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Anthropogenic Change Alters Ecological Relationships via Interactive Changes in Stress Physiology and Behavior within and among Organisms

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Synopsis Anthropogenic change has well-documented impacts on stress physiology and behavior across diverse taxonomic groups. Within individual organisms, physiological and behavioral traits often covary at proximate and ultimate timescales. In the context of global change, this means that impacts on physiology can have downstream impacts on behavior, and vice versa. Because all organisms interact with members of their own species and other species within their communities, the effects of humans on one organism can impose indirect effects on one or more other organisms, resulting in cascading effects across interaction networks. Human-induced changes in the stress physiology of one species and the downstream impacts on behavior can therefore interact with the physiological and behavioral responses of other organisms to alter emergent ecological phenomena. Here, we highlight three scenarios in which the stress physiology and behavior of individuals on different sides of an ecological relationship are interactively impacted by anthropogenic change. We discuss host–parasite/pathogen dynamics, predator–prey relationships, and beneficial partnerships (mutualisms and cooperation) in this framework, considering cases in which the effect of stressors on each type of network may be attenuated or enhanced by interactive changes in behavior and physiology. These examples shed light on the ways that stressors imposed at the level of one individual can impact ecological relationships to trigger downstream consequences for behavioral and ecological dynamics. Ultimately, changes in stress physiology on one or both sides of an ecological interaction can mediate higher-level population and community changes due in part to their cascading impacts on behavior. This framework may prove useful for anticipating and potentially mitigating previously underappreciated ecological responses to anthropogenic perturbations in a rapidly changing world.

Introduction

Because all organisms interact with members of their own species and other species within their communities, the effects of human-related stressors on one organism can impose indirect effects on one or more other organisms, resulting in cascading changes across interaction networks. One mechanism by which individual organisms may respond to environmental change is through physiological responses to stressors. Stress can covary with behavior (Packard et al. 2016), meaning that it can affect how organisms interact with their biotic and abiotic surroundings. While relationships between stress physiology and behavior are inconsistent across species, stress–behavior associations of variable directions and magnitudes are well-documented at short-term (plastic within the lifetime of an individual, e.g., response to chronic and acute stressors; Thaker et al. 2009; Adamo and Baker 2011; Allan et al. 2015) and longer-term timescales (e.g., evolutionarily selected co-variation in suites of stress- and behavior-related traits, Réale et al. 2010; Baugh et al. 2017; but see Royauté et al. 2018). The specific nature of these relationships may be context-dependent and difficult to predict, but within an individual, physiological and behavioral changes induced by anthropogenic change can covary and impact one another.

Interwoven changes in behavior and physiology often take place in parallel among individuals involved in ecological relationships. The consequences

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of global change may differ from what would be expected if these factors are considered independently, with possible amplifying, stabilizing, and non-additive effects (Tylianakis et al. 2008; Ferrari et al. 2017; Gunderson et al. 2017b). Moreover, environmental stressors can alter relationships between physiological and behavioral traits (Killen et al. 2013). An integrative approach must be employed to understand and describe such relationships in the context of modified and altered environments.

Here, we highlight ecological scenarios in which changes in stress physiology and behavior in interacting individuals coping with anthropogenic stressors can trigger changes at higher levels of biological organization. We are not the first to call attention to the role that behavioral and physiological responses to global change may play in mediating community-level dynamics (e.g., Gunderson et al. 2017a; Warne et al. 2019). However, this perspective offers a mechanistic view, examining how changes in the stress physiology of two or more interacting "partner organisms" intermingle to induce vertical changes on higher levels of biological organization, thereby attenuating, amplifying, or otherwise altering the biological interaction. In contrast to previous work, we concentrate on three specific ecological interactions—host–pathogen/parasite dynamics, predator–prey relationships, and beneficial partnerships—to elucidate how responses to anthropogenic stressors may alter these interactions.

Stress is notoriously multifaceted and difficult to define. Here, we define it as a response that occurs when a physiological system is faced with an external or psychological challenge that pushes the system out of the scale of normal daily, circannual, or life-history-transition based variation (Wingfield et al. 1998; Romero et al. 2009). This often involves the sympathetic adrenomedullary system and the hypothalamic pituitary adrenocortical (HPA) axis. While we acknowledge that stress and glucocorticoids (GCs) are not equivalent (MacDougall-Shackleton et al. 2019), our perspective does rely heavily upon the large body of empirical evidence for behavioral responses to stressors via the HPA axis. However, we also point toward other, relevant components of the physiological stress response that may be important, particularly in non-vertebrate systems (e.g., heat shock proteins, oxidative stress; Ottaviani and Franceschi 1996; Gunderson et al. 2017a). We define anthropogenic change inclusively (i.e., climate change, invasive species, overexploitation, and habitat degradation/loss, including pollution and human presence). Each ecological interaction is likely impacted by multiple components of anthropogenic change, but we first review the types most pertinent for each of our three ecological relationship foci (host–pathogen/parasite dynamics, predator–prey relationships, and beneficial partnerships). We then explore how changes in stress physiology and behavior within individuals on different sides of the relationship could impact larger ecological and evolutionary phenomena. These non-exhaustive examples contribute to a simplified framework with the aim of identifying common processes vulnerable to anthropogenic change across seemingly disparate areas of study.

Host–pathogen relationships

While many facets of anthropogenic change impact disease dynamics (Daszak et al. 2001), two particularly relevant drivers in host–pathogen/parasite relationships are habitat alteration (Pongsiri et al. 2009) and introduced/invasive species (Crowl et al. 2008). Habitat modification can impact disease dynamics via changes in resource availability and distribution, which have downstream consequences that alter disease exposure and transmission rates (Becker et al. 2015; Flint et al. 2016; Altizer et al. 2018). For instance, food provisioning has been associated with increased host densities, inter-individual contact rates, and endoparasite infections (Wright and Gompper 2005; Blanco et al. 2017). Humans also introduce pathogens into novel areas, often via domestic animals or commercial trade, thereby exposing organisms to pathogens with which they have no evolutionary history (Epstein et al. 2006; O'Hanlon et al. 2018). These and other human-related activities can impact a host's likelihood of contracting a pathogen and, often less appreciated, a pathogen's ability to infect.

Stress responses of individuals can mediate many of these emergent dynamics (Fig. 1A and Box 1A). For example, the recent onslaught of disease-related wildlife declines (Pongsiri et al. 2009) may be related to chronic stress in individuals exposed to multiple, simultaneous human-related stressors (Hing et al. 2016). Chronic stressors can reduce individual quality and cause immunosuppression, leading to increased disease susceptibility (Dhabhar and McEwen 1997; Apanius 1998; Gervasi et al. 2017). At the same time, individuals experiencing acute or chronic stress varying in stress reactivity (e.g., proactive vs. reactive personalities, Réale et al. 2010) can exhibit different behavioral traits, including altered foraging and risk-taking behaviors (Martins et al. 2007; Baugh et al. 2017; Vindas et al. 2017; Moyers et al. 2018a; but see Royauté et al. 2018; Westrick et al. 2019). In turn, certain behaviors

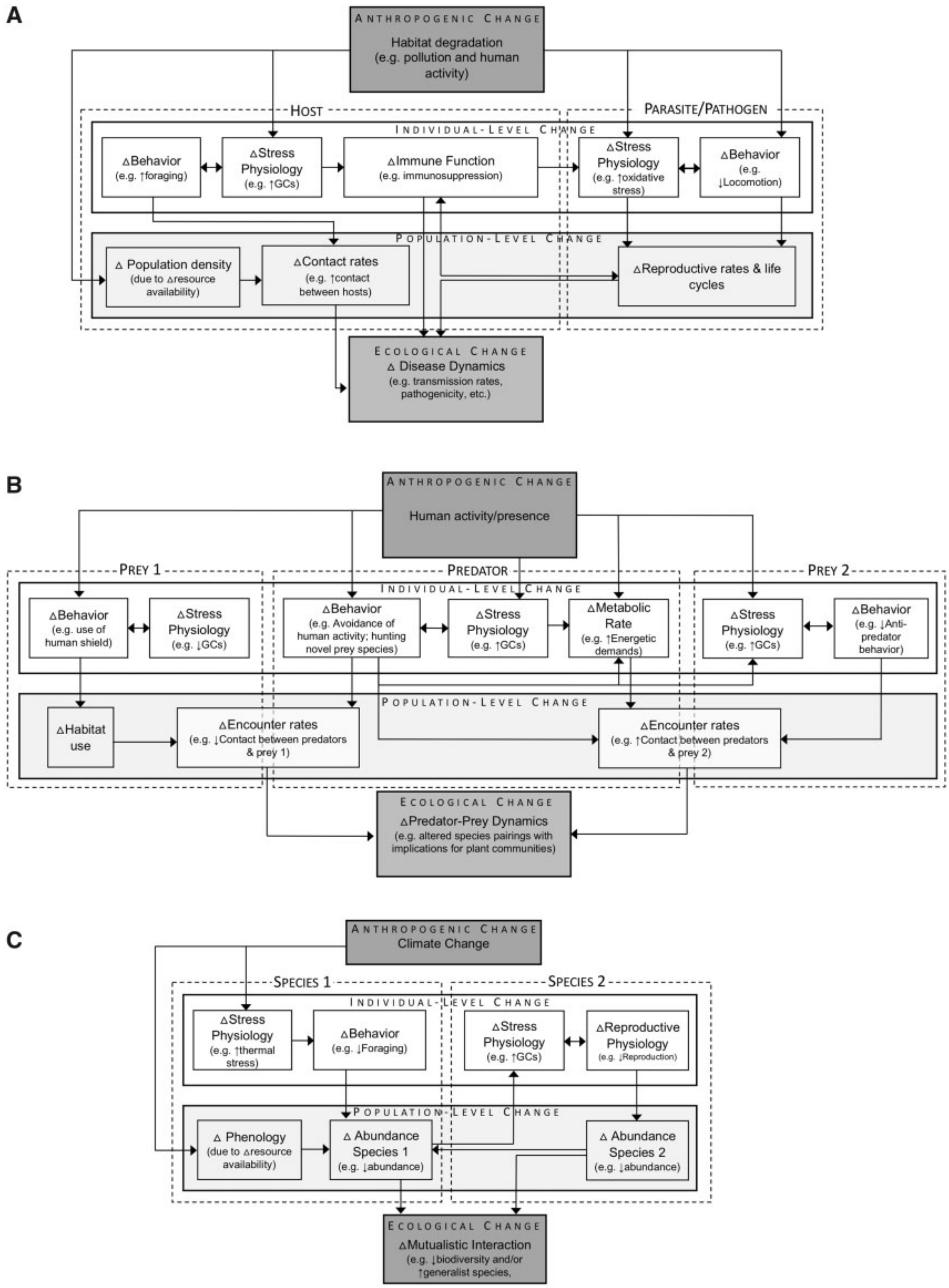


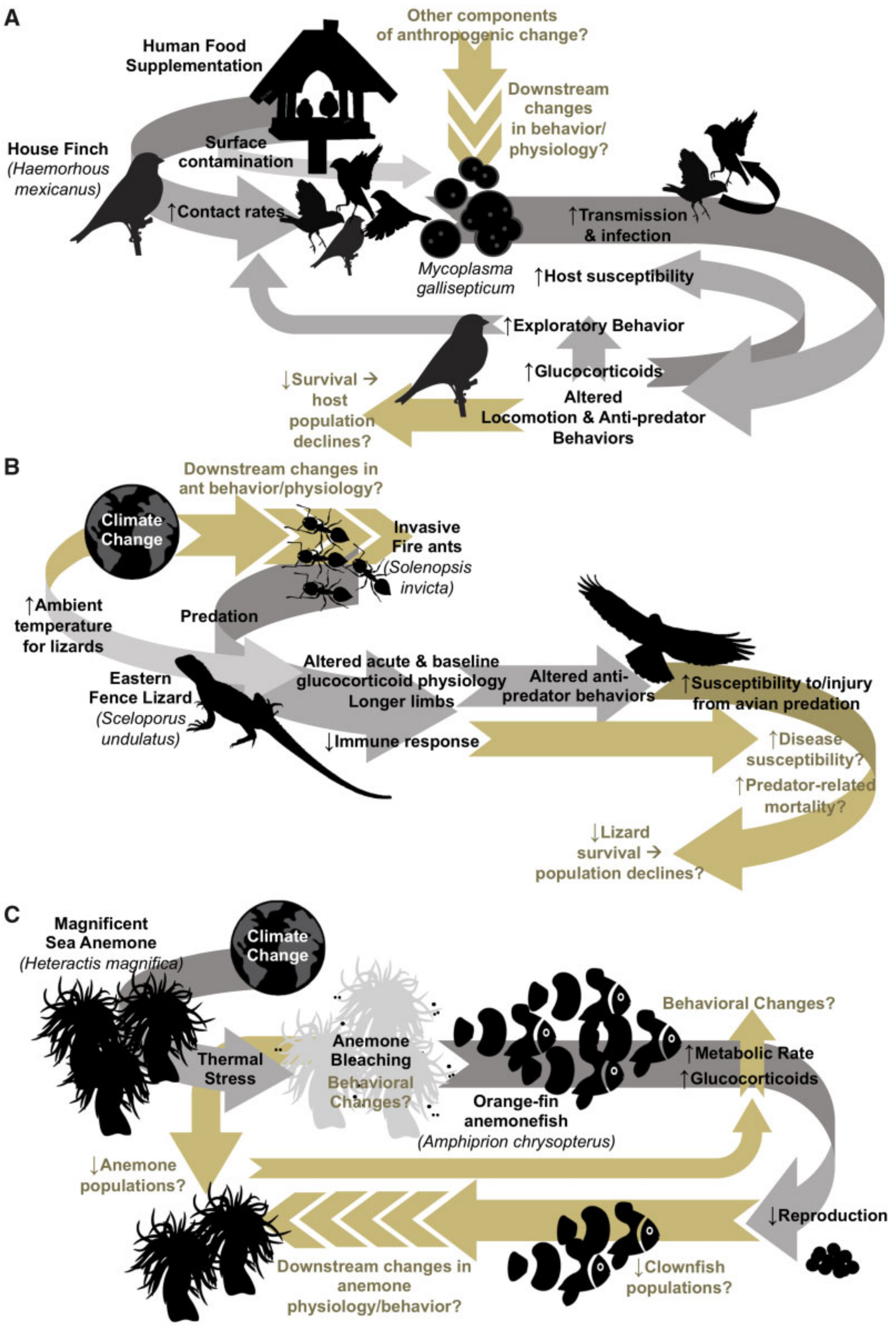
Fig. 1 Flowcharts exhibiting a set of possible relationships between anthropogenic change and interrelated changes in stress physiology and behavior in the context of three ecological interactions: (**A**) host–pathogen dynamics, (**B**) disease dynamics, and (**C**) beneficial relationships. Individual-level changes in physiology and behavior can have bidirectional, horizontal impacts and can contribute to higher, system-level changes, with potential consequences for populations, species interactions, and biodiversity.

are linked to population-level contact and disease transmission rates (Adelman et al. 2015; Adelman and Hawley 2017; Sih et al. 2018). Altogether, co-varying behavioral and physiological traits may alter disease transmission via two linked mechanisms: altered susceptibility (often via physiological changes) and exposure (often via behavioral changes; Hawley et al. 2011), both of which respond to human

Box 1

Schematics illustrating relationships among anthropogenic change, stress physiology, behavior, and higher-level impacts on interspecific relationships. Relationships (casual or correlative) supported by empirical data are shown in gray/black; relationships not yet examined in the respective systems (but in some cases with support in other related systems) and which could be focused on in future studies are shown in spotted rather than solid fill (online version: yellow instead of gray fill), with associated statements followed by question marks.

(**A**) Avian–Mycoplasma host–pathogen system: Human food supplementation can facilitate higher local densities of free-



living house finches (Mertz and Brittingham 2000), alter contact rates among house finches (Moyers et al. 2018b), and promote contaminated feeder surfaces (Adelman et al. 2015). These changes have consequences for transmission and infection rates of the bacterium *Mycoplasma gallisepticum* (Adelman et al. 2015; Fischer and Miller 2015). Infection with this pathogen can lead to increased GCs (Lindström et al. 2005; Love et al. 2016), decreased roost-site fidelity that may further increase contact rates (Dhondt et al. 2006), and can inhibit antipredator responses (Adelman et al. 2017). Moreover, in house finches, seasonal increases in GCs are correlated with periods of *Mycoplasma gallisepticum* outbreaks (Lindström et al. 2005), and individual differences in GCs are associated with increased exploratory behavior (Moyers et al. 2018a), which may further alter finch contact rates (Moyers et al. 2018a). The direct impacts of other aspects of anthropogenic change (e.g., climate change) on *M. gallisepticum*'s behavior and physiology have not yet been explored in this context, but ultimately these dynamics could lead to reductions in host populations.

(B) Fire Ant–Lizard Predator–Prey System: Invasive fire ants prey upon eastern fence lizards, resulting in changes to their GC physiology (Graham et al. 2012, 2017; McCormick et al. 2017; Sprayberry et al. 2019), immune responses (McCormick et al. 2019; Sprayberry et al. 2019), and limb morphology (Langkilde 2009). Changes in GC physiology and an evolutionary history of exposure to fire ant predation in members of this species are also associated with altered anti-predator behaviors that are thought to reduce susceptibility to fire ant predation but to increase susceptibility to avian predation (Trompeter and Langkilde 2011; Thawley and Langkilde 2017). Although not yet explored, increased injury from avian predation (Thawley and Langkilde 2017) in combination with immune function changes related to fire ant exposure (Sprayberry et al. 2019) could make lizards more susceptible to certain diseases and mortality, with potential downstream consequences for population numbers. While the direct impacts of climate change on these dynamics have yet to be explored, recent work has suggested that increased temperatures can further contribute to changes in GC physiology in fence lizards (Telemeco et al. 2019), with unexplored consequences for/interactions with fire ants.

(C) Anemone–clownfish mutualism: Climate change causes thermal stress-induced bleaching in the magnificent sea anemone. Bleaching has been found to increase metabolic demands (Norin et al. 2018) and to induce a GC stress response in the anemones' associated anemonefish, the orange-fin anemonefish (Beldade et al. 2017). In turn, these changes have been associated with decreased reproduction in anemonefish (Beldade et al. 2017). The downstream consequences of these dynamics on anemone and anemonefish populations in this particular system and the role of anemone or anemonefish behavior in mediating these changes are not yet understood.

modifications of habitat structure and resource distributions.

Concurrent physiological and behavioral changes take place in the parasites and pathogens that infect human-impacted hosts. Relationships between anthropogenic change, stress, and behavior have largely been examined from the perspective of the host, but pathogens and parasites also have stress pathways (Vonlaufen et al. 2008; Keppel et al. 2016) and are susceptible to anthropogenic change (Carlson et al. 2017). Certain types of environmental change are known to directly impact their physiology and behavior. For example, in helminth parasites, pollution can inhibit reproductive (Gheorghiu et al. 2007) and encystment physiology (Morley et al. 2003) and can alter behavior by impairing locomotion and the ability to find hosts (Pietrock and Marcogliese 2003). Parasites and pathogens are also known to respond negatively to certain extreme environmental conditions (e.g., higher than usual temperatures, Stevenson et al. 2013; or lower than usual pH, Marcogliese and Cone 1996).

Studies examining hosts or parasites in isolation often conclude that anthropogenic stressors have negative impacts on fitness for each group, but the consequences of these changes for higher-level disease dynamics depend upon interactive effects (e.g., Ezenwa et al. 2016) and the relative susceptibilities of hosts versus parasites to environmental change (Rohr et al. 2008; Sonn et al. 2017; Decker et al. 2018). If pathogens or parasites incur higher costs than hosts, it is possible that environmental change could lead to unexpected benefits for host populations. For example, some parasites can act as "pollutant sinks" accumulating pollutants and thereby reducing the host's exposure (Sures et al. 2003, 2017). On the other hand, the ability of parasites and pathogens to use hosts as a buffer to their direct exposure to environmental change may allow these organisms to persist while taking advantage of immunocompromised hosts.

There is an urgent need for work characterizing the physiological and behavioral responses of pathogens and parasites to anthropogenic change, and how these responses interact with simultaneous impacts on infected hosts. Unsurprisingly, technological advances are opening doors for studies of disease ecology; proximity sensors, movement tracking, and passive integrated transponder (PIT) tags may be useful for mapping out contact/transmission dynamics. Studies of the house finch–mycoplasma system provide a particularly elegant, thoroughly explored case-study off of which future work could be modeled (Box 1A).

Predator–prey dynamics

Human activities are known to affect predator–prey dynamics directly, via human presence or direct killing, and indirectly via the introduction of invasive species and habitat alteration. Introduced species have had devastating impacts on native species with cascading effects on ecological communities (Nelson et al., 2010; Murphy et al. 2019). Habitat modification—particularly modification that involves changes in food availability (e.g., supplementation: Rodewald et al. 2011; overexploitation: Baum and Worm 2009; hunting: Ritchie and Johnson 2009)—has obvious impacts on predator–prey dynamics. More subtly, habitat modifications that impact sensory ecology—for example noise and light pollution—can alter susceptibility to predation and/or hunting ability (Siemers and Schaub 2011; Minnaar et al. 2015).

In comparison to other ecological interactions, there is a relatively large body of literature examining behavior- and stress-mediated impacts of humans on predator–prey dynamics. Predator–prey interactions are inherently behavioral, and there are clear impacts of humans on space use (Muhly et al. 2011; Ordiz et al. 2013; Suraci et al. 2019a), activity rhythms (Ordiz et al. 2017), and other behaviors relevant to predators and prey (Smith et al. 2015; Ortiz et al. 2019). Humans can also act or be perceived as direct predators, which can induce stress-mediated, non-consumptive impacts on animal physiology (Ellenberg et al. 2006; Pereira et al. 2006; Casas et al. 2016). Because humans are "super-predators" (Darimont et al. 2009; Suraci et al. 2019a), their activities can trigger stress–responses (Creel et al. 2002, 2013; Van Meter et al. 2009) in both prey and predator species. Such physiological changes can be linked to further downstream changes (e.g., Thaker et al. 2009), such as acting to inhibit anti-predator behaviors in prey (e.g., Allan et al. 2015; Hammond et al. 2019; but see Lawrence et al. 2017). Altogether, these physiological and behavioral changes could make already-stressed prey more susceptible to predation. It is difficult to predict the overall impacts of humans on predator–prey relationships without balancing the costs and benefits of human activity on each member of the relationship.

Interactions between changes in the physiology and behavior of predators and prey have cascading consequences that can mediate eco-system level changes (Hammond et al. 2007; Hawlena and Schmitz 2010; Guiden et al. 2019; Fig. 1B). For example, when predators avoid human settlements, the same areas can function as a shield for prey species, providing a low-risk area for foraging and reproducing (Berger 2007; Muhly et al. 2011). This in turn alters dietary choices of prey, which can impact native plant communities (Schmitz et al. 1997; Killen et al. 2013; Suraci et al. 2019a). Altered prey availability in low-risk areas (Berger 2007; Muhly et al. 2011) may leave predators nutritionally stressed, forcing them to either hunt novel or non-preferred species, or to become willing to hunt in high-risk areas, thereby incurring further physiological costs. Alternatively, when prey perceive humans as predators, subsequent changes in stress physiology may lead to inhibition of anti-predator behaviors (Clinchy et al. 2013) and altered energy flow up the food chain (Hawlena and Schmitz 2010). When the performance curves of predator and prey species differ with respect to environmental traits, one species may be favored as the environment changes (Miller et al. 2017). Alternatively, fitness costs for both groups of animals may be amplified when chronically stressed predators hunt for poor-quality, declining prey.

Ultimately, anthropogenic stressors may drive selection for generalist and bold-type predators, which may be more successful in environments with scarce prey options (Terraube et al. 2011; Mella et al. 2015). Personality types in predators can alter predation rates and non-consumptive impacts on prey species (Sih et al. 2012; Toscano and Griffen 2014). Similarly, certain stress phenotypes in prey may be favored in modified environments, and if stress physiology is linked to behavioral phenotypes (Martins et al. 2007; Øverli et al. 2007; Atwell et al. 2012; Baugh et al. 2017; but see Royauté et al. 2018; Westrick et al. 2019), there may be parallel, selective impacts on prey temperament. Selection on animal temperaments can in turn influence community structure (Toscano et al. 2016; Moran et al. 2017; Sih et al. 2018).

Exploring stress- or behaviorally-mediated effects of anthropogenic change on both sides of predator–prey relationships is a difficult task, particularly for larger-bodied, longer-lived, and more far-ranging organisms like mammalian carnivores. Long-term datasets will likely be critical in this pursuit (Langkilde 2009; Smith et al. 2017b). Studies of invasive, predatory fire ants and fence lizards provide an elegant example that future work may benefit from emulating (Box 1B).

Beneficial partnerships

Certain types of anthropogenic change may be most likely to impact beneficial interaction networks, in which the behavior and physiology of two or more individuals is linked through a mutualistic (between heterospecifics; Fig. 1C) or cooperative (between conspecifics) relationship. For example, climate change and invasive species can change species assemblages (Williams and Jackson 2007; Rogers et al. 2017) thereby altering the likelihood of mutualistic species interacting. In contrast, direct killing, which can remove key individuals from social groups (Packer et al. 2011) and human presence, which can alter grouping of conspecifics (Li et al. 2017), may impact cooperative networks. Theory and existing evidence suggest that humans may impose contrasting pressures on these relationships, acting to disrupt mutualisms (Tylianakis et al. 2008; Dunn et al. 2009; Aslan et al. 2013), but to promote cooperation (Raulo and Dantzer 2018).

While mutualistic relationships are thought to ameliorate environmental stressors for the involved species (Stachowicz 2001), there is little empirical research exploring how anthropogenic stressors imposed on one partner may indirectly act as a stressor upon an associated partner, thereby contributing to biodiversity loss because associated species are bound to common fates (Toby Kiers et al. 2010). One key example comes from the impacts of climate change on a marine mutualism. Temperature-induced anemone bleaching can indirectly harm anemones' associated anemonefish by increasing metabolic demands (Norin et al. 2018), triggering the fish's GC response, and ultimately significantly suppressing reproductive output (Beldade et al. 2017). This fascinating study system has been illustrated in Box 1C. Indirect effects of global change may also negatively affect cleaner mutualisms via the stress axis in other systems. Mutualistic relationships can be subject to cheating (Bshary and Grutter 2005), thus, if anthropogenically-mediated changes in stress are associated with certain behavioral types or responses, then selfish behaviors may change in frequency. Moreover, stress activation can have masking impacts on relationships between physiology and behavior, sometimes resulting in a homogeneity of behavioral types (Killen et al. 2013).

Relatively fewer studies have explored the potential for humans to trigger stress responses to modify patterns of cooperation within social species. Evidence for the role of the HPA-axis in promoting or inhibiting social behavior comes mainly from studies of reproduction (Montgomery et al. 2018; Raulo and Dantzer 2018). Mating behavior and parental care are generally inhibited by HPA activation (Wingfield et al. 1998; Kirby et al. 2009; but see Blumstein et al. 2016), including, potentially, human-induced HPA activation. However, stressors can also promote coordinated, group-level cooperation (von Dawans et al. 2012; Schweda et al. 2019) and increase social network cohesion (Crockford et al. 2008), both of which can positively impact individual fitness of social animals (Silk 2007; Smith et al. 2017a). Such findings can be extended to generate hypotheses about the impacts of human-induced stressors on cooperative behaviors (e.g., cooperative hunting, group defense/vigilance). For example, human-induced disturbances can promote group-level vigilance in ungulates or birds (Hunter and Skinner 1998; Blumstein 2006). These effects may shape community processes by altering rates of herbivory or depredation by non-human predators. Although the strength of these effects likely varies with sex, species, and the intensity/duration of the stressor, human-induced stressors may promote group-level cooperation to alter population demography, spatial distributions, and persistence.

The extent to which social cooperation can buffer anthropogenic challenges remains poorly understood. Cooperatively breeding vertebrates do occur disproportionately in unpredictable environments (Guindre-Parker and Rubenstein 2018; Schradin et al. 2019), but the extent to which this flexibility in offspring care behavior reduces vulnerability to anthropogenic change is understudied. Even for non-cooperatively breeding animals, social bonds can shield the effects of everyday stressors (Young et al. 2014), suggesting that sociality may help animals to buffer some costs of global change. However, in other species, individuals sacrifice their personal thermal preferences to maintain social cohesion (Cooper et al. 2018), suggesting that sociality may constrain appropriate responses to warming global temperatures. Going forward, technological advances such as animal–worn sensors that monitor stress-reactivity in real-time (Young et al. 2014; Lee et al. 2016) in combination with data collected from long-term studies (Packer et al. 2011; Smith et al. 2017b) could offer insights into the effects of physiological and beneficial partnerships shaping higher-level processes.

Conclusions and future directions

The exposure of multiple parties in an ecological relationship to simultaneous anthropogenic stressors may be greater or less than the sum of its parts (Jackson et al. 2016). We focused on three, classic ecological relationships here, but many other interactions could be examined with a similar perspective (e.g., competition, pollination, animal-mediated seed dispersal, herbivory). We also did not touch upon the extensive ways that early life stress and maternal stress may impact these dynamics (Pryce et al. 2002), nor upon higher-level interactions between interactions, for example, the impacts of predator–prey relationships on disease dynamics (Buss and Hua 2018; Sprayberry et al. 2019). Stress and stress-mediated changes are not inherently "bad," and may facilitate wildlife persistence in the face of environmental change (Boonstra 2013). In some cases, anthropogenic change-induced stress responses may interact to facilitate or stabilize ecological dynamics. Still, while impacts of anthropogenic change on interacting organisms may sometimes counterbalance each other in a network, when multiple changes are made to a carefully tuned system disruption is more likely than stabilization (Tylianakis et al. 2008). These dynamics are context-dependent, and ideally should be studied against the backdrop of altered environments.

It is challenging and often logistically impossible to simultaneously study stress and behavior on multiple sides and/or levels of an ecological interaction. However, systematically studying species responses to environmental change in isolation from the ecological relationships and modified habitats they exist within may yield biased conclusions. When attempting to predict or characterize one species' response to anthropogenic change, meta-analyses that integrate seemingly disparate literatures may be valuable in examining how that same type of environmental change impacts other species that are ecologically bound to the focal species (Winfree et al. 2009; Becker et al. 2015). HormoneBase, a new repository of vertebrate hormone levels, may be a useful online resource in this pursuit (Vitousek et al. 2018). Simulations and modeling may also be required (Gilman et al. 2010). Studies that experimentally manipulate physiological or environmental parameters (e.g., with hormone implants, or mesocosms) will be critical in teasing apart the causality of hormone–behavior–anthropogenic change relationships in modified habitats. Finally, while it is more easily suggested than done, another possible solution to this logistical challenge is for multiple research groups studying disparate sides or levels of the same ecological relationship to combine forces. This approach may be most useful when long term or museum-based datasets are also available, or when studies can be preemptively designed with both groups in mind. Moreover, it will be important to reach outside of comfort zones to pair seemingly diverse datasets (e.g., behavioral/movement datasets from telemetry, GPS, or accelerometers in combination with ecosystem function studies that integrate data on stable isotopes or nutrient flow; Nakamura and Sato 2014; Schmitz et al. 2018).

Stress-mediated ecological changes will have evolutionary consequences for wildlife communities. For example, species that have spent many generations in urbanized conditions can exhibit altered physiological and behavioral traits, potentially due to evolutionary change (Partecke et al. 2006; Donihue and Lambert 2015; Charmantier et al. 2017; Tennessen et al. 2018). In the face of environmental change, novel species assemblages (Williams and Jackson 2007), and altered phenology (Rafferty et al. 2015), the target species involved in pathogenic, predatory, or mutualistic relationships may change. Generalist species with flexible life histories may emerge as "winners" (Dunn et al. 2009; Le Viol et al. 2012; Hammond et al. 2018). The stress response may be one process at play in these shifting community dynamics, allowing species to modulate several mechanisms of response to novel conditions (e.g., behavior, reproduction, metabolic expenditure, etc.). Species exist within ecological interactions. When attempting to predict the impacts of anthropogenic change on one species, we must also consider the ways that it may directly or indirectly impact the physiology and behavior of partner species.

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