studies have actually examined the relationship between physiological capacities and distribution boundaries in endotherms (e.g., McNab 2002, Swanson & Bozinovic 2011). Most involve birds and suggest that ambient temperature and avian northern boundaries are related (e.g., Canterbury 2002, although cf. Olson et al. 2010). For mammals, Humphries et al. (2002) employed a bioenergetic model to predict the range distribution of the little brown bat, *Myotis lucifugus*, in northern North America. They not only suggest that thermal effects on hibernation energetics constrain the distribution of *M. lucifugus* but also provide a mechanistic explanation of how energetics, climate, and biogeography are related. In addition, Lovegrove (2000) reported significant differences in basal metabolic rate (BMR) for similar-sized mammals from the six geographic zones, i.e., Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, and Palearctic. Lovegrove showed that Nearctic and Palearctic mammals had higher BMRs than their Afrotropical, Australasian, Indomalayan, and Neotropical counterparts and explained this pattern with a model describing geographic variance in BMR in terms of the influence of climate variability. Thermal environmental conditions hold considerable significance for most levels of biological hierarchies. Because environmental temperature varies in time and space at different times and scales, organisms are continually challenged to maintain homeostasis. Thus, thermal physiology may be a significant factor underpinning the ecological and evolutionary success of animals. Rezende et al. (2004) and Bozinovic & Rosenmann (1989) reported a good correlation between maximum thermoregulatory metabolism (MMR) of rodent species and environmental temperature. Rodríguez-Serrano & Bozinovic (2009) analyzed the diversity of physiological responses in nonshivering thermogenesis (NST) among species of rodents from different geographic areas. They demonstrated a negative correlation between NST and geographic temperature, which suggests that selection may act on thermoregulatory performance. The absence of phylogenetic signal in these traits suggests that interspecific differences in MMR and in NST could be partially explained as adaptive to different thermal environments. These results further suggest that temperature imposes a high selective pressure on maximum thermoregulatory capabilities (both MMR and NST) in rodents in particular and perhaps in small endotherms in general. This supports the thermal niche expansion model, which proposes that high metabolic rates evolved because they allow animals to increase the range of environmental temperatures in which they can function (Block & Finnerty 1994, Swanson & Bozinovic 2011). Also, many records of species-specific metabolic rates show that these physiological traits are often evolutionarily labile (absence of phylogenetic signal for mass-independent values) and negatively correlated with environmental temperature. In fact, because greater or lower values of metabolic rates among endothermic species are associated with acclimatization to cool and short days or to warm and long days, respectively, some phenotypic plasticity may partially account for these results. Indeed, there is evidence that, for example, NST is the most plastic of metabolic variables because its heat-producing machinery (brown fat with sympathetic innervation) increases quickly after cold exposure. Nevertheless, and in spite of the plasticity of this trait, a clear geographic pattern exists in the sense that species that evolved in cold climates exhibit higher mass-independent metabolic rates than species from warmer habitats (Rodríguez-Serrano & Bozinovic 2009).

The pattern of increasing thermal tolerance, e.g., increasing mass-independent NST with increasing latitude, provides support and possibly an explanation for Rapoport's rule. As the mean temperature experienced by species decreases with latitude, animals require a higher level of energy expenditure and hence a broader thermal tolerance to survive and persist in the colder habitat,

Maximum thermoregulatory metabolism (MMR): maximum thermogenic capacity, which in eutherian mammals may be decomposed as the sum of basal metabolic rate, nonshivering thermogenesis, and shivering thermogenesis

Nonshivering thermogenesis (NST): the increase in heat production owing to the enhancement of normal calorogenic metabolic processes, which are dependent mainly upon brown adipose tissue metabolism

Thermal niche expansion model: high metabolic rates evolved because they allow animals to increase the range of environmental temperatures in which they can function and maintain homeostasis

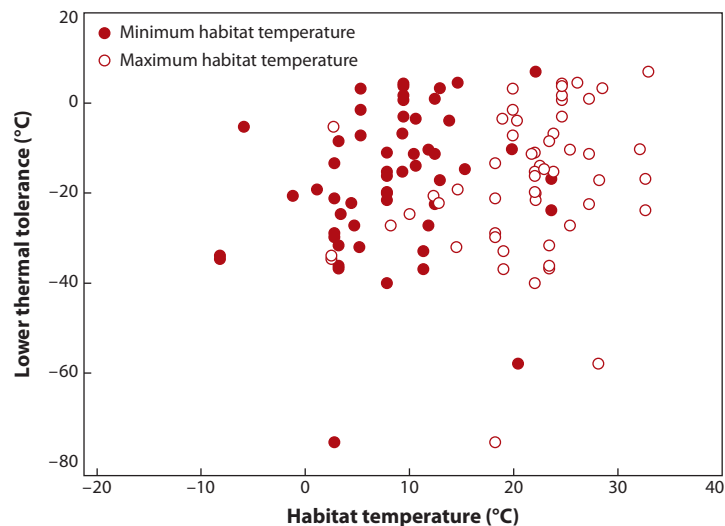


Figure 1

Relationships among mean minimum ($T_{\min}$, filled dots) and maximum ($T_{\max}$, open dots) habitat temperatures and lower thermal tolerance (T_{ll}) for 55 rodent species from different biogeographic regions. Statistics for Spearman rank order correlations are: $T_{\text{ll}} - T_{\max}$ ($r = 0.37$, $P = 0.005$); $T_{\text{ll}} - T_{\min}$ ($r = 0.36$, $P = 0.007$). Accordingly, as the mean temperature experienced by rodent species decreases with latitude or altitude, animals require a mass-independent broader thermal tolerance to survive and persist in the habitat. As a consequence, species and populations can become more widely distributed. Each point represents one species. Data from Bozinovic & Rosenmann (1989).

and as a consequence species can become more widely distributed (**Figure 1**). Nevertheless, even though some studies provide good evidence that long-term average temperatures could affect thermogenic capabilities on an evolutionary scale, these physiological traits are plastic and dependent on several environmental factors as well as species-specific ones, which have been taken only partially into account. One underlying assumption of these studies is that metabolic plasticity lies within a limited range characteristic of each species or population, although migration could mitigate fundamental differences at this level. Many authors reported differences in thermogenic capacity after acclimating to cold and warm temperatures. However, developmental acclimation cannot be ruled out as a possible explanation when reported data could reflect genetic adaptation and/or specialization to a particular thermal environment during ontogeny (i.e., developmental plasticity). Estimating the relative importance of ontogeny to metabolic flexibility is clearly important. A second limitation arises from the character of the study itself. Comparative studies often sacrifice precision for generality. The use of coarse meteorological variables, for instance, may not accurately reflect the thermal microclimates that species experience in situ as well as the whole geographic range of each species; alternatively, certain species may not be representative of the range of physiological abilities of a clade. Even a decade later, one of the key questions posed by Spicer & Gaston (1999, p. 189), “How well do between-species patterns in physiological diversity predict patterns across populations?” particularly when attempting to link physiological diversity and range limits, is still unresolved.

Ectotherms and the Metabolic Cold Adaptation Hypothesis

Much controversy and speculation has surrounded the metabolic cold adaptation hypothesis (MCA; Scholander et al. 1953) and the latitudinal compensation hypothesis

Metabolic cold adaptation (MCA) hypothesis and latitudinal compensation hypothesis (LCH):

at equivalent environmental temperatures, the metabolic rate of ectothermal species and populations from cold climates is greater than that of their warm-climate relatives

(LCH; Levinton & Monahan 1983, Scholander et al. 1953). These hypotheses derive from observations that at equivalent environmental temperature the metabolic rate of ectothermal species and populations from cold climates is greater than that of their warm-climate relatives (i.e., temperate or tropical). The increase in metabolic rate is considered to be adaptive, i.e., there is compensation for the short period of favorable environmental conditions for development, growth, and reproduction (Addo-Bediako et al. 2002, Clarke 1993, Scholander et al. 1953). MCA has also been extended to explain metabolic differences in altitude, latitude, and habitat conditions, because it is thought to be a general evolutionary adaptation among ectotherms to compensate for low environmental temperature (for reviews see Gaston 2003, Gaston et al. 2009). An example is found in Jacobsen & Brodersen's (2008) work on the characterization of metabolic rates of larvae of Andean insect species inhabiting high altitudes, which appear to possess inherently higher metabolic rates when compared with species found at lower elevations.

Several studies support the MCA hypothesis, particularly for terrestrial insects (Addo-Bediako et al. 2002, Gaston et al. 2009). However, several authors have failed to find an increase in O_2 consumption at lower environmental temperatures in marine organisms (Clarke 1991, Rastrick & Whiteley 2011, Steffensen 2002). Direct comparisons over altitudinal or latitudinal gradients mostly employ between-species differences; few published data address intraspecific comparisons for ectotherms (e.g., Levinton & Monahan 1983, Sømme et al. 1989). Nevertheless, several methodological issues arise when comparing the metabolic rates of organisms from different geographic areas. Factors such as acclimatization and laboratory acclimation, activity level, sex, reproductive status, food intake, and experimental technique employed may strongly influence the results if these factors are not taken into account.

Environmental gradients are common in nature, and particularly in widespread ectotherm species, intraspecific clinal patterns of variation are frequently attributed to the action of natural selection and, hence, are presumed to reflect genetic adaptation within populations to local conditions (e.g., Lardies et al. 2004). An important approximation for the study of the MCA hypothesis is comparisons at a geographic level, especially on a latitudinal scale, because mean annual temperature decreases toward high latitudes. To clarify, we understand MCA to be a component of the general term "cold adaptation," which encompasses all those aspects of an organism's physiology that allow it to inhabit cold (including polar) regions (Clarke 1991), apparently while maintaining aerobic scope levels via increasing mitochondrial capacity and density among other cellular and biochemical traits (Johnston 1987, Morley et al. 2009, Sommer & Pörtner 2002). Empirical support for the MCA hypothesis is not strong and comes principally from meta-analysis of data sets on insects (see Addo-Bediako et al. 2002). At the intraspecific level, decreases in metabolic rates have been reported for high-latitude populations of vertebrate and invertebrate ectotherms (Angilletta 2001, Peck 2002). Lardies et al. (2004), who put into place many impressive controls, demonstrated the opposite of the pattern predicted by the MCA hypothesis for woodlice across 13° of latitude, i.e., metabolic rates increased toward low latitude within experimental temperatures. This does not support the idea that elevated metabolism is advantageous to small terrestrial isopods occupying cooler habitats (see also Sømme et al. 1989).

A greater rate of metabolism has been interpreted as advantageous in ectotherms, especially in insects inhabiting high latitude/altitude environments, because it enables them to metabolize foodstuffs more rapidly, to develop faster, and thus to complete their life cycle in a period of time compatible with a reduced growing season (Gotthard et al. 2000). Nevertheless, for an iteroparous organism that has a life cycle in excess of one year and is active throughout the year (as is the case for many terrestrial isopods; Warburg 1987), higher values are not an advantage, because individuals can grow until the next reproductive season and then increase their reproductive success (i.e., by producing more offspring of better quality). In this sense, as Clarke (1993) pointed out, metabolism

represents a cost to the organism, not a benefit, which therefore makes it an improbable selective benefit for maintaining or elevating respiration. This is because elevated metabolic rates impose a cost on growth and development, which are necessary for life cycle completion in relatively short and cold growing seasons in high latitude/altitude zones (Addo-Bediako et al. 2002). Apparently, the MCA hypothesis is more applicable to semelparous, ectothermic organisms with annual cycles, which need to grow and develop faster to reach reproductive size in one season (Addo-Bediako et al. 2002, Gotthard et al. 2000). In this sense, MCA is more likely to be found in species that show latitudinal compensation in growth (Levinton & Monahan 1983) or the inverse Bergmann's rule (an inverse trend between latitude and body size) (Masaki 1978). Resting metabolism is, by far, the largest component of energy budgets of animals; energy lost to metabolism accounts for 80% of annual energy expenditure (Green & Ydenberg 1994). Therefore, the MCA hypothesis is probably linked to the LCH; for example, in the polychaete worm, *Ophryotroca* sp., a shift in growth efficiency in species and populations adapted to different thermal habitats, or the inverse Bergmann's rule, was reported (Levinton & Monahan 1983).

Not a corollary, but analogous to the MCA in bathymetric terms, is the idea that metabolic rate decreases with increasing depth, a feature that could allow some deep-water species to live in low-oxygen areas (e.g., the oxygen minimum layer) (Childress & Seibel 1998). A strong reduction in mass-specific metabolic rates with depth has been documented for pelagic fishes, cephalopods, and crustaceans (Childress 1995, Seibel & Carlini 2001). Childress & Mickel (1985) proposed the visual interactions hypothesis to explain this pattern: Reduced metabolic rates are found among some deep-sea pelagic taxonomic groups as the result of selection for strong locomotory abilities for visual predator-prey interactions in the (light-limited) deep sea. However, more recently, Seibel & Carlini (2001) reanalyzed data for pelagic cephalopod metabolic rates as a function of minimum depth of occurrence using phylogenetic-independent contrasts; they confirmed the existence of a significant negative relationship between oxygen uptake and minimum depth but also highlighted that phylogenetic history was very important. The challenge represented by the impending global change, particularly in marine habitats (owing to the synergistic action of global warming, ocean acidification, and the increase in hypoxic events; see Rosa & Seibel 2009), has thus renewed interest in comparing the physiological abilities of shallow-water and deep-sea organisms (e.g., Pane & Barry 2007). The intent is to identify whether different degrees of physiological vulnerability exist between the two groupings and to estimate how such changes might alter the vertical distribution and fitness of deep-sea organisms.

PHYSIOLOGICAL PLASTICITY

Pervasive Plasticity

Numerous organisms are able to adjust their physiological abilities (including metabolic rates and thermal limits) following daily and seasonal fluctuations of environmental variables (e.g., Bozinovic et al. 1990, 2003; Naya et al. 2009; Overgaard et al. 2006; Sinclair et al. 2003; Worland & Convey 2001). Physiological acclimatization can thus allow individual organisms to exploit broad (or broader) thermal capacity windows as well as express broader thermal tolerance and capacity ranges. This represents a form of plasticity that must be a major component of intra- and interindividual physiological variation (Spicer & Gaston 1999; along thermo-latitudinal gradients also see Hoffmann & Watson 1993). Where present, it clearly could modulate species and population resilience to climatic changes (Stillman 2002). Plasticity is a pervasive trait that can be extended equally to both physiological limits (tolerance) and performances (capacities). Although the ecological and evolutionary relevance of plasticity is widely recognized (Ghalambor et al. 2007,

Huey et al. 1999), few investigations have focused on measuring plasticity in relationship to species and population biogeography (Calosi et al. 2008a,b, 2010; Hoffmann & Watson 1993; Klok & Chown 2003; Naya et al. 2008; Stillman & Somero 2000).

The Climatic Variability Hypothesis and Brattstrom Hypothesis

The CVH (Gaston 2003) posits that as the range of climatic variability experienced by terrestrial animals increases with latitude, individuals from populations inhabiting higher latitudes require a broader range of physiological tolerances to persist at that site. In addition, a wider range of physiological tolerance allows species to become more extensively distributed. Given that the range of tolerance of an organism is related to its phenotypic flexibility, the CVH implies that the physiological flexibility of species (and/or its populations and individuals) should increase with latitude (Chown et al. 2004). In this vein, populations may cope with genetic differentiation in fitness-related traits that allows them to adjust their mean phenotypes to prevailing environmental factors across generations (Kawecki & Ebert 2004). Second, organisms may show within-generation changes in their phenotypes in response to environmental changes, which is indeed phenotypic plasticity (see sidebar on Phenotypic Variation Along Environmental Gradients). Plastic responses include modifications in physiological, morphological, developmental, behavioral, and life-history traits (Schlichting & Pigliucci 1998). Theoretically, this flexibility allows organisms to adjust to changing biotic and abiotic conditions through increases in performance and likely Darwinian fitness (e.g., Spicer & El-Gamal 1999). Thus, unsurprisingly, documented cases exist in which most intraspecific and interspecific physiological variation can be attributed to phenotypic plasticity.

Plasticity for capacity. Among vertebrates, the flexibility of traits associated with digestive function is an excellent case study and a useful model of physiological flexibility. This is because digestive tract function and structure represent the link between energy intake, maintenance, and energy allocation and fitness-related traits (Secor 2001). Both theoretical and experimental studies have demonstrated that animals adjust their digestive attributes to maximize overall energy return (Sibly 1981 and references therein). To evaluate the CVH, Naya et al. (2007, 2008) applied a meta-analytical approach to data on rodents' small intestine length flexibility. Naya et al. (2008) found a positive correlation between small intestine length flexibility and latitude as well as between the former variable and the number of habitats occupied by different species. This broad statistical analysis is important evidence of the adaptive value of physiological flexibility in small mammals,

PHENOTYPIC VARIATION ALONG ENVIRONMENTAL GRADIENTS

Patterns of within-species phenotypic variation along environmental gradients—or lack thereof—are significant starting points to formulate general hypotheses and/or to undertake mechanistic studies aimed at understanding the ecology and evolution of species along geographic ranges. This knowledge may be useful to predict the ecological and evolutionary responses of populations or species to current and predicted climate change. For example, on one hand, the commonly found pattern of increased body size with latitude in endotherms (e.g., Bergmann's rule) often has been explained by considering that the lower surface-to-volume ratio of larger organisms allows a reduced heat loss rate in colder environments. On the other hand, for example, along an aridity gradient in small endotherms, larger individuals are found in the driest regions, presumably because conservation of metabolic water is maximized when the evaporative surface-to-volume ratio is minimized.

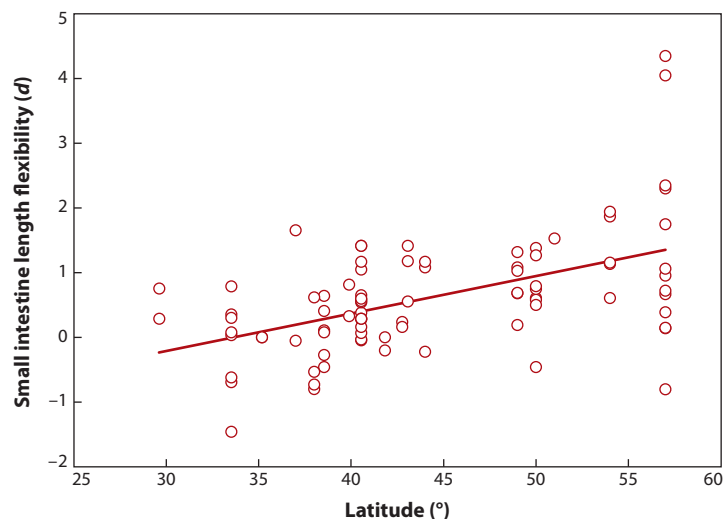


Figure 2

Relationship between maximum small intestine length flexibility and geographic latitude for species of rodents. Small intestine length flexibility is the difference between control and experimental group means (d), expressed in units of pooled standard deviation and corrected for small sample bias (Hedges' difference). In agreement with climatic variability hypothesis predictions, a highly significant positive relationship between latitude and small intestine length flexibility is observed along geographic ranges ($r = 0.51$, $P < 0.0001$). Modified from Naya et al. (2008).

which is consistent with the CVH (**Figure 2**). Testing the adaptive value of flexibility also requires demonstration that the phenotype evoked by each environment has higher relative fitness than the alternative phenotypes (Thompson 1991). As suggested by Naya et al. (2008), a final test of the adaptive flexibility hypothesis might be to artificially extend the range of phenotypes within environments, which is logistically problematic (Schmitt et al. 1999). Ideally, one should conduct between-species comparative studies to evaluate the adaptive value of phenotypic flexibility within a macrophysiological framework, ideally paired with laboratory evolution experiments, to attempt to draw more definitive conclusions (Huey & Rosenzweig 2009).

Plasticity for tolerance. Brattstrom (1968) published an extensive study on “Thermal acclimation in Anuran amphibians as a function of latitude and altitude.” Later Snyder & Weathers (1975) reanalyzed Brattstrom's data to test whether temperate zone organisms have relatively broad thermal tolerances (see Sunday et al. 2011 for a more comprehensive, although not exhaustive, analysis). Spicer & Gaston (1999, p. 170) used these data as evidence for the existence of a relationship between species' upper and lower thermal tolerance and altitudinal distribution. Finally, Ghilambor et al. (2006) used Brattstrom's data to revise Janzen's (1967) hypothesis and answer the fundamental question of whether mountain passes are higher in the tropics. Interestingly, these analyses focused on the relationship between species tolerance and latitudinal and/or altitudinal distribution. In contrast, the focus of Brattstrom's work on the thermal acclimatory ability of amphibian species is largely overlooked. He produced a graph, subsequently reproduced by Spicer & Gaston (1999) (**Figure 3**), showing the relationship between species critical thermal maximum acclimatory ability and geographic range size. However, few studies have experimentally investigated the potential importance of species plasticity as a determinant of animal distribution.

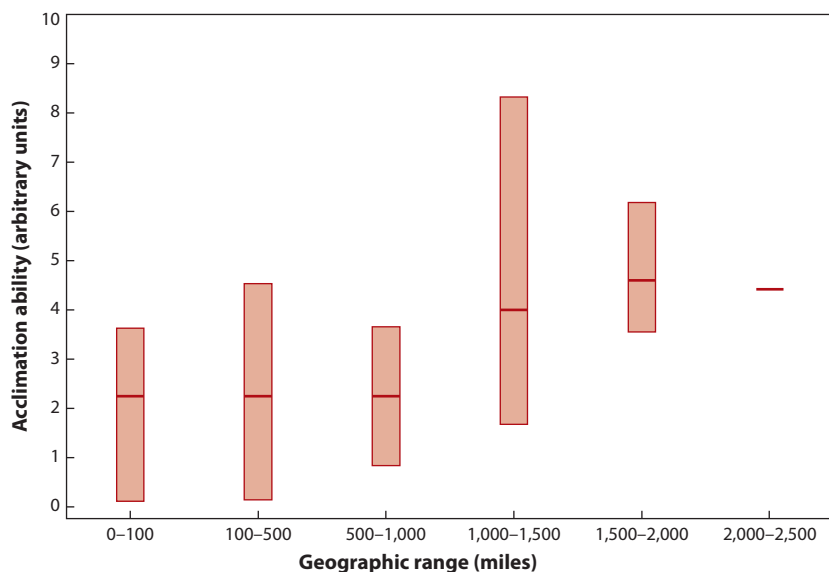


Figure 3

Relationships between acclimation ability and geographical range for frog species (Brattstrom 1968). Acclimation ability was tested as the rate of adjustment of critical thermal maxima (CT_{max}), for a 20°C change in the temperature at which individuals were kept. The horizontal lines represent mean values, whereas the vertical boxes represent the range of CT_{max} adjustment. Hence, anuran amphibians with restricted geographic ranges reveal less ability to acclimate CT_{max} to temperature changes than do broadly distributed species. Modified from Spicer & Gaston (1999), after Brattstrom (1968).

The positive relationship between thermal acclimation ability and geographic range size observed in ectothermic animals has been identified recently as the Brattstrom hypothesis (Gaston et al. 2009), although it must be recognized that the hypothesis is nested within the CVH conceptual framework (see also the jack-of-all-trades concept in Gaston & Spicer 2001). Recently, while investigating the thermal tolerance levels and plasticity of several taxa of European diving beetles (*Deronectes*), Calosi et al. (2008a, 2010) found a positive relationship between species' heat tolerance acclimatory ability and the size and position of their geographic range, thus showing that widespread species appear to possess a higher degree of plasticity. In particular, such ability in *Deronectes* seems to be coupled with high tolerance levels in widespread species (Calosi et al. 2008a). However, no relationship was found between tolerance to cold and its plasticity in *Deronectes* even though a surprising negative relationship of cold tolerance plasticity and range size appears to exist (Calosi et al. 2010).

Investigation of the evolution of physiological traits is essential for the interpretation of physiographic and ecographic patterns, and these patterns should be verified on a broader taxonomic scale. Stillman & Somero (2000) and Stillman (2002) have shown that in porcelain crabs (genus *Petrolisthes*), tolerance levels and their related plastic response are negatively related, thus indicating the existence of an evolutionary physiological trade-off between these traits, both for tolerance to heat and cold. Although we currently cannot say that differences in these patterns in thermotolerance (Calosi et al. 2008a, Stillman 2002) characterize the different physiological evolution of freshwater and marine organisms, this idea needs to be explored (Figure 4). However, as Stillman has suggested (J.H. Stillman, personal communication), the pattern described above may be generated by differences in the evolutionary trajectory of thermal tolerance in diving beetles

Brattstrom hypothesis: a positive relationship may exist between thermal acclimation ability and geographic range size among ectotherms

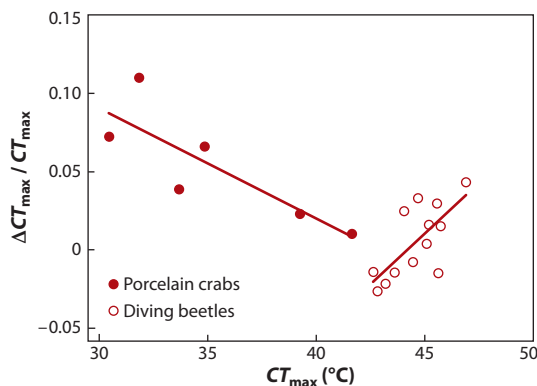


Figure 4

Relationships between tolerance to heat ($CT_{\max}$) and relative acclimatory ability ($\Delta CT_{\max}/CT_{\max}$) in Pacific porcelain crab species of the genus *Petrolisthes* ($y = -0.007x + 0.30$, $n = 6$, $r = 0.84$; data from Stillman 2002) and European diving beetle species of the genus *Deronectes* ($y = 0.013x - 0.57$, $n = 13$, $r = 0.71$, data from Calosi et al. 2010). Circles represent raw data for individual species, and lines represent significant relationships ($P < 0.05$) between studied variables.

and crabs. In fact, although crabs evolved into the upper intertidal zone from subtidal ancestors (and thus $CT_{\max}$ evolved from cooler to warmer and thermally more variable habitats), diving beetles evolved into aquatic environments from terrestrial ancestors (and thus $CT_{\max}$ evolved from warmer to cooler and thermally less variable habitats). Additionally, the apparent discrepancy between the patterns observed in porcelain crabs and diving beetles may be because the diving beetles examined by Calosi et al. (2008a) were much more closely phylogenetically related to each other, and more ecologically similar, than were the porcelain crab species examined by Stillman & Somero (2000) and Stillman (2002).

Hawes & Bale (2007) proposed a relationship between cold tolerance and its plasticity in different cryotypes of arthropods. They suggested that these two traits should be negatively related (i.e., evolutionary trade-off) in freezing-tolerant arthropods and positively correlated (i.e., coevolution) in freezing-avoidant arthropods. However, when Chown et al. (2008) formally tested these suggestions, there was no evidence for an evolutionary physiological divergence in these two cryotypes. Instead, they showed that cold tolerance and its plasticity were related positively in both groups, thus suggesting that these traits have coevolved in terrestrial arthropods. Calosi et al. (2008a,b) and Strachan et al. (2011) found no evidence for an evolutionary trade-off or coevolution of cold tolerance and its plasticity in diving beetles and *Drosophila* larvae, respectively, whereas Stillman (2002) described an evolutionary trade-off between these traits in porcelain crabs (Stillman 2002, Stillman & Somero 2000). Explanation of these examples of potential ecological evolution is more challenging.

In conclusion, there is a need to advance our current understanding of the relationship between species and population plastic responses (e.g., Klok & Chown 2003) and their influence on determining the geographic distribution of taxa. Ultimately, this will lead to a better understanding of the relationship among tolerance, capacity, and plasticity and will guide the integration of these traits in the investigation of what determines a species range size. The debate on how to integrate different traits (not exclusively physiological), or how to better parameterize every trait considered fundamental for the modeling of species geographic range and limits determinants, is a lively one (see Gaston et al. 2009, Kearney & Porter 2009; see also sidebar on From Molecules to Biogeography).

FROM MOLECULES TO BIOGEOGRAPHY

The phrase “from molecules to biogeography” is the holy grail of ecological physiologists. However, the possibility of constructing simple models in which the actions of one or a group of molecules can predict biogeography seems remote—but perhaps not impossible. For example, magnesium has long been recognized as a muscle relaxant, and the knowledge that an increased extracellular magnesium concentration is linked with reductions in activity and temperature in crustaceans is now established. For sandhoppers, below a critical low temperature, activity ceases, metabolism is dramatically reduced, and extracellular magnesium increases three- to fourfold (Spicer et al. 1994). The switch that triggers magnesium flooding of the extracellular space at a particular low temperature could restrict the geographic distribution of this species by reducing the amount of time the species can be active during the year. Frederich et al. (2001) proposed that the absence of crabs and lobsters in Antarctica was because of poor magnesium regulation in the cold. Thus, the relaxant properties of magnesium would impose limitations on cardiac and ventilatory performance at low temperatures, thus compromising tissue oxygen supply. In such a scenario, crustaceans with lower, better-regulated extracellular magnesium (such as shrimps, amphipods, and isopods), although they may bear higher costs associated with such ionoregulation, would be expected to outcompete their reptant decapods in polar regions.

GLOBAL CLIMATE CHANGE, PHYSIOLOGY, AND DISTRIBUTION

Physiological Ecology in a Warming World

Earth's climate is changing rapidly. Data from the Intergovernmental Panel on Climate Change (IPCC 2007) signal a trend toward increasing global temperatures that is evident, but not identical, on all five continents. The causes of these patterns are complex and associated with a network of events in which anthropic action appears to have a determining role (Parmesan & Yohe 2003). Although rapid climate change is expected to result in pervasive effects on the biota, the nature, span, and final consequences of climate change must differ among taxa, even among individuals, because of the vast diversity in physiological traits and ecological associations evident in the fauna (Calosi et al. 2008a, Stillman 2002). Understanding the nature of differential effects of climate change on animal species is one of many urgent interdisciplinary challenges faced by contemporary science.

Two main principles in ecological physiology are that populations exposed to environmental change may crash when most individuals deteriorate and that individuals decline when they reach a physiological state that prevents them from maintaining homeostasis—that is, the proper internal equilibrium through time (Spicer & Gaston 1999). Disruption of homeostatic functions ultimately leads to reduction in fitness, loss of genetic variation at a population level, and possibly local or even global extinction. It follows that the effects of future climate change on species can be assessed not from the type, magnitude, or time scale of the perturbation but instead from the physiological states caused by it, and that the same pattern may be deleterious for one species or population and neutral to another. In addition, knowledge of climatic change effects on animals' range of terrestrial ecosystems is lacking. In terrestrial ecosystems, for example, most analyses of such abiotic effects have been restricted to the level of primary and secondary productivity and geographic biodiversity; none have examined their presumed effects on physiological function, which is the real method through which climate affects individuals and their fitness. Thus, the narrow approaches to the study of the effects of global change on animal biodiversity are limited

because by and large they ignore the constellation of physiological mechanisms that organisms use to cope with environmental changes. [However, see Cowling et al. (2004) on the invasiveness of the landhopper *Arcitalitrus dorrieni* in Britain as well as Chown et al. (2007) on phenotypic plasticity-mediated responses to climate change among indigenous and invasive springtails in sub-Antarctic Marion Island.] Here we identify and assess weaknesses in the few current approaches to the eco-physiological and mechanistic bases of global climate change biology and its putative consequences on distribution ranges. This complex problem requires an understanding of the regional impact of climate change, the physiological mechanisms (tolerance, capacity, and plasticity) by which animals cope with change during their life cycles, and the nature of the differential effects of climate change on the ecology and life history of species and populations living in different geographic areas (Somero 2011).

The Intertidal Ecosystem: A Model for Climate Change Physiology

With few exceptions, intertidal invertebrates and algae are of marine origin and constantly face an oscillation between marine conditions during high tide and terrestrial conditions during low tide. This tidal oscillation generates steep gradients in submersion time, temperature, pH, salinity, and oxygen availability over only a few meters that may last a few hours. Most notable are the changes in ambient temperature. On one hand, during high tides, when marine conditions prevail, the ambient temperature will be that of the sea submerging these organisms. On the other hand, during low tides, when terrestrial conditions prevail, ambient temperature may reach values far in excess of the warmest sea temperatures (Southward 1958) and may fall well below freezing during early morning winter low tides at higher latitudes. Probably the most conspicuous feature of rocky shores worldwide is the organization of intertidal invertebrates and algae into distinct vertical bands, a pattern frequently referred to as zonation (Newell 1979). The lower limits to the distribution of intertidal organisms are usually attributed to biological factors such as competition and predation, whereas upper limits are attributed to desiccation and thermal stress (Robles & Desharnais 2002). The idea that desiccation and thermal stress determine the upper zonation limits of intertidal organisms has been held as a paradigm for many years, and ecologists have explored the relationship between vertical and latitudinal range of distribution [e.g., Harley et al. (2003) found a strong relationship between bathymetric distribution and geographic range size in marine algae and invertebrates]. Such patterns (again) could be explained as the by-product of variation in physiological traits. The most comprehensive investigation of the relationship between species physiological ability and their relative position along the vertical gradient of a shore is that conducted by Stillman (see Stillman & Somero 2000, but also Davenport & MacAlister 1996). However, most studies historically did not include in their analysis or discuss information on the thermal environment experienced by the organisms under examination (Helmuth 2002). Such an omission may limit our ability to critically evaluate the outcome of such investigations. Given this observation, it is perhaps surprising that little is known about what species actually experience in terms of thermal regime. Only recently has commercially available technology allowed the recording of in situ temperature over extended periods of time and at multiple locations (Helmuth 2002). Once matched to the thermal properties of the study organisms, these data loggers provide a measure of the actual thermal conditions experienced by organisms over a fixed period of time. A current limitation in the use of this method is that often thermal regimes are recorded only for the duration of the study or for a period determined by logger capacity. It is possible that unusual events that occur every few to tens of years (in fact, these events might not be so unusual; see Spicer & Gaston 1999 for discussion) may be responsible for some of the patterns

we observe today. An alternative method of evaluating the effects of environmental stresses on invertebrates and on their local ecological ranges involves a combination of direct measures of the thermal regimes and modeling of the main components affecting the organism's body temperature. Given measurements of solar radiation, air temperature, relative humidity, and wind speed, body temperatures can be estimated to within a few degrees using a thermal energy budget (Porter & Gates 1969, Porter et al. 1973), which can be validated against in situ recorded temperature data. This kind of model, which was originally formulated for terrestrial ectotherms (e.g., by Porter et al. 1973), was applied by Helmuth (1998) and Finke et al. (2009) to intertidal mussels along the Pacific coast of North and South America to estimate body temperatures under different scenarios of changes in climatic conditions when in situ body temperature measurements are not available. Thus, because thermal energy budget modeling incorporates an organism's physiological performance, it has the potential to be a helpful tool for answering questions regarding spatial distribution and geographic range changes in the face of global warming over finer temporal and spatial scales.

Understanding and explaining the selective pressures underlying differences in individual performance within and across species has been a major topic among evolutionary physiological (and biophysical) ecologists, and now it should be used as an analytical approach to study the impact of climate change in terms of both means and variability on individual, population, and species performance. For instance, one of the few studies testing for the effects of daily thermal amplitude on physiological and life-history traits was that of Folguera et al. (2009), who found that populations of terrestrial isopods submitted to daily thermal amplitudes exhibit greater physiological resistance to fluctuating regimes. This response to climate also suggested that thermal fluctuation may be an important selective factor in nature. In addition, the experimental effects of different environmental thermal conditions are directly related to the thermal safety margin, which is defined as the difference between an organism's thermal optimum and its current climate temperature (Deutsch et al. 2008). Folguera et al. (2009) showed that higher values of thermal amplitude are correlated with lower values of physiological performance. Many physiological traits are adaptive, although there are costs involved (Hoffmann 1995).

In summary, for the global change biologist, the lack of physiological approaches is the primary barrier to the successful prediction of the ecological effects of climate change. A lack of mechanistic understanding of how organisms work makes it difficult to predict the potential threats to life on earth.

SYNTHESIS AND CONCLUSIONS

We have reviewed and critically analyzed existing evidence for the presence of a relationship between physiological traits and ranges of geographic distribution of animals, taking into account the role that clade evolution, ecology, and phylogenetic history will play in shaping intra- and interspecific diversity. We explored what (if any) are the physiological constraints (in terms of tolerance and capacity as well as their plasticity) that restrict range expansions into different environments found within a geographic area, including constraints imposed by physiological traits (e.g., Kellerman et al. 2009), the presence of evolutionary trade-offs (e.g., Pörtner et al. 2006, Stillman 2002), and the coevolution of physiological traits (e.g., Calosi et al. 2008a, 2010; Naya et al. 2008). Also, we attempted to evaluate the physiological vulnerability of species to global warming (Calosi et al. 2008a,b; Deutsch et al. 2008; Huey et al. 2009), their ability to employ behavioral responses (and their plasticity) to maintain a thermal optimum status (Huey & Tewksbury 2009, Kearney et al. 2009), and their ability to respond by adapting, via natural

selection, to different geographic ranges. Although behavioral traits are more labile and thus more complex to investigate and predict, and scope for adaptation is still a poorly explored area of science with the exception of a few model organisms (e.g., *Escherichia coli*, *Drosophila* sp.), it is prudent to critically evaluate the mechanistic basis for known physiographic patterns if one aims to identify likely new (or lack of) physiological responses of animals to new climatic conditions at the limits of their geographic ranges. Indeed, one of the principal challenges for ecologists today is to assess the ecological impact of global changes caused by natural processes and human activities, which range from the loss of habitat and introduction of alien species to the injection of CO₂ and pollutants into the biosphere.

Although adaptive diversity and variation are key characteristics of life, remarkably, few analyses exist that investigate the relationship among global climatic change and variability on physiological traits and physiological responses of animals (and plants) in geographic areas. In addition, it seems desirable to explain how high levels of environmental variability encountered over large geographic distances affect physiological traits. Clearly, the impact of rising temperatures depends on the physiological vulnerability of organisms to climate change and can be defined by species safety margins. Thus, it seems necessary to evaluate patterns of physiological diversity as a function of different ecological regions oriented to obtain mechanistic explanations regarding the likely new (or lack of) physiological responses of animals to new climatic conditions along geographic ranges. Theoretical models (Katz et al. 2005) as well as empirical data (Easterling et al. 2000) have concluded that climate change also impacts temperature variability. Importantly, most current studies and analyses of global changes have used mean values, paying less attention to the role of fluctuations in climatic variables. Thus, experimental studies testing not only the effect of increases in mean temperature but also changes in temperature variability on phenotypic traits may be important at different evolutionary, ecological, and physiological scales (Travis & Futuyma 1993). Moreover, environmental temperature changes in different and complex ways along latitudinal and altitudinal gradients (Montgomery 2006, Rind 1998). Particularly, daily thermal amplitude, measured as the difference between mean diurnal and nocturnal temperatures, is expected to change dramatically between highland and lowland environments. Indeed, future geographic comparisons between populations may indicate higher sensitivity to thermal amplitude in lowland rather than in highland individuals, which indicates that important effects on biodiversity may be expected in the context of increasing thermal amplitude. Taken together, future studies of environmental thermal variability may produce important results on physiological diversity along geographic gradients. Therefore, to develop more realistic scenarios of the effects of global climate change on biodiversity, the effects of means as well as variability need to be examined simultaneously.

Finally, the question of why a species or population has a restricted distribution, given its present physiological traits, is still puzzling (Kirkpatrick & Barton 1997, Sexton et al. 2009). Comprehensive empirical studies of the relationships between physiological properties within and between species and the limits of species distribution, undertaken for both current and predicted climatic scenarios, may help ecologists and evolutionary biologists to answer questions such as: Is there a limit to the range of environmental factors to which a species can adapt? What prevents a species from adapting further and extending its range of distribution for an indefinite period, given the potential for single-amino acid replacements to adapt a protein to a new thermal range (see Somero 2010)? Thus and finally, what limits the geographic range of a species and a population is still an open question (Futuyma 1998). The debate on how to integrate physiological traits as well as how to better parameterize all the traits considered fundamental for the modeling of species' geographic range limits is a vigorous topic in ecology and evolutionary biology.

SUMMARY POINTS

1. Over the past decade many climate-based hypotheses about variation in distribution range have emerged. These use data on physiological traits, focusing mainly on variation in latitude and altitude, to predict how climate may affect the geographic range of assemblages, species, and populations.
2. Physiological constraints determine the relationship between abiotic variables and the distributional limits of species, but the processes explaining such patterns remain poorly understood.
3. Physiology on a landscape scale with spatially explicit models of physiological and biophysical ecology may quantify and predict the consequences of future climate scenarios and shifts in distribution range.
4. Thermal variation in the intertidal habitat may have a major impact on the distribution of invertebrates, which is reflected by the strong correlation between the level of environmental variability along the bathymetric gradient they occupy and the size of their latitudinal range.
5. Species of endotherms that evolved in cold climates exhibit higher mass-independent metabolic rates than species from warmer habitats.
6. Because the tolerance range of an organism is related to its phenotypic flexibility, the physiological flexibility of species, populations, and individuals should increase with latitude.
7. A lively problem is how to integrate different physiological traits or how to parameterize all the traits considered fundamental for the modeling of species' geographic range and limits determinants.
8. The absence of a physiological approach is one of the primary difficulties in the successful prediction of the ecological and biogeographical effects of climate change.

FUTURE ISSUES

1. It is important to critically evaluate the mechanistic basis for known physiographic patterns to identify the physiological responses to new climatic conditions at the limits of organisms' geographic ranges.
2. It is critical to describe and explain how high levels of environmental variability encountered over large geographic distances affect physiological traits.
3. We must combine at different ecological scales the experimental investigation of the effect of changes in mean levels of climatic variables and of the effect of changes in levels of climatic variability on physiological traits.
4. We need to determine species' and populations' scope for adaptation to rapid environmental changes as well as the presence of evolutionary trade-offs with plasticity levels.
5. It is important to describe patterns of physiological diversity as functions of different ecological regions.

6. It is critical to use approaches from, for example, molecular biology, climatology, and computer science to investigate the relationship between global change and species'/populations' physiological responses in geographic space.
7. We must investigate the relationships between physiological properties within and between species and their distribution limits, both under current and predicted climatic scenarios.

DISCLOSURE STATEMENT

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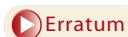
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