Integrative and Comparative Biology

Integrative and Comparative Biology, volume 0, pp. 1–6
https://doi.org/10.1093/icb/icaf143

Society for Integrative and Comparative Biology

SYMPOSIUM INTRODUCTION

Identifying the Physiological Mechanisms That Underlie Phenotypic Responses to Rapid Environmental Change

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Presented at the annual meeting of the Society for the Integrative and Comparative Biology on January 7th, 2025, in Atlanta, GA 30303.
From the symposium "Identifying the physiological mechanisms that underlie phenotypic responses to rapid environmental change" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7th, 2025.

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Synopsis In response to rapidly changing environmental conditions, many organisms are experiencing shifts in geographic ranges and in the timing and expression of key life-history traits, which have important effects on fitness. However, the physiological mechanisms that mediate these phenotypic responses, such as endocrine and other signaling pathways are not well understood. This information will be critical for predicting organismal responses to climate change because physiological mechanisms are often highly responsive to environmental cues and influence the phenotypic variation available to selection. Additionally, they often integrate suites of correlated traits and are thus expected to influence the evolutionary response to selection. The overarching goals of this symposium were to gain novel insights into the physiological mechanisms that underlie organismal responses to rapidly changing environmental conditions and to identify gaps in knowledge and experimental approaches to advance the field. Here we review and discuss the symposium contributions and the research themes that emerged as important foci for future studies.

Introduction

Over the last century, global temperatures have increased by an average of 1°C (Karl 2009). Simultaneously, the frequency of extreme weather events, including heat waves, cold snaps, and storms has also risen (Kornhuber et al. 2024; Parmesan and Yohe 2003; Vasseur et al. 2014). In response to these rapidly changing environmental conditions, many organisms have shifted their geographic distributions and altered diverse phenotypic traits, including the timing of breeding and migration, as well as body size and shape, which have important effects on fitness and population viability (Parmesan and Yohe 2003; Scheffers et al. 2016). However, the physiological mechanisms that mediate these responses are poorly understood, despite the importance of this information for predicting evolution-

Advance Access publication September 4, 2025

ary responses to rapidly changing environmental conditions (Briscoe et al. 2023; Ketterson et al. 2009; Names et al. 2024; Riddell et al. 2023; Seebacher and Franklin 2012; Taff et al. 2024).

Physiological mechanisms such as endocrine and other signaling pathways that regulate vital processes (e.g., temperature regulation, water balance, nutrient sensing, metabolism, stress responses, growth, and reproduction) are expected to play an important role in enabling organisms to respond to rapidly changing conditions (Ketterson et al. 2009; Names et al. 2024; Seebacher and Franklin 2012; Taff et al. 2024). One reason for this is that physiological mechanisms mediate the relationship between the organism and the environment and hence the phenotypic variation available for selection. Although selection can favor physiological mechanisms that better enable organisms to cope with changing environmental conditions, it is unclear whether there will be sufficient time for evolution to keep pace with rapid environmental changes (Kelly 2019). Importantly, physiological mechanisms are often highly responsive to environmental cues and enable organisms to respond plastically to varying environmental conditions (i.e., when the same genotype can produce a different phenotype in response to different environmental conditions), which may allow organisms to better match the prevailing circumstances (Anderson and Song 2020; Ghalambor et al. 2007; Kelly 2019). For example, in many butterfly species, wing coloration represents a balance between selection to absorb more solar radiation (thus increasing body temperatures, activity times, and ultimately net energy gain and reproductive output) and selection to avoid overheating (and declines in egg viability) in response to thermal extremes (Buckley and Kingsolver 2019). In some butterfly species, individuals that develop during late spring and summer under warmer, longer days, have lighter wing coloration than individuals that develop during cooler, shorter days (Nijhout 2003b; Rountree and Nijhout 1995). This seasonal plasticity in wing coloration is regulated by ecdysone signaling (Nijhout 2003b; Rountree and Nijhout 1995), and may allow individuals to better match the prevailing thermal conditions. Both phenotypically plastic responses within individuals and evolutionary changes across generations (including changes in the degree of phenotypic plasticity) are expected to be important in mediating organismal responses to rapidly changing environmental conditions. However, the relative importance of these processes is poorly understood and is anticipated to have significant evolutionary and ecological implications (Anderson and Gezon 2015; Kelly 2019). For example, although phenotypic plasticity may enhance fitness over shorter time scales and allow organisms to persist in place, it could also reduce the strength of selection and slow the pace of evolution over longer time scales (Gienapp et al. 2008; Kelly 2019).

Additionally, because physiological mechanisms such as endocrine and other signaling pathways often integrate suites of phenotypic traits, they could influence the pace of evolution by facilitating rapid coordinated responses across the phenotype or constraining the independent responses of individual traits (Ketterson et al. 2009; Names et al. 2024; Seebacher and Franklin 2012; Taff et al. 2024). For example, using the butterfly example above, in addition to influencing wing coloration, ecdysone signaling is also involved in regulating molting and transitions between developmental stages (Nijhout 2003a). If selection favors changes in ecdysone levels, this could result in a high degree of trait integration and constrain the independent evolution of traits sensitive to ecdysone signaling, such as wing coloration and the transitions between developmental stages (Cox et al. 2022; Ketterson and Nolan 1999; Lipshutz et al. 2019). Alternatively, if selection favors changes in tissue sensitivity to ecdysone, this could permit ecdysone-sensitive traits to evolve more independently of one another (Cox et al. 2022; Ketterson and Nolan 1999; Lipshutz et al. 2019). Interestingly, recent research in common buckeye butterflies (*Junonia coenia*) demonstrated that selection for the genetic assimilation of wing coloration (when a formerly phenotypically plastic trait is produced in the absence of the original environmental cue) was likely driven by changes in regulatory alleles of downstream wing-patterning genes that changed sensitivity to ecdysone (van der Burg et al. 2020). This finding is consistent with the idea that selection on phenotypically plastic traits may often favor downstream changes in tissue sensitivity to allow for tissue- and trait-specific modifications without impacting cue detection or other traits.

Knowledge about the physiological mechanisms that mediate phenotypic responses to changing environmental conditions will also be essential for accurately forecasting population-level responses, including range shifts and extinction risk (Briscoe et al. 2023; Riddell et al. 2023). The environmental variables that are rapidly changing can vary over both temporal and spatial scales and physiological mechanisms mediate the way in which organisms experience this environmental variation (Briscoe et al. 2023). For example, over the past century, small mammal communities have remained relatively stable in the Mojave Desert, whereas many bird communities have collapsed (Riddell et al. 2021). Models that incorporated information about heat flux, particularly the amount of water required for evaporative cooling, suggest that this is because birds and mammals experienced very different levels of warming in this same area due to differences in microhabitat use (e.g., mammals burrow underground, whereas birds do not) (Riddell et al. 2021). Although this example focuses on broad taxonomic differences, it also applies to differences among populations and individuals. Thus, it is becoming increasingly clear that incorporating information about the physiological mechanisms that mediate organismal responses to changing environmental conditions will be essential for predicting long-term outcomes related to these changes (Briscoe et al. 2023; Riddell et al. 2023).

Goals of the symposium

As a scientific community, we must generate robust predictions about which individuals, populations, and species will be more vulnerable to these environmental challenges. To achieve this, we need to understand the physiological mechanisms that underlie organismal responses to rapid environmental change. The overarching goals of the symposium were to: (1) gain a deeper understanding of the physiological mechanisms that mediate rapid responses to changing environmental conditions, (2) provide rich networking opportunities to enhance idea generation and collaboration, and (3) identify and discuss the key outstanding research questions and experimental approaches necessary to advance the field and more accurately predict organismal responses to rapid environmental change. Below, we first provide a brief overview of the seven symposium contributions and then highlight some important areas of future research generated from these contributions and during the symposium and roundtable discussion.

Overview of the symposium contributions

Previous research has tended to focus on increasing temperatures and less is known about the impacts of other environmental variables or the potential interactions among environmental variables that are changing in response to climate change. In this issue, Riddell and Porter (2025) examine the underexplored wind niche and how changes in wind speed will affect organismal heat and water exchange. One of their important findings is that temperate regions are predicted to experience reduced wind speeds along with increased temperatures. By incorporating microclimate data and biophysical simulations, they determined that wind will likely interact with solar radiation and organismal traits such as body size and solar absorptance to influence water loss and the realized temperatures that terrestrial plants and animals experience. Thus, wind is expected to be an important and largely neglected environmental variable that should be incorporated into future models to better predict organismal responses to rapidly changing environmental conditions.

As highlighted above, changing environmental variables are often expected to interact to influence organismal responses to climate change, but these interactions are less well understood. For example, both temperature and atmospheric carbon dioxide concentrations (CO2) are increasing in response to climate change. Here, Denney and Anderson (2025) experimentally manipulated both environmental variables in a growth chamber and examined the potential effects on several ecologically important traits in *Boechera stricta* (*Brassicaceae*) accessions sourced from populations along an elevational gradient in Colorado. Interestingly, they found that the phenotypically plastic responses of some of these traits (e.g., root-to-shoot ratio and leaf dry matter content) to these environmental variables did not align with the direction of selection, suggesting that plasticity is not always adaptive. Nevertheless, the direction of plasticity did align with patterns of natural selection in some traits, such as root mass fraction, which is a key resource allocation trait. In that case, the plasticity in response to temperature variation is likely adaptive. Taken together, these results underscore the idea that plastic responses to multiple changing environmental variables are likely to be complex and do not always have positive effects on fitness.

As environments change rapidly, the ability of organisms to flexibly change their phenotypes may be a critical fitness determinant. In this issue, Taff et al. (2025) highlight flexibility in the glucocorticoid stress response as a potentially important mechanism of adaptation to temperature variability. Although individual variation in the speed of responsiveness and the scope (i.e., how much glucocorticoid levels increase), has been suggested to be important, it has been difficult to test these ideas empirically because large sample sizes are necessary. In the current paper, Taff et al. use a large comparative dataset to test for species-level differences in glucocorticoid flexibility. They found differences among species in reaction norms for baseline corticosterone, corticosterone produced in response to a standardized stressor, and the speed of corticosterone increase in relation to temperature. Across species, the speed of the glucocorticoid response increased when minimum temperatures were lower than 0–2°C, whereas elevated temperatures had less of an effect. With sufficient sample sizes, cross-species or cross-population comparisons of glucocorticoid flexibility may be helpful for predicting resilience to the effects of climate change.

Traditionally, to determine how sensitive organisms are to climate change, performance has been measured across different body temperatures to assess the thermal sensitivity of performance and then, to calculate the fitness implications of climate variability. One limitation of this approach is that it does not account for potential acclimation to prior thermal stressors. Here, Buckley et al. (2025) test how recent thermal stress may affect current thermal responsiveness, including damage, repair, and carryover effects by applying a model to an extensive dataset of experimental manipulations of realized temperatures for English aphids (*Sitobion avenae*). Heat stress was observed to start at the upper limit of performance and intensified with increased temperatures and duration of exposure to elevated temperatures. Importantly, aphids were able to extensively utilize repair mechanisms near the thermal optimum. These results highlight the potential for more accurate assessments of the fitness consequences of climate variability by accounting for recent thermal history, damage, recovery, and repair.

Continuing the theme of recovery from stressors, Rujuta et al. (2025) extend this approach to document the time course of the cellular heat shock response in a marine copepod, *Tigriopus californicus*. At the cellular level, the responses to heat stress can involve changes in gene expression, which is what is typically quantified, but may also include changes in exon usage through differential expression. The gene expression and exon usage of copepods were different at each time point after heat shock (30 min, 1 h, 2 h, and 24 h) with the greatest effects observed at the time points closest to the heat stress. A minority of genes, primarily those that code for peptidases and chitin synthesis, responded to heat shock by altering both gene expression and exon usage. Most genes altered only one of these mechanisms. Genes for heat shock proteins, as well as those related to cellular growth and differentiation, altered their expression levels in response to heat stress. Conversely, genes related to cellular metabolism and cytoskeletal elements changed their exon usage. These results highlight the need to incorporate more qualitative analyses of changes in exon usages to better understand how organisms respond to environmental change.

Physiological mechanisms can be influenced by both environmental and genetic factors and predicting how organisms will respond to climate change will require careful experimental approaches that can tease apart the relative importance of these two processes, such as common gardens and reciprocal transplants. In egg-laying vertebrates, this can involve artificially incubating developing embryos. Although this is often done in non-avian reptiles, and precocial birds like chickens, quail, and ducks, this is notoriously difficult in most altricial bird species. Here Names and Heidinger (2025) use house sparrows (*Passer domesticus*), a widespread songbird, as a case study and demonstrate an approach that can be used to optimize aspects of artificial incubation, including temperature, humidity, egg mass loss, and egg turning to achieve very high hatching success. This study is expected to expand the possibility of adopting experimental approaches that require artificial incubation in songbirds to shed new light on the mechanisms that mediate responses to rapidly changing environmental conditions and may also aid in the conservation management of threatened songbird species.

Another consideration is that the fitness consequences of exposure to adverse environmental conditions may carry over across generations when maternal physiology during gestation is altered by the demands of thermoregulation and hydroregulation, as seen in terrestrial ectotherms. Brusch et al. (2025) test the consequences of elevated temperatures and water deprivation on the offspring of the common lizard (*Zootoca vivipara*) and found that warmer daytime temperatures increased offspring growth and survival. However, warm temperatures at night were more challenging for both mothers and offspring, and offspring survival was reduced when both day and night temperatures were warm. Although water deprivation challenged maternal homeostasis, both mothers and offspring were resilient to water restriction. This study highlights the importance of considering how future climate change may have cascading effects across generations to make more accurate predictions of potential fitness consequences.

Future directions and conclusions

We highlight several reoccurring and overlapping themes that emerged from the symposium as foci for future research. One general theme centered around the complexity of rapid environmental changes. We need a much richer understanding of how interactions among environmental variables are changing in response to climate change (e.g., precipitation, humidity levels, CO_2, and wind speed) and shaping organismal responses. Furthermore, the degree of variation in many of these environmental variables is also increasing and may be even more significant in shaping organismal responses than mean changes. However, this variation has been largely neglected. Some of the specific questions related to this general theme that were generated during the roundtable discussion include: (1) How do multiple environmental drivers (e.g., temperature and CO_2) and spatial and temporal variation in these factors influence evolutionary potential? (2) How do other environmental factors such as habitat fragmentation and pollution influence organismal responses to climate change? (3) What are we missing when characterizing changing environments (that is, how are we constrained by our own umwelt)? (4) How much do environmental means versus variation matter and how do we account for this when measuring physiological responses?

Given that the intensity of climate change varies dramatically across both small and large spatial and temporal scales, it will be critical to better characterize how these different scales of variation influence organismal responses. Significant advances in understanding in this area are expected to be made through the formation of collaborative networks focused on longitudinal, across population-level studies. Some specific questions include: (5) How can we best match scales of spatial and temporal variability to organismal sensitivity to predict organismal responses? (6) How do we support and fund networks for large-scale comparisons across time and space? (7) How can we increase cross-institution collaboration to address the effects of climate change? (8) How can we better utilize historical data from museums, as well as large-scale collaborative research projects (e.g., NEON) and citizen science data, to address questions related to physiological mechanisms? (9) How can we best use modeling, and in some cases historical collections, to hindcast and forecast to better predict organismal responses?

Another general theme that emerged is that organismal responses to rapidly changing environmental conditions are complex and involve coordination across multiple physiological systems and varied life stages. We need much more information about the mechanisms that mediate these responses, including the degree to which this variation is due to phenotypic plasticity and/or microevolutionary change. We need to increase our capacity to link differences in thermal performance, stress responsiveness, and other physiological mechanisms for coping with changing environmental conditions to fitness. Some of the specific questions include: (10) How does environmental variability influence phenotypic plasticity, and how often are organisms inhabiting high-variability environments less plastic? (11) Does the evolutionary history of a specific population impact its evolutionary potential or plasticity? For example, might refugial populations behave differently than those in a new part of the species range? (12) How polygenic is heat tolerance, and how does the number of genes associated with heat tolerance compare across taxa? (13) How do we integrate across multiple different responses to better understand whole-organism responses? (14) When do behaviors constrain physiological responses and vice versa? (15) How do we deal with multivariate climate changes given the sampling constraints of physiology? (16) What is the most efficient mix of omic and physiological approaches to understand and anticipate phenotypic change? (17) What are the best proxies for physiological performance? (18) How does life stage influence thermal sensitivity? (19) How do temperature regime differences across life stages interact to shape thermal tolerance? (20) Across plants and animals do certain life history stages respond differently to ecological stressors than others? (21) How do we incorporate life history effects into climate change resilience models? (22) How does fitness scale with different traits? If traits respond differently, how do we know which is most important?

Going forward, taking a more integrative approach to understanding the physiological mechanisms that mediate organismal responses to rapidly changing environments will be essential for accurately predicting long-term responses to climate change. For example, future integrative research in this field would benefit from including understudied environmental variables, such as wind, as well as variation in climate variables and their averages. Moreover, environmental variables are likely to interact with consequences for organismal adaptation, making this another area where an integrative, physiological approach will be beneficial. Integrative approaches may also involve incorporating various types of study methods, including common gardens, reciprocal transplants, simulations, models, cross-species comparisons, transcriptomics (and other -omics), and museum studies, among others. Finally, several authors are utilizing diverse approaches across levels of organization to demonstrate how recent thermal, light, and hydric challenges impact damage, recovery, and repair within and across generations. Together, the symposium and this issue highlight important future challenges and opportunities in understanding and anticipating organismal responses to climate change.

Funding

This symposium “Identifying the physiological mechanisms that underlie phenotypic responses to rapid environmental change” was generously supported by the Division of Comparative Endocrinology, the Division of Ecology and Evolution, the Division of Animal Behavior, the Division of Comparative Biomechanics, and the Division of Evolutionary Developmental Biology of the Society for Integrative and Comparative Biology. J.L.G. was also supported by NSF DBI 2216648, and B.J.H. was also supported by NSF IOS–185974.

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