STUDENT AWARDEE PAPER

An Integrative Perspective On the Mechanistic Basis of Context-Dependent Species Interactions

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Synopsis It has long been known that the outcome of species interactions depends on the environmental context in which they occur. Climate change research has sparked a renewed interest in context-dependent species interactions because rapidly changing abiotic environments will cause species interactions to occur in novel contexts and researchers must incorporate this in their predictions of species' responses to climate change. Here, we argue that predicting how the environment will alter the outcome of species interactions requires an integrative biology approach that focuses on the traits, mechanisms, and processes that bridge disciplines such as physiology, biomechanics, ecology, and evolutionary biology. Specifically, we advocate for quantifying how species differ in their tolerance and performance to both environmental challenges independent of species interactions, and in interactions with other species as a function of the environment. Such an approach increases our understanding of the mechanisms underlying outcomes of species interactions across different environmental contexts. This understanding will help determine how the outcome of species interactions affects the relative abundance and distribution of the interacting species in nature. A general theme that emerges from this perspective is that species are unable to maintain high levels of performance across different environmental contexts because of trade-offs between physiological tolerance to environmental challenges and performance in species interactions. Thus, an integrative biology paradigm that focuses on the trade-offs across environments, the physiological mechanisms involved, and how the ecological context impacts the outcome of species interactions provides a stronger framework to understand *why* species interactions are context dependent.

Introduction

Ecologists have long been interested in the consequences of species interactions like competition, predation, facilitation, and parasitism (e.g., Thompson 1988; Cornell and Lawton 1992; Chamberlain et al. 2014; Thompson et al. 2021). These interactions are central to many ecological and evolutionary processes that regulate populations, structure communities, drive the evolution of niche differentiation, and determine species distributions (; Chase and Leibold 2003; Sexton et al. 2009); Vellend 2010; Alexander et al. 2022). While traditional models of species interactions (e.g., interspecific competition, predator–prey dynamics) often assume static coefficients to describe the impact one species has on another, there is a growing appreciation that the outcome of species interactions can be dynamic, fundamentally changing with the environmental context (e.g., Chamberlain et al. 2014). Recognition that the environmental context plays a role in determining the outcome or importance of species interactions is not new, indeed it was first hinted at by Darwin (1859) and has interested biologists since. Specifically, Darwin argued that species interactions should play a more important role in restricting distributions in more benign environ-

ments compared to climatically more stressful environments. Dobzhansky (1950) and MacArthur (1972) later extended this idea, which in turn has inspired a large body of research, particularly related to elevational and latitudinal gradients (see also Louthan et al. 2015; Lynn et al. 2019; Paquette and Hargreaves 2021). An extensive meta-analysis on the context dependency of species interactions by Chamberlain et al. (2014) revealed that a broad range of environmental conditions (abiotic, spatial, temporal, biotic) and types of species interactions (competition, predation, mutualism) are affected by the environmental context. The increasing number of studies, reviews, perspectives, and meta-analyses (e.g., Morris et al. 2007; Tylianakis et al. 2008; Gilman et al. 2010; Larimer et al. 2010; Chamberlain et al. 2014; Louthan et al. 2015; Lynn et al. 2019; Spence and Tingley 2020; Paquette and Hargreaves 2021; Alexander et al. 2022) reveal that context dependent interactions are widespread across diverse types of interactions, environments, and taxa.

Species interactions can generally be defined as context dependent if a change in the abiotic or biotic environment results in a change in the outcome of the interaction (Chamberlain et al. 2014). However, such a general definition obscures the diverse ways interacting species respond to environmental variation, and how these responses in turn influence and are influenced by the outcome of their interactions. For example, context dependent species interactions can be viewed as a strictly environmentally driven process, independent of any functional differences among the interacting species. Such a perspective is commonly invoked in the *stress-gradient hypothesis* which predicts that a shift from benign to stressful environmental conditions (e.g., high vs low elevation/latitude, or high vs low water availability) will induce a shift from competition (−/−) to facilitation (+/+) among interacting species (Bertness and Callaway 1994; Callaway et al. 2002; Liancourt et al. 2005; Maestre et al. 2009; Chamberlain et al. 2014).

Yet, there is also the recognition that differences among species in environmental tolerance and performance during species interactions lead to interactions whose outcomes depend on the environment in which they occur (Morse 1974; Grime 1977; Connell 1983; Dunson and Travis 1991; Martin 2015). For example, dominant species commonly outcompete and exclude subordinate species from benign regions of environmental gradients, but lack the environmental tolerance to the stressful part of gradients where subordinate species are able to persist (e.g., Connell 1961; Chappell 1978; Bertness 1981; Robertson and Gaines 1986; Martin and Martin 2001; Pasch et al. 2013). An underlying theme to this repeated pattern is that species appear to be unable to maintain high performance during biotic interactions and tolerate a wide range of environmental conditions, such that there is a trade-off between physiological tolerance and some aspect of performance during the biotic interaction (Martin 2015). For many species interactions, this pattern may manifest itself as a "specialist-generalist" trade-off (Huey and Hertz 1984; Futuyma and Moreno 1988; Huey and Kingsolver 1989) in which broad environmental tolerance is thought to compromise performance in specific environments. Overall, such variation between species in the traits that underlie environmental tolerance and performance may explain why conceptual frameworks based strictly on environmentally driven context dependency often fail to predict the outcome of species interactions (e.g., Maestre et al. 2006, 2009).

Here, we advocate for a trait-based framework that focuses on understanding the trait(s) that determine both environmental tolerance and performance during species interactions (e.g., Dunson and Travis 1991), and how they influence each other (e.g., trade-offs). A trait-based framework focuses attention on the set of traits involved in environmental tolerance (e.g., thermal breadth, desiccation tolerance, salinity tolerance) and those involved in performance when interacting with another species (e.g., aggression, prey capture efficiency, escape ability), and how they are related (e.g., connected by the shared influence of growth rates, body size). Perhaps most importantly, a trait-based approach allows for identifying how adaptations for environmental tolerance and performance in species interactions interact along an environmental gradient, including evaluating if and how these responses are functionally connected. Focusing on traits related to environmental tolerance and performance during species interactions thus facilitates an understanding of the physiological mechanisms underlying context dependent interactions. This perspective can more generally be viewed as an integrative biology approach, because it focuses on the mechanisms and processes that bridge disciplines such as physiology, biomechanics, ecology, and evolutionary biology (e.g., Ketterson et al. 2009; Mykles et al. 2010; Cox et al. 2016; Burnett et al. 2020). Thus, an integrative biology paradigm that focuses on the physiological mechanisms underlying environmental tolerance and performance in species interactions can help us better understand *why* the outcome of species interactions are context dependent.

Below, we offer such an integrative perspective on context dependent species interactions as a framework for ecologists interested in physiological mechanisms and physiologists interested in the mechanisms underlying ecological interactions. Within this context, we first discuss a general framework for studying context

dependent interactions by focusing on traits related to environmental tolerance, traits related to performance in interactions, and the potential for trade-offs between them. Next, we discuss some physiological mechanisms that contribute to environmental tolerance and performance during species interactions, and why trade-offs are likely to be common. We then highlight some ecological concepts regarding how a trait's relationship to fitness and biotic interactions can be altered by the environment.

Environmental tolerance and performance during species interactions: an integrative perspective on context-dependency

Understanding the mechanisms limiting an organism's tolerance to the abiotic environment and quantifying how whole-organismal performance changes across different environmental conditions motivates studies at the intersection of physiology, ecology, evolution, and global change biology (Huey and Stevenson 1979; Arnold 1983; Ghalambor et al. 2006; Deutsch et al. 2008; Martin 2015; Riddell et al. 2021). Yet, despite the long-held recognition that variation in physiological tolerance and performance can impact biotic interactions between species (see Dunson and Travis 1991), physiological studies of tolerance and performance tend to be done outside the context of ecological studies examining species interactions. Granted, there is a simple explanation for why this is often the case: it is challenging. This is both because the breadth of knowledge and skill required to bridge physiology and community ecology is immense and because physiological experiments in non-model organisms can be limited in scope due to logistical reasons. Here we attempt to alleviate some of these challenges by discussing integrative biology concepts that will help researchers studying how physiological tolerance and performance shape biotic interactions across environmental gradients (Figure 1). While our perspective is biased towards competition and predatory-prey interactions between animal species because of our own research interests, we consider the framework general enough that it can be applied to context dependent species interactions in many different taxa.

Tolerance, performance, and context-dependent species interactions

Why species interactions change across different environmental contexts is rooted in several implicit assumptions. First, interacting species must have some degree of overlap in their physiological tolerances, otherwise they would never have an opportunity to interact with each other. However, rarely is the breadth of physiological tolerance across interacting species quantified. A second related and also often untested assumption, is that interacting species do not differ in their tolerance to environmental variation (Maestre et al. 2009; He et al. 2013). Yet, there are good reasons to question these assumptions, as species often exhibit significant variation in the physiological breadth of their environmental tolerance (Spicer and Gaston 2009). Thus, quantifying the limits of environmental tolerance and performance for interacting species is essential when making predictions about how they will respond to different environmental contexts. For example, coexisting aquatic insect species can exhibit significant differences in their upper thermal tolerance and performance can vary between predators and prey, despite experiencing the same thermal regimes (Shah et al. 2017, 2020). Such variation among interacting species can be quantified by measuring the breadth of environmental tolerance (i.e., difference between minimum and maximum limits) and some related measure of performance in the *absence* of the species interaction (Fig. 1A). The most familiar example of such an approach would be a thermal performance curve for locomotion or another ecologically important function, where the lower and upper critical limits characterize the breadth of thermal tolerance (e.g., Huey and Stevenson 1979; Sinclair et al. 2016; Tüzün and Stoks 2018). A similar approach could be used test how other potential environmental factors (e.g., pH, salinity, water availability, oxygen availability) impact some measure of performance (e.g., growth rate, aerobic scope). In practice, the measurements in these approaches are obtained by conducting controlled lab experiments, field transplant experiments, or removal experiments (Leimu and Fischer 2008; Kellermann et al. 2019; Martin and Ghalambor in review). Overall, measuring tolerance and performance in the absence of the interacting species is a critical step in isolating and partitioning responses due to the environment versus those due to species interactions (Fig. 1A), and assessing how these responses interact.

Another often untested assumption is that interacting species have symmetric impacts on each other, despite evidence that the outcome of context-dependent interactions will change if interactions are asymmetric (Lin et al. 2012; Cameron et al. 2019). Across a wide range of taxa and types of interactions (competition, mutualism, predator-prey), differences in traits like body size can result in consistently asymmetric impacts of one species on another (Grime 1977; Connell 1983; Denno et al. 1995; Martin et al. 2017; Cameron et al. 2019; Miller-ter Kuile *et al.* 2022). Indeed, situations where one species is consistently dominant over a sub-
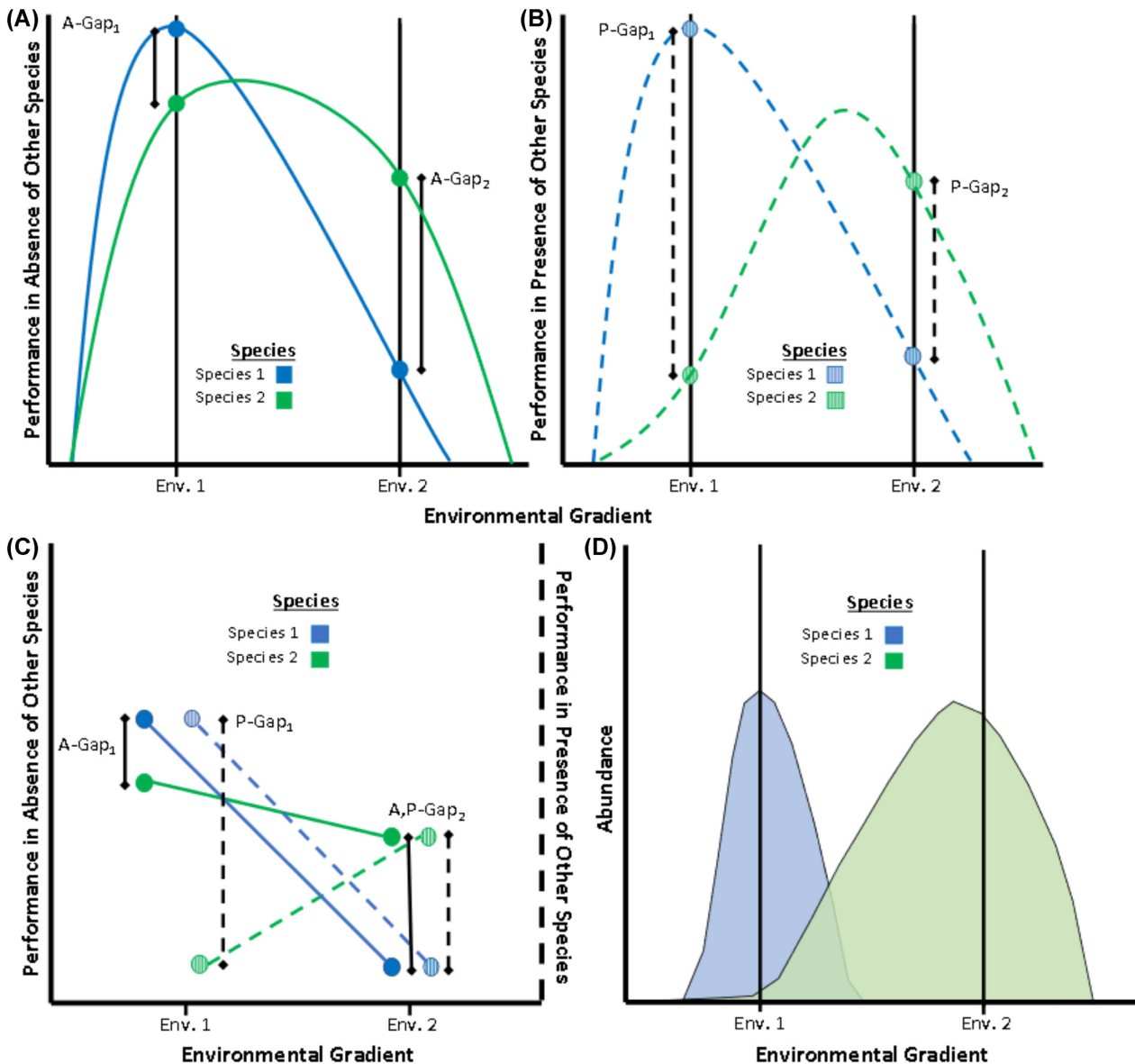
Fig. 1 Here we systematically breakdown a hypothetical context dependent species interaction that illustrates what can occur when two species dramatically differ in how they respond to the environment and how they respond to the interaction with the other species. **(A)** The performance curves of two species across an environmental gradient (temperature, salinity, pH, etc.) in the *absence* of the other species. Hence, performance is purely a function of how the species respond to environmental factors along a gradient. At two specific environments along the gradient (Env. 1, Env. 2) the performance values of the two species are compared. Differences between those values are depicted as "performance gaps in the *absence* of the other species" gaps (A-$Gap_{1,2}$). In this scenario, species 1 performs slightly better than species 2 in environment 1 but performs much worse than species 2 in environment 2. This is indicative of species 1 having a narrower environmental tolerance and species 2 having a broader environmental tolerance. **(B)** The performance curves of the two species across the same environmental gradient as in panel A, but performance is measured in the *presence* of the other species, capturing the interaction between the species. Differences between performance in the same two environments are depicted as "performance gaps in the *presence* of the other species" gaps (P-$Gap_{1,2}$). In environment 1 where species 1 has higher environmental tolerance, it significantly outperforms species 2. In environment 2 where species 1 has lower environmental tolerance, species 2 outperforms species 1. **(C)** The combined results from panel A (solid lines/circle) and panel B (dashed lines/circles), shows how performance in the presence and absence of the interacting species potentially shapes species distributions along an environmental gradient. Species 1 performance is purely a function of the environment (dashed and solid lines are parallel) whereas species 2 performance is most significantly affected by the presence or absence of species 1 (the solid line has a shallow slope whereas the dashed line has a steep slope). This pattern is consistent with species 1 being a "specialist" and species 2 being a "generalist" in terms of environmental tolerance, and species 1 being dominant in the interaction and species 2 being subordinate in the interaction. **(D)** The ecological impact of the performance of these two species can be seen in their abundance across the environmental gradient. Species 1 is only found near environment 1 because of its narrow environmental tolerance. Species 2 is not found in environment 1 where species 1 is highly abundant and it is subordinate to species 1. Species 2 abundance gradually increases along the gradient toward environment 2 as the abundance/density of species 1 decreases.

ordinate species and wins the majority of contests (i.e., asymmetric interaction) tend to be the norm rather than the exception (see Connell 1983; Denno et al. 1995; Kaplan and Denno 2007; Aschehoug et al. 2016; Martin et al. 2017). Thus, testing and predicting how the environmental context impacts the outcomes of species interactions requires measuring performance of interacting species across environments (Fig. 1B). Quantifying performance during interactions can take many forms such as: direct measures of behavioral aggression during competition like biting (e.g., Vanhooydonck et al. 2005; Husak et al. 2006) or chasing and displacement (e.g., Seghers and Magurran 1991; Martin and Ghalambor 2014), measures of locomotor performance such as escape ability during predator-prey encounters (e.g., Walker et al. 2005), tracking the outcome of the interaction (e.g., winners vs losers, escape vs capture), or longer term consequences of the interaction (e.g., gain or loss of body mass, changes in survival or fecundity). Measuring performance across environments in nature must also consider the indirect influences of the environment, because the distributions of age, size, condition, density, or sex of individuals within species can vary with subsequent consequences for species interactions (e.g., Stiles 1973). In these cases, variation in performance in species interactions across environments (Fig. 1B) can be caused by among-individual variation in performance coupled with non-random distributions of individuals across environments, rather than within-individual changes in performance in interactions as a function of the environment. Overall, combining measures of environmental tolerance and performance in the absence (Fig. 1A) and presence (Fig. 1B) of interactions provides a simple, yet powerful way of visualizing and partitioning how the environmental context impacts species' responses to environmental challenges versus interactions with another species (Fig. 1C and D).

Given that a change in the environmental context can impact interacting species through their physiological sensitivity (Fig. 1A) or performance during the interaction (Fig. 1B), predicting how a given amount of environmental change is likely to impact the outcome of the interaction will depend on the "gap" or difference in performance exhibited by each species in a particular environmental context. In the hypothetical performance curves depicted in Figure 1, Species 1 is a habitat specialist (i.e., has a narrower tolerance breadth), exhibiting higher performance in Environment 1 compared to Species 2, and lower performance in Environment 2 compared to Species 2 (Fig. 1A). Thus, differences in tolerance and performance to the environment result in measurable gaps between the two species, which in this case reverse between Environments 1 and 2 (Fig. 1A). A similar pattern is depicted in the performance during the biotic interactions (Fig. 1B), where Species 1 has an advantage in Environment 1 (e.g., increased competitive or escape ability) and Species 2 has an advantage in Environment 2. When these two sets of responses are combined, the gaps between the species in their performance to environmental challenge and during interactions can be directly compared (Fig. 1C). In this specific case, the interpretation would be that Species 1 is unlikely to persist or perform well in Environment 2 (Fig. 1D), primarily because it lacks the environmental tolerance which also impacts its performance in interactions with Species 2 (Fig. 1C). In other words, the context dependent nature of the species interaction is a function of reduced environmental tolerance (Fig. 1A) that also reduces performance during the interaction (Fig. 1B). The exact shape of these performance curves will vary between species and even between traits within a species (Kellermann et al. 2019; Iverson et al. 2020), but by separating the responses to the environmental challenge from the interaction, the independent and joint responses to different environmental contexts can be assessed. Furthermore, by assessing the contributions of different traits to variation in performance in different environments, we can generate hypotheses about the physiological mechanisms underlying how and why species interactions are context dependent.

Physiological mechanisms underlying context-dependent species interactions

By taking a trait-based approach to studying context-dependent interactions, the mechanisms underlying organismal responses to environmental variation can be more clearly identified. Numerous patterns and trends regarding the interaction between the environment and species interactions have been documented (see above paragraphs), but a general understanding of the mechanisms generating variation in the outcomes of species interactions remains elusive. This is in part because the mechanism per se has not been the focus of many species interaction studies. Indeed, Chamberlain et al (2014) concluded their meta-analysis by urging future researchers to study context dependency itself rather than just the mean outcomes of species interactions. The mechanistic basis of context dependent species interactions will become easier to identify by focusing on the set of traits involved in environmental tolerance, those involved in species interaction, and the connections and potential trade-offs involving these traits. Below, we briefly discuss some of these mechanisms and how they can contribute to establishing more causal relationships between environmental context,

organismal responses, and changes to the outcome of species interactions.

Thermal sensitivity and energetics

The impact of body temperature is pervasive across biochemical reactions, cellular processes, tissue function, and whole organism performance (Angilletta 2009). The influence of temperature is particularly important in ectotherms (although endotherm performance is also influenced by temperature (Levesque and Marshall 2021)), where minimum energy demands increase with temperature and constrain allocation to the competing demands of growth, activity, and other components of fitness (e.g., Dillon et al. 2010; Huey and Kingsolver 2019; Jutfelt et al. 2021). The relationship between temperature, thermal breadth, and measures of performance are often conceptualized in the thermal performance curve (Huey and Stevenson 1979), providing a framework for exploring the mechanisms underlying context-dependent species interactions (Fig. 1; see also Tüzün and Stoks 2018). If interacting species differ in their thermal performance as a function of their body temperature, a priori predictions can be made about how the outcome of interactions will change as a function of time of day (e.g Thomas and Holway 2005), along thermal gradients (e.g., Taniguchi and Nakano 2000), or across larger geographic areas (Tüzün and Stoks 2018). For example, the degree to which predators and their prey have performance gaps (Fig. 1B and C) can predict how predation risk changes as a function of temperature (Grigaltchik et al. 2012; Öhlund et al. 2014; Pintanel et al. 2021) or how predation pressure on prey with different levels of performance across temperatures can result in "enemy release" for the more successful prey species (e.g., Fey and Herren 2014). Similarly, differences in the thermal sensitivity of performance between competing species can either lead to the loss or gain of competitive dominance depending on the environmental temperature (e.g., Taniguchi and Nakano 2000; Thomas and Holway 2005). Why species differ in their thermal sensitivity reflects a diversity of mechanisms ranging from enzyme and membrane structure (e.g., Hochachka and Somero 2002; Bowler 2018) to the capacity for mitochondrial, circulatory, and respiratory systems to meet oxygen demand (Pörtner et al. 2006). Yet, thermal performance can also be plastic within an organism's lifetime (Sinclair et al. 2016) and can evolve (Tüzün and Stoks 2018). Thus, understanding variation in the ability to exhibit plasticity and evolvability of thermal performance should play a role in mediating species interactions over shorter time scales through acclimation, or longer time scales through adaptation.

While changes in environmental temperature allow for predicting some aspects of organismal responses (e.g., minimum energy demands, performance), there are other complicating factors which can impact the mechanisms by which temperature alters the outcome of species interactions. These complicating factors, not easily captured in thermal performance curves of interacting ectothermic species, include how temperature directly or indirectly impacts resource availability, access to food resources, the efficiency of digestion and assimilation, patterns of energy allocation, and thermosensory behavioral adjustments (e.g., O'Connor et al. 2009; Dillon et al. 2010; Abram et al. 2017; Bernhardt et al. 2018; Huey and Kingsolver 2019; Jutfelt et al. 2021). For example, Huey and Kingsolver (2019) describe a biophysical model where warmer temperatures result in accelerating metabolic costs, reduced growth rates, temperature-induced restrictions on activity, and reduced food intake. They refer to the combined energetic costs of warming and reduced access to food as a "metabolic meltdown" (Huey and Kingsolver 2019). It is not difficult to imagine how such costs are further augmented by interactions with competitors or predators (Huey and Kingsolver 2019) and why understanding how temperature impacts the food supply, the ability to assimilate food resources, and meet energy demands is crucial to a mechanistic understanding of context-dependent species interactions. Jutfelt et al. (2021) provide another mechanistic hypothesis based on the specific dynamic action associated with digestion and assimilation, arguing that with increasing temperatures, the aerobic costs of feeding can take up much of an ectotherm's aerobic scope. Thus, ectotherms may reduce food intake and suffer from reduced growth rates to protect their aerobic scope (Jutfelt et al. 2021). Yet, the degree to which ectotherms should protect aerobic scope for energy demanding activities like locomotion or growth is likely to be impacted and shaped not only by temperature but also by their interactions with predators (i.e., the need to maintain escape ability or pursue prey) and competitors (i.e., the ability to access food).

The importance of thermal challenge and energetics extends to endotherms as well. Temperature extremes require added energetic expenditures or adaptations to maintain thermal homeostasis, and these added costs or costly adaptations can compromise the abilities of species in interactions. For example, cold environments favor increased investment in insulation (e.g., fur, feathers) at the expense of growth and muscle (Scholander 1955) and shorter appendages to reduce heat loss (e.g., snout, ears, legs; Allen's Rule) (Allen 1877; Nudds and Oswald 2007), both of which could compromise performance in species interactions involving competitors

or predators. Cold environments like the arctic are also characterized by periods of low resource availability that can favor smaller-sized organisms that require less energy for growth, survival, and reproduction (Peters 1986; Blanckenhorn 2000). Thus, small species, like the arctic fox (*Vulpes lagop*us), can persist in cold arctic environments while the larger red fox (*V. vulpes*) cannot (Pål 1991; Bartoń and Zalewski 2007); even as the larger and more powerful red foxes readily displace and kill arctic foxes where they meet (Hersteinsson and Macdonald 1992; Elmhagen et al. 2017). Climate warming has enabled a northward range expansion of red fox at the expense of arctic fox (Elmhagen et al. 2017) but predicting the extent of this displacement will require an understanding of how interactions between the species vary as a function of temperature and temperature-related challenges (e.g., limited food; snow cover), and other environmental contexts (e.g., human food subsidies; Elmhagen et al. 2017). In short, the mechanisms by which temperature, energy demands, and performance underlie context-dependent species interactions remains a largely unexplored field at the interface of physiology and ecology, and yet understanding these mechanisms is important for our understanding of species distributions and for predicting human impacts on them.

Homeostatic challenges

High levels of organismal performance typically occur within a particular range of internal conditions that are maintained by homeostatic regulation. For example, basic physiological functions such as gas exchange and water balance require acid-base and ion homeostasis. Thus, any environmental condition which differentially impacts an organism's ability to maintain homeostasis (e.g., a change in environmental pH, O_2 availability, water availability, salinity, temperature, etc.) has the potential to impact performance to both environmental challenge (Fig. 1A) and species interactions (Fig. 1B). In these cases, the physiological response to an environmental challenge involves deploying molecular, cellular, and physiological mechanisms to reestablish homeostasis under the new environmental conditions (Hochachka and Somero 2002). For example, one of the biochemical responses to hyperoxia in fish is to alter ion fluxes across the gills in order to maintain ion homeostasis (Goss and Wood 1990; Evans et al. 2005). Hence, differences between species in their ability to maintain physiological homeostasis can alter performance and the outcomes of species interactions. For example, Warner et al (1993) conducted a mesocosm experiment and found that by changing the pH of the water they could alter the outcome of competitive interactions be-

tween tadpoles of *Hyla femoralis* and *Hyla gratiosa*. Similarly, the invasive mosquitofish (*Gambusia holbrooki*) is able to outcompete a native cyprinodont fish (*Aphanius fasciatus*) at low salinities, but loses this advantage with increasing salinity (Alcaraz et al. 2008). Differences in salinity tolerance also can alter the competitive abilities of plant species and shape distributions along salinity gradients (Kenkel et al. 1991). While temperature has received considerable attention, the ecological consequences of homeostatic regulation in response to other abiotic factors remains understudied.

Many homeostatic mechanisms and measures of performance are under endocrine control (e.g., Husak et al. 2009; Lorenz and Gäde 2009; McCormick 2009; Hau et al. 2016). Because hormones are known to have pleiotropic effects and generate trait correlations (Ducrest et al. 2008; Dantzer and Swanson 2017), there are strong reasons to expect traits associated with adaptation to environmental challenge (Fig. 1A) could be correlated with traits associated with performance during species interactions (Fig. 1B). For example, Lorenz and Gäde (2009) provide a compelling argument for the role of adipokinetic hormones as a general regulator of homeostasis and as part of the mechanism underlying energy metabolism during locomotor performance. Similarly, hormones like testosterone, cortisol/corticosterone, and arginine vasopressin/vasotocin play important roles in various homeostatic functions regarding energy metabolism, ion homeostasis and water balance, but also impact a suite of performance traits involved in common species interactions, such as aggression, territorial defense, escape performance, and immune function (Husak et al. 2009; John-Alder et al. 2009; Ketterson et al. 2009; McCormick 2009). The hormonal integration of traits associated with the maintenance of homeostasis and those associated with performance during species interactions should be considered as a potential mechanism underlying context dependent species interactions.

Functional morphology and body size

Organismal structure is closely associated with function and performance (e.g., Wainwright and Reilly 1994; Irschick et al. 2008; Lailvaux 2018). However, all organisms are bound by physical laws which constrain the limits of form and function and dictate the range of possible solutions organisms use to achieve certain levels of performance (Vogel 1988). The fields of biomechanics, functional morphology, and ecomorphology seek to understand how organisms achieve different solutions to different environmental challenges by viewing form and function through the lens of these physical laws. For example, by describing how a given bird

generates the aerodynamic forces of thrust and lift to overcome drag and gravity through muscle contractions and the kinematics of wingbeats, reasonable predictions can be made regarding the limits to its flight performance (Tobalske 2007; Altshuler et al. 2014). In the context of species interactions, such a perspective can provide explanatory power for why larger species are dominant to smaller species, owing to their ability generate greater force for a given acceleration (Martin and Ghalambor 2014). Similarly, larger lizards typically can generate greater bite force when fighting other males for dominance (Verwaijen et al. 2002; Husak et al. 2006). However, the relationship between organismal design and performance can also be context dependent, which in turn can have implications for species interactions. Altshuler (2006) provides an example of a reversal in competitive ability and dominance, where the short-winged hummingbird *Selasphorous rufus* is dominant at low elevations over the long-winged hummingbird *Selasphorus playcercus*, but the pattern reverses at high elevations. In this case, differences in wing length alter the burst ability for vertical flight performance at high elevation where the density of air is lower, shifting the competitive advantage away from shorter wings to longer wings (Altshuler 2006). Evidence to date suggests that such dominance reversals along environmental gradients are rare (Martin et al. 2017; Martin and Ghalambor, in review); however, few studies have identified the links between the environment, form, and performance during a species interaction.

Trade-offs as a general framework for studying context-dependent species interactions

Why can't a species tolerate a wide range of environmental factors (temperatures, pH, air density, etc.) and simultaneously maintain high performance in biotic interactions? The answer to this question falls under the broader goal in ecology, evolution, and physiology to understand the mechanism(s) underlying trade-offs (Dunson and Travis 1991; Angert et al. 2009; Mauro and Ghalambor 2020). Below, we provide an overview of conceptual models used to study trade-offs and how they can inform species interactions.

One of the most commonly invoked mechanisms for trade-offs is that they arise when different traits or functions compete for the same pool of finite resources such energy, time, or space (Zera and Harshman 2001; Garland et al. 2022). Such allocation trade-offs play a central role in explaining diverse aspects of organismal biology, ranging from the evolution of different life history strategies (Van Noordwijk and de Jong 1986; Roff 1992) to developmental constraints on the size of differ-

ent morphological structures (Nijhout and Emlen 1998; Moczek and Nijhout 2004). Similar allocation trade-offs have also been proposed to mediate biotic interactions with predators and herbivores (e.g., Coley et al. 1985), competitors (Grime 1977), and context dependent changes along elevational and latitudinal gradients (Hargreaves et al. 2014; Louthan et al. 2015; Paquette and Hargreaves 2021).

Mechanistically, allocation trade-offs should impact performance during biotic interactions when an organism can no longer support its minimum energy and/or repair demands caused by exposure to a given environment (Sokolova 2013). Hence, if interacting species have evolved divergent tolerances to an abiotic factor (like in the above temperature examples), they will allocate different amounts of energy to cope with it. For example, a species that has evolved a narrow thermal tolerance may spend more energy coping with suboptimal temperatures over a range of environmental temperatures than a species that has evolved a broad thermal tolerance. If these species interact in a novel thermal environment, each will be left with different amounts of remaining energy to power their interaction, leading to one species dominating the other during the interaction (e.g., Liancourt et al. 2005; Kroeker et al. 2014). How often energy allocation trade-offs drive the outcome of species interactions along environmental gradients in nature is not known because such trade-offs are rarely addressed in research and constitute a sizeable gap in our knowledge of species interactions.

Another way that abiotic tolerance and performance during an biotic interaction can trade-off is when both traits are controlled by the same biological network in such a way that a change in one trait that increases fitness necessitates a change in the other trait that decreases fitness (Mauro and Ghalambor 2020). Biological networks or physiological response networks (Cohen et al. 2012) broadly refer to all the components of an organism that connect its genome to its phenome (Martin et al. 2011) (i.e., genes, RNA, proteins, hormones). Hence, pleiotropic genes or hormones that affect abiotic tolerance and performance during a biotic interaction can lead to trade-offs that mediate species interactions (Roff and Fairbairn 2007; Dantzer and Swanson 2017; Mauro and Ghalambor 2020). For example, hormones like AVT and cortisol can affect both aggression and salinity tolerance in euryhaline fish, and we hypothesized that this is the mechanism that underlies the inability of the euryhaline fish *Poecilia reticulata* to be a good competitor in brackish water and expand it range into brackish water (Mauro and Ghalambor 2020; Mauro et al. 2021). Similarly, genetic pleiotropy underlies a range restricting trade-off between abiotic-stress

tolerance and herbivory defense in the plant *Boechera stricta* (Olsen et al. 2019).

Energy allocation and overlapping biological networks are not mutually exclusive mechanisms that can underlie trade-offs (Bourg et al. 2019; Mauro and Ghalambor 2020). For instance, certain signaling hormones (i.e., JH, insulin signaling, testosterone) that regulate energy expenditure can also effect behavior and stress tolerance (Flatt and Kawecki 2007; Harshman and Zera 2007; Hau and Wingfield 2011). Hence, investigating both mechanisms when possible is ideal. For example, Kelly et al. (2016)used transcriptomics to investigate the mechanism underlying a trade-off between heat tolerance and salinity tolerance in the copepod *Tigriopus californicus*. They found that the negative impact of combined heat and salinity stress on *T. californicus* was due to the increased energetic demand needed to increase heat and salinity tolerances simultaneously and not because heat and salinity tolerance share stress response pathways (Kelly et al. 2016). Ultimately, understanding the contribution of energy allocation and pleiotropic mechanisms to trade-offs is important because it influences how those trade-offs will plastically respond to environmental change and potentially evolve in response to environmental change (Mauro and Ghalambor 2020), which can affect species interactions in the short and long term respectively.

Trade-offs can also occur when the traits involved in adaptation to environmental challenge are the same as those involved in species interactions, but the optimal trait values for each function differ. A classic example involves distinct interacting strains of *Escherichia coli* that are differentially adapted to bacteriaphage viral infection (Lenski 1988; Bohannan et al. 2002). Membrane receptors in *E. coli* that facilitate the uptake of nutrients are simultaneously used by viruses to infect the bacteria. Mutations that modify these receptors to reduce viral infection come at a cost of reduced nutrient uptake and metabolism, such that virus-resistant *E. coli* have slower growth and are poor competitors against virus-susceptible *E. coli*. This example illustrates how traits involved in adaptation to challenge (in this case, to viral infection) can also impact interactions with other species (competition with another strain of *E. coli*), and where the competitive costs of viral resistance also depend on environmental context (resource availability, temperature; Lenski 1988; Bohannan and Lenski 2000; Bohannan et al. 2002). Similar examples are likely widespread, particularly in the case of influential traits like body size that affect physiology (e.g., energetics, water loss), biomechanics (e.g., costs of locomotion), life history (e.g., survival, annual reproductive effort), and ecology (e.g., resource use) (Peters 1986;

Bonner 2006) and simultaneously can determine the outcomes of species interactions (e.g., outcomes of aggressive contests, risk of predation) (Morse 1974; Peters 1986; Martin and Ghalambor 2014).

Ecological considerations for understanding context-dependent species interactions

The dynamic nature of environmental gradients

Environmental gradients are often viewed as static, yet many environmental factors fluctuate in both space and time (e.g., shifts along the x-axis Fig. 1). For instance, the magnitude of temperature variation differs seasonally and daily as a function of elevation and latitude (Ghalambor et al. 2006) while salinity gradients fluctuate seasonally and daily with the tides (Rice et al. 2012; Ghalambor et al. 2021). This means organisms must either track shifting environmental gradients through dispersal, plastically adjust their environmental tolerance/performance, or potentially suffer a decline in performance (Bozinovic et al. 2011). As species can differ in their capacity to avoid this decline in performance, temporal fluctuations in the environment can lead to shifting (context dependent) species interactions at a single point in space (e.g., Kordas and Dudgeon 2011). This can allow for species coexistence as no one species has a stable advantage (Price and Kirkpatrick 2009). For example, researchers found that the intensity of competition between sympatric species of marsh grasses varied latitudinally, but also temporally with the seasons and wet/dry years (Bertness and Ewanchuk 2002). Thus, considering the temporal nature of gradients when studying species interactions can explain discrepancies between observations in nature and experiments that are restricted to environmental conditions at a single point in time.

Even when environmental gradients vary continuously or linearly, the environment's effect on organismal performance may not be linear or continuous in nature (Shah et al. 2020). For instance, even though salinity gradients typically vary continuously along estuarine rivers (Rice et al. 2012; Ghalambor et al. 2021), euryhaline fishes' physiological responses to salinity challenges may not vary continuously and may instead be described as a threshold response. Most euryhaline fish maintain a homeostatic internal osmolality (an iso-osmotic threshold) of around 12psu (Evans et al. 2013) and have mechanisms that allow them to osmoregulate by expelling salt ions and increasing water retention in hyperosmotic (above threshold) conditions and do the reverse in hypoosmotic (below threshold) conditions

(Evans et al. 2013; Kultz 2015). Thus, physiological responses to salinity may not be linear, but rather change abruptly at different levels of salinity (e.g., Whitehead et al. 2011). Under this "threshold" model, we would not expect a trade-off between salinity tolerance and a fish's ability to perform during a biotic interaction until this threshold is crossed. Thus, when experimental designs are restricted to a few test conditions, consideration should be given to the physiological tolerance of the organism (linear vs. threshold response) when choosing the test conditions expected to impact species interactions.

Lastly, multiple environmental factors covary along environmental gradients (e.g., temperature and the partial pressure of oxygen along elevation (Birrell et al. 2020)) which can each impact an organism's performance during biotic interactions. This makes it challenging to know which aspect of the environment to use when examining tolerance/performance curves (like those in Fig. 1). For example, at southern sites within the Cape Cod region, canopy forming algae have a positive impact on underlying intertidal barnacles through shading and a reduction in thermal stress, whereas in northern sites the algal canopy has a negative impact on barnacles because it attracts gastropod predators (Leonard 2000). Hence, to fully understand why a biotic interaction is context dependent, researchers may have to investigate multiple aspects of the environment and consider how multiple stressors or different aspects of the environment jointly shape organismal tolerance and performance.

Behavior and Natural History

The natural histories and behaviors of interacting organisms can influence the links between the biotic interaction, the environment, and fitness. This is readily evident in plant-pollination mutualisms in which the phenology of the interacting species must be in sync for the interaction to occur (Rafferty et al. 2015) and the phenology of the species can be greatly affected by the environment (Forrest 2016; Piao et al. 2019; Stewart et al. 2021). However, this can occur in less obvious, indirect interactions as well. For instance, predator foraging strategy can interact with temperature to influence the relative prey capture success of competing predators (Twardochleb et al. 2020). As an example, *Enallagma annexum*, a sit-and-wait aquatic invertebrate predator, increased capture success relative to an active predator, *Notonecta undulata*, as temperature increased (Twardochleb et al. 2020) because its predation strategy allowed it to hunt more efficiently at warmer temperatures. By incorporating the natural history of the predators as a factor, researchers were able to in-

vestigate how different functional groups (sit-and-wait vs active predators) and their interactions might change under environmental change scenarios (Twardochleb et al. 2020).

The behavioral mechanism determining the outcome of an interaction can also vary with the environment adding another challenge when attempting to uncover the mechanism underlying context dependent species interactions. For example, in a study on two competing species of salmonoids, the mode of competition appeared to change along a lab-simulated environmental gradient. At high temperatures, interference competition between Whitespotted char (*Salvelinus leucomaenis*) and Dolly Varden trout (*S. malma*) could explain why *S. malma* did not expand further downstream into warmer waters as *S. leucomaenis* was dominant over *S. malma* at high temperatures. However, their dominance relationship could not explain why *S. leucomaenis* was not found further upstream in cold waters as *S. leucomaenis* never became subordinate to *S. malma*. One potential explanation is that poorer starvation resistance in *S. leucomaenis* could be restricting its ability to expand into colder waters because those waters tend to be less productive which means it may not be able to acquire enough energy to compete with *S. malma* (Taniguchi and Nakano 2000). This implies that over a temperature/food gradient, the mode of competition switches from interference competition, in which the dominant species is able to actively exclude the subordinate species from a resource, to exploitative competition, in which the dominant species is the one that is more efficient at acquiring a scarce resource (Amarasekare 2002). Hence, in addition to considering multiple factors along environmental gradients, consideration must also be given to how different environmental factors shape the nature and type of interactions among species.

Conclusion

Here, we have advocated for taking an integrative biology perspective to better understand the mechanisms that can explain how and *why* species interactions are context dependent. This approach seeks to connect the physiological mechanisms involved in environmental tolerance and performance with those involved in determining the outcome of ecological species interactions. A critical aspect of this perspective is that the traits involved in environmental tolerance are likely to be intimately linked to traits that determine the outcome of species interactions because they share underlying physiological, biomechanical, or integrating mechanisms. This perspective differs from a strictly environmentally driven perspective (e.g., by classifying

environments as stressful or not), and instead focuses on how organismal performance changes across environments in the presence and absence of interacting species (Fig. 1). In practice, we envision researchers adopting this approach will begin by observing a pattern in nature that could be caused by a species interaction (e.g., the replacement of one by another along an environmental gradient) and investigate the traits and mechanisms underlying environmental tolerance in the presence and absence of the species interaction. The details of this work will vary depending on the taxa involved, but ideally requires an experimental approach in the lab or other controlled environment, in combination with transplant or removal experiments in nature to test for a causal links between performance, the outcome of the species interactions, and the ecological pattern. Indeed, the ability to conduct field experiments and "return to nature" is the gold standard when testing for the causal links between species interactions and ecological patterns because they retain the ecological complexity that laboratory and mesocosm studies are unable to replicate (Martin et al. 2017; Martin and Ghalambor, in review).

Ultimately, as the mechanisms that generate context dependency are understood, general rules governing species interactions will emerge and help generate better predictions on the outcome of species interactions in a changing world. Indeed, there is strong motivation to understand how rapidly changing climatic conditions will alter environments (e.g., temperature, salinity, pH) and in turn alter species interactions or lead to novel species interactions (Deutsch et al. 2008; Tylianakis et al. 2008; Gilman et al. 2010; Donelson et al. 2019). If the single greatest challenge in predicting the effects of climate change on ecosystem function is determining how biotic interactions will change under climate change (Tylianakis et al. 2008), then it is critical we work towards providing a mechanistic and predictive framework for how environmental change will alter species interactions.

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