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SYMPOSIUM INTRODUCTION

Indirect Effects of Global Change: From Physiological and Behavioral Mechanisms to Ecological Consequences

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Synopsis A major focus of current ecological research is to understand how global change makes species vulnerable to extirpation. To date, mechanistic ecophysiological analyses of global change vulnerability have focused primarily on the direct effects of changing abiotic conditions on whole-organism physiological traits, such as metabolic rate, locomotor performance, cardiac function, and critical thermal limits. However, species do not live in isolation within their physical environments, and direct effects of climate change are likely to be compounded by indirect effects that result from altered interactions with other species, such as competitors and predators. The Society for Integrative and Comparative Biology 2017 Symposium "Indirect Effects of Global Change: From Physiological and Behavioral Mechanisms to Ecological Consequences" was designed to synthesize multiple approaches to investigating the indirect effects of global change by bringing together researchers that study the indirect effects of global change from multiple perspectives across habitat, type of anthropogenic change, and level of biological organization. Our goal in bringing together researchers from different backgrounds was to foster cross-disciplinary insights into the mechanistic bases and higher-order ecological consequences of indirect effects of global change, and to promote collaboration among fields.

Introduction

The impact of human activity on the Earth is now of such magnitude that geologists are referring to the current epoch as the "Anthropocene" (Waters et al. 2016). Not surprisingly, our influence on the abiotic environment has enormous consequences for the biosphere. Species distributions are shifting (Chen et al. 2011), the dynamics of nutrient and energy flow through ecosystems are changing (Ernakovich et al. 2014), and species are going extinct at rates several times higher than background levels (Ceballos et al. 2015; Urban 2015).

If we are to accurately predict and successfully mitigate the consequences of global change, we need to understand the mechanisms that underlie concomitant biological change (Pacifici et al. 2015; Urban et al. 2016). The mechanisms that drive population responses to global change are often described as falling into two general categories: direct effects and indirect effects (Cahill et al. 2013; Ockendon et al. 2014). Direct effects on a population result from the influence of abiotic factors on the physiology and behavior of that population. Examples include the effect of changing $p\mathrm{CO_2}$ on photosynthetic rates (Smith and Dukes 2013), temperature effects on metabolic rates (Dillon et al. 2010), and behavioral avoidance of habitat that has become unsuitable (Eby and Crowder 2002; Swaddle and Ingrassia 2017). Indirect effects on a population result from changes in the strength and kind of species interactions that the population experiences as conditions change. Examples of indirect effects include temperature-dependent shifts in parasite infection (Pounds et al. 2006; Mignatti et al. 2016), predator attack rates (Englund et al. 2011; Pincebourde et al. 2012; Dell et al. 2014), competition

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(Dallalio et al. 2017), and symbioses (Cunning et al. 2015).

Although direct and indirect effects of global change are sometimes described as two different phenomena, changes in species interactions must ultimately be driven by direct effects on at least one species within a system. For example, climate change indirectly affects migratory bird populations by driving mismatches between the arrival of birds on their breeding grounds and the emergence of their prey; these mismatches result from the direct effects of abiotic conditions on bird and prey phenology (Jones and Cresswell 2010; Senner et al. 2017). Similarly, the direct effects of climate on species range limits can lead species to experience novel and more harmful competitors, predators, and parasites (Alexander et al. 2015). Therefore, there is a need to develop approaches that translate our understanding of direct effects of global change into predictions of indirect effects. In this issue, we bring together researchers that study the indirect effects of global change from multiple perspectives in terms of habitats (marine and terrestrial), type of anthropogenic change (temperature and ocean acidification), biological fields (physiologists, behaviorists, and ecologists), and levels of biological organization (from molecules to whole communities). Our goal is to foster cross-disciplinary insights into the mechanistic bases and higher-order ecological consequences of indirect effects of global change.

Species interactions in the context of physiological and behavioral performance

In animal systems, changes in species interactions will be mediated by direct effects of environmental change on physiology and behavior, both of which are tightly linked to each other (Fig. 1). The importance of physiology and behavior for species interactions is straightforward: physiology and behavior jointly determine where individuals of a given species will be, when they will be there, and the level of performance they can achieve in fitness-related tasks. The direct effect of abiotic factors on many physiological (Angilletta 2009) and behavioral (Gunderson and Leal 2015; 2016) traits can be summarized in terms of performance curves, which describe how a biological process changes as a function of abiotic conditions (Huey and Stevenson 1979; see Sinclair et al. (2016) for a critique of the application of performance curves). Performance curves provide a powerful means of conceptualizing how species interactions can be affected by abiotic change (Fig. 2). Imagine two interacting species such as competitors or predator and prey. Under certain conditions the species may have similar performance such that no species has the upper hand. However, a change in abiotic conditions can change the dynamics, granting one species a performance advantage (Fig. 2). For example, performance curves for temperature-dependent locomotor performance, which influence ecologically relevant factors such as the ability to catch prey or evade predators, have been used extensively to investigate the consequences of global warming on species interactions (Tylianakis et al. 2008; Dell et al. 2011; Gibert et al. 2016).

Because performance is likely to be critical for determining the outcome of many species interactions, it is important to be able to predict the shape of performance curves and how performance curves are affected by acclimation (Agrawal 2001; Gunderson and Stillman 2015; Seebacher et al. 2015). Luhring and DeLong (2017) use a mechanism-based model of temperature-dependent chemical reaction rates to investigate changes to the shape of organism-level thermal performance curves under different temperature acclimation regimes, using data on population growth rates of *Paramecium bursaria*. They find that acclimation to intermediate temperatures generally lead to increased thermal breadth and the highest growth rates at high temperatures. Their analysis also suggests lower-level biochemical mechanisms (i.e., temperature-dependent heat capacity and enthalpy of enzymes) that could drive the differences in performance curve shape (Luhring and DeLong 2017).

An important means by which abiotic conditions can affect physiology and subsequently behaviors important for species interactions is through effects on sensory physiology. If individuals have reduced ability to detect predators, prey, or competitors, they are likely to be at a disadvantage (Amo et al. 2004). For example, numerous sensory modalities are known to be temperature sensitive, including vision (Aho et al. 1988; Cunningham and Hyde 1995; Ala-Laurila et al. 2004; Reilly and Thompson 2007), audition (Campbell 1969; Hubl and Schneider 1979; Franz and Ronacher 2002; Wysocki et al. 2009), and mechanoreception (French and Kuster 1982). For marine organisms, another abiotic change that can influence sensory function is ocean acidification (Nilsson et al. 2012). Ashur et al. (2017) review the literature on the consequences of ocean acidification for sensory perception and behavioral responses to environmental cues. They outline extensive evidence for ocean acidification to influence responses to chemosensory, auditory, and visual cues in both vertebrates and

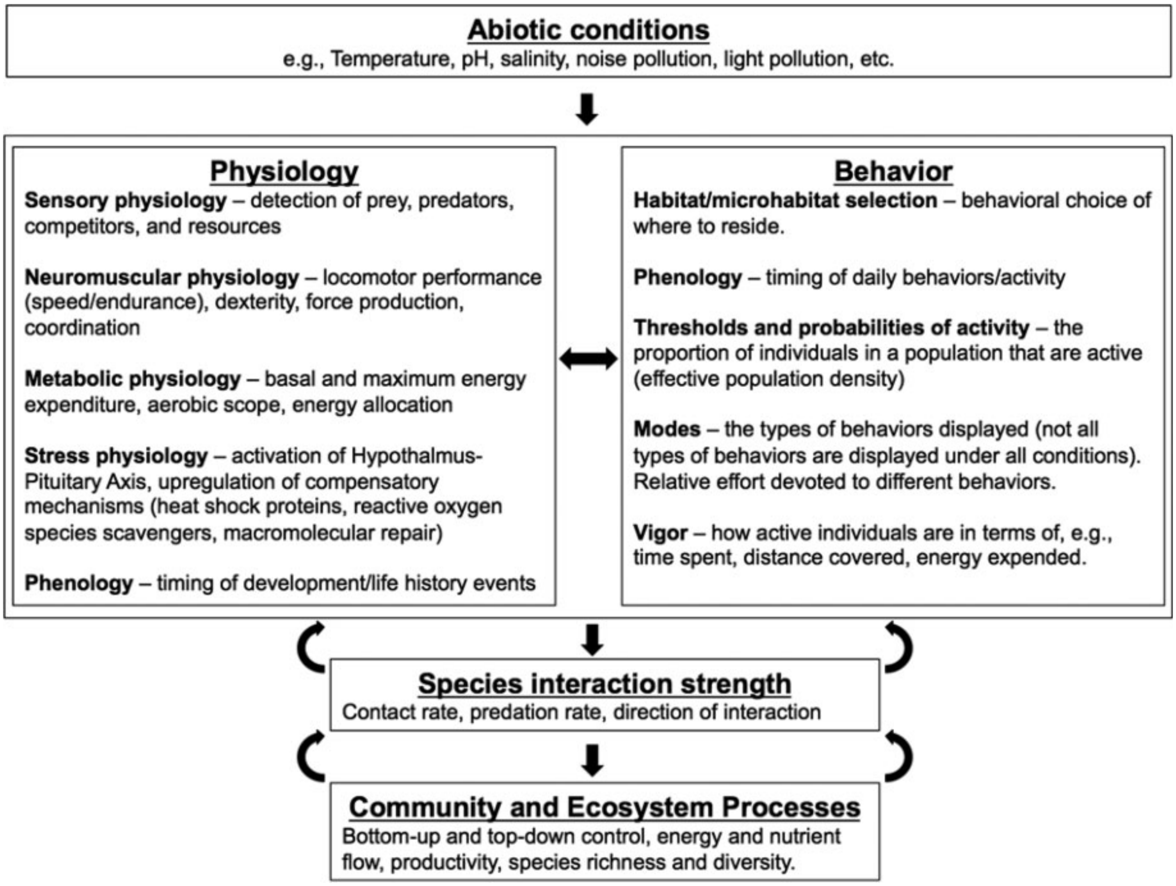

Fig. 1 An overview of some environment-dependent physiological and behavioral processes likely to influence species interactions and subsequent higher-order community and ecosystem processes. Abiotic factors will directly affect physiology and behavior, as well as the interaction between physiology and behavior. These direct effects will influence community- and ecosystem-level processes through their effects on species interactions. In addition, these higher-order effects are likely to feed back on physiology and behavior.

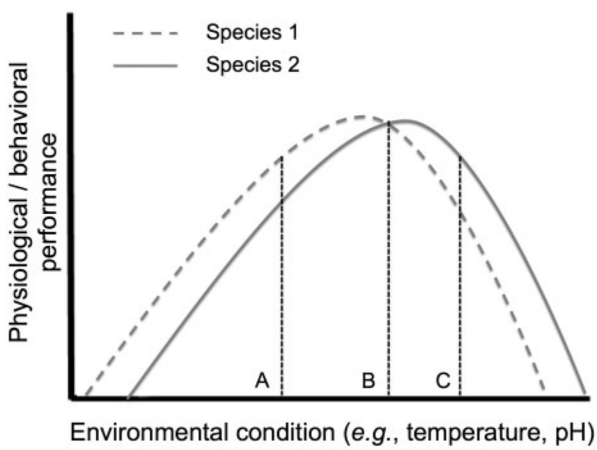

Fig. 2 Graphical example of how physiological and behavioral performance can influence the strength of species interactions under changing environmental conditions. Species 1 has a performance advantage under condition A, while species 2 has a performance advantage under condition C. Neither species has an advantage under condition B.

invertebrates. They also highlight potentially large ecological consequences of these effects, including focal species ignoring cues that would guide them to habitats with symbionts, shifts toward preferences for predator olfactory cues, and decreasing detection of prey (Ashur et al. 2017).

Ferrari et al. (2017) experimentally investigated the consequences of high pCO_2 on prey by monitoring behavior and survival of damselfish (*Pomacentrus amboinensis*) on reefs after pre-exposure to different levels of pCO_2 and predation (i.e., alarm) cues in the laboratory. They found an antagonistic effect of predation cues on responses to elevated pCO_2. In the absence of predation cues, fish pre-exposed to elevated pCO_2 exhibited more high risk behaviors and had lower survival on the reef compared to fish pre-exposed to control conditions. However, fish pre-exposed to both elevated pCO_2 and elevated predation cues did not differ from controls in either metric. Therefore, the behavioral and ecological consequences of high pCO_2 can be influenced by interactive effects with other environmental factors (Ferrari et al. 2017).

Mechanistic frameworks for predicting indirect effects of global change

Because physiological and behavioral traits influence species interactions, it is possible that knowledge of these traits can be used to make mechanism-based predictions of the outcome of species interactions under changing conditions. Gilman (2017) develops a mechanistic framework for predicting the indirect effects of warming using intertidal predator/prey systems as models. The framework is built around the influence of body temperature on energetic expenditure (through metabolic rates) and energy acquisition (through feeding). One prediction of this framework is that prey size can have an impact on predator energetics independent of prey abundance by influencing the energetic gain per prey individual consumed. Gilman tested this hypothesis with experiments in which predatory whelks (*Nucella ostrina*) were subjected to three different temperature treatments while feeding *ad libitum* on either small or large barnacles (*Balanus glandula*). She found that whelks fed small barnacles had lower heat tolerance than whelks fed large barnacles, even though more small barnacles were eaten. Therefore, direct effects of warming on prey, such as temperature effects on size, can potentially influence predators even if prey numbers are not affected.

Diamond et al. (2017) test trait-based hypotheses regarding the consequences of warming within communities of competing ant species. They conducted experiments at two different latitudes using field enclosures in which ground and nest temperatures could be experimentally warmed. They also measured the physiological heat tolerance of all species in the experiment. During the experiments, they monitored the densities and nest occupancy dynamics of all species under ambient and warmed conditions. At both sites, they found that species with lower physiological tolerances for heat were more likely to be affected by the presence of other species under warmed conditions. In other words, the indirect effects of warming were more severe for heat intolerant species. Their results suggest that data on relatively simple physiological metrics such as heat tolerance, which is likely to be correlated with the temperature dependence of many other physiological and behavioral traits (Angilletta et al. 2006), can be powerful in predicting the influence of anthropogenic global change on species interactions (Hein et al. 2014).

Murrell and Barton (2017) investigated the temperature-dependence of species interactions across three trophic levels in an agricultural setting including a primary producer (alfalfa), an herbivore (pea aphid), and a predator (ladybeetle) in fields subjected to conventional and organic farming methods. They found that aphids grew better on conventional alfalfa, and that estimated predation strength was significantly affected by predator density, temperature treatment, and whether or not the alfalfa was organic or conventional. In particular, they found that warming had no effect on predation strength in organic fields under any predator density, but that warming significantly reduced predator effects under low density in conventional fields. The density- and context-dependent results highlight how the consequences of warming on predator/prey systems can depend on complex interactions with other factors, such as the conditions under which lower trophic levels develop.

Incorporating species interactions into species distribution models

Predicting how global change will influence species distributions is a central focus in ecology and conservation research (Buckley et al. 2010; Guisan et al. 2013). Nonetheless, most species distribution models do not incorporate interactions with other species (Araújo and Luoto 2007). Lany et al. (2017) develop an approach to species distribution modeling that integrates the direct effects of environmental conditions with interactions between species. The interacting species in this case are an intertidal zone predator (the seastar *Pisaster ochraceus*) and its prey (the mussel *Mytilus californianus* and the barnacle *B. glandula*). Building on observations that the strength of species interactions are often context dependent (Sanford 1999; Chamberlain et al. 2014; Diamond et al. 2017; Gilman 2017; Murrell and Barton 2017), they allow interaction strength to change based on environmental conditions including water temperature, upwelling strength, and seawater chlorophyll content. Their model is developed using years of survey data on species abundances and environmental conditions at sites covering over 10° latitude on the US West Coast. In general, they find that prey abundance had a positive effect on predator abundance but that the predator had little effect on prey abundance. Models of this kind have great promise for increasing the reliability of species distribution predictions.

Applying knowledge of species interactions to conservation management decisions

With models of the extent to which species interactions are influenced by global change, one can incorporate species interaction effects into management decisions about species that should be targets of conservation efforts. Urban et al. (2017) argue that the species that should be the primary targets of conservation efforts are those that are both sensitive to the direct effects of global change and have a disproportionate influence on other members of biological communities. They refer to these species as “biotic multipliers” of global change, and contend that biotic multipliers within communities are most likely to be top consumers. They then define eight testable, non-mutually exclusive hypotheses to mechanistically explain why top consumers act as biotic multipliers. These hypotheses range from the strictly ecological (top-down control of lower trophic levels) to the behavioral (top consumer have greater mobility than lower trophic levels) and physiological (top consumers have greater metabolic sensitivity than lower trophic levels)(Urban et al. 2017).

Species as stressors

In general, the stress associated with global change is expected to result from direct effects of abiotic drivers on species physiology, which then influences interactions between species. However, there is also the possibility that species interactions themselves can be stressful. Gunderson et al. (2017) investigate the stress of species interactions in a pair of competing intertidal zone crabs and review the literature on the consequences of species interactions for cellular stress and the cellular stress response (CSR) in predator/prey and competitor systems. Though interactions between their focal crab species did not lead to an increased CSR in either species, their review found considerable evidence that species interactions induce cellular stress. They found that predator cues often lead to increased cellular stress and induction of CSR genes in prey, even in the absence of direct interactions such as pursuit and physical contact. They also found some evidence that competitive interactions can induce cellular stress, though this has been far less studied. The stress of species interactions is therefore a potentially important but little studied consideration in global change research given that global change is leading to novel communities and interactions between species (Urban et al. 2012).

Concluding remarks

Assessing the joint impact of direct and indirect effects of global change on populations will be necessary to effectively predict and mitigate biodiversity loss. The papers in this symposium highlight mechanisms likely to mediate both direct and indirect effects on populations, and they provide approaches for integrating these mechanisms into predictions of global change consequences and management strategies. Although the complexity of ecological systems make accurate predictions difficult to achieve, an increased mechanistic understanding of ecological processes can hopefully improve our ability to maintain biological diversity in the face of myriad environmental challenges.

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