

# Integrating animal behaviour into research on multiple environmental stressors: a conceptual framework

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## Abstract

While a large body of research has focused on the physiological effects of multiple environmental stressors, behavioral effects remain far less studied. However, behavioural plasticity can not only directly drive responses to stressors but can also mediate physiological responses. Here, we provide a conceptual framework incorporating four fundamental tradeoffs explicitly linking animal behaviour to life history-based pathways for energy allocation, shaping the impact of multiple stressors on fitness. We first address how small-scale behavioural changes can drive conflicts between the effects of multiple stressors and alternative physiological responses. We then discuss how animal behaviour gives rise to three additional understudied and interrelated trade-offs: balancing the benefits and risks of obtaining the energy needed to cope with stressors, allocation of energy between life-history traits and stressor responses, and larger-scale escape from stressors in space or time via dispersal or dormancy. Finally, we outline how these trade-offs interactively affect fitness and qualitative ecological outcomes resulting from multiple stressors. Our framework suggests that animal behavior could underlie the extensive context dependence in results from stressor research, highlighting promising avenues for future empirical and theoretical research.

## Introduction

Physiologists and ecologists have long studied environmental stressors, which we define broadly as abiotic (e.g., chemical toxin, low oxygen, ocean acidification, pH, temperature) or biotic (e.g., disease, predation risk, food scarcity) factors that negatively affect individual fitness or the growth, abundance or persistence of a population or community (Boone *et al.* 2007; Pincebourde *et al.* 2012; Killen *et al.* 2013) (Box 1). But stressors rarely act in isolation, stimulating a recent focus on multiple stressors (see Figure 1 and Box 2, Figure 2) and their potential for synergistic impacts (Przeslawski *et al.* 2015; Cote *et al.* 2016; Cambronero *et al.* 2018; Petitjean *et al.* 2019). Despite this effort, Orr *et al.* (2020) concluded that “over the past 20 years. . . very few, if any, general patterns have emerged from meta-analyses (Crain *et al.* 2008; Holmstrup *et al.* 2010; Dieleman *et al.* 2012; Jackson *et al.* 2016; Yue *et al.* 2017; Lange *et al.* 2018)” addressing the effects of stressor combinations. Our thesis is that a clear theoretical understanding of behavioural and life-history plasticity in response to multiple stressors can help explain the observed context-dependent variation in stressor effects.

Conceptual models of how organisms respond physiologically to environmental variation (e.g, the Allostatic Load (McEwen & Wingfield 2003; Wingfield 2013) and Reactive Scope Models (Romero *et al.* 2009) provide

frameworks for understanding how stressors affect fitness (or performance). These effects are expressed through physiological mediators, both within a range that does not reduce fitness (the reactive scope) and in scenarios that push organisms into an overload that reduces survival. Behaviour plays a role in these models through feeding, locomotion, aggression, anxiety, fear, fleeing, vigilance, and migration, and mediates the physiological responses to stressors (see Table 1 in Romero *et al.* 2009). But a full, trade-off based integration of behavioural mechanisms and life-history implications is essential to achieve a deeper, more predictive understanding of these relationships. Organismal responses are triggered by cues (whether single or multiple), which provide information on the nature and intensity of stressors. Whether and how organisms respond, and the effectiveness of their responses, can depend critically on the reliability of cues, and how cues interact (see Box 3).

In this synthesis, we outline a conceptual framework that integrates animal behaviour, bioenergetics and life history trade-offs to identify ways that behaviour and life history plasticity shape the impacts of stressor exposure on individual fitness (Figure 1). First, in addition to physiological responses, small-scale behaviours (e.g., incremental shifts in space use or activity schedules) that reduce exposure to one stressor can simultaneously alter an organism’s vulnerability to the effects of a second stressor, or alter the magnitude of these effects on fitness (**trade-off 1**). Second, because responding physiologically to stressors requires energy, foraging activity can increase in response to stressors, thereby enhancing exposure to additional risks, e.g., predation (**trade-off 2**). If the organism has obtained the energy it requires, it will then need to allocate energy between behavioural or physiological stress responses and fitness-enhancing life history demands (i.e. reproduction and growth; **trade-off 3**). **Trade-offs 2** and **3** emphasize how stressors can reduce fitness indirectly by limiting overall energetic budgets, increasing foraging-related risks or drawing energy away from alternative life history needs. Finally, at a larger spatial or temporal scale, organisms can respond to stressors by actively escaping exposure through space (e.g., via longer-distance dispersal) or time (e.g., via dormancy or diapause). Escape in space or time typically incurs other costs (**trade-off 4**).

Our integrated framework highlights 1) the relative importance of direct versus indirect costs of stressors, where, for example, the indirect costs of an abiotic stressor might include increased predation risk or reduced mating success; 2) the role of the scales of spatial and temporal correlations between stressors, resources and other risks; and 3) the need to better understand mechanisms resulting in ‘fitness cliffs’ – situations where a relatively small increase in stressor levels results in a large decrease in fitness. In the following sections, we provide detailed descriptions of each of the four fundamental and interrelated trade-offs (Fig. 1) and the broad insights they offer.

### **Trade-off 1: Small-scale energetic and behavioural tradeoffs**

Physiologists have rigorously investigated physiological trade-offs – where the physiological mechanism of response to stressor A either enhances (cross-tolerance) or interferes with (cross-susceptibility) the physiological mechanism of response to stressor B (Todgham *et al.* 2005; MacMillan *et al.* 2009; Sinclair *et al.* 2013; Hintz *et al.* 2019). Here, we focus on additional, less studied behavioural and energetic mechanisms, whereby exposure to stressor A changes the fitness costs of stressor B.

Many organisms respond to environmental stressors by adjusting their space use (Clusella-Trullas & Chown 2014; Sears *et al.* 2016) or temporal activity patterns (Gaynor *et al.* 2018; van der Vinne *et al.* 2019) to reduce exposure to stressors and, thus mitigate physiological costs. These behavioural responses can occur over small scales, which we refer to as ‘avoidance’, or large scales, which we refer to as ‘escape’ (e.g., dispersal or dormancy, which we discuss later: trade-off 4). The small-scale responses that we discuss here differ from larger-scale escape responses in being relatively rapidly reversible and typically requiring lower energy costs.

Behavioral responses can interact with physiological responses to determine not only the net effect of a stressor on an organism, but also whether multiple stressors interact antagonistically or synergistically. Put simply, when two stressors require conflicting adaptive behavioural responses, where the response to either increases exposure to the other, the negative impact of the stressor pair can be enhanced. A core concept from standard behavioural ecology trade-off theory (Houston & McNamara 1999) suggests that a key factor

is the degree to which multiple stressors are positively versus negatively correlated in space or time (see Box 4 for further discussion of these correlations). If stressors are positively correlated (e.g., if the same locations have high levels of both stressors, while other locations have low levels of both), then avoidance of one tends to also reduce exposure to the other; if the stressors are negatively correlated (e.g., places with high levels of one stressor have low levels of the other), then organisms face the trade-off where avoidance of one could increase exposure to the other. For example, salamander larvae avoid exposure to damaging ultraviolet radiation by going to deeper water, but doing so exposes them to higher predation risk from fish (Garcia *et al.* 2004).

Invoking parallel theory on avoidance of multiple predators (Matsuda and Abrams 1996; Sih *et al.* 1998), we can predict how organisms should respond behaviourally to multiple stressors. If avoidance of one stressor increases exposure to the other, then organisms should more heavily weigh avoidance of the more detrimental stressor(s). This weighting could depend on both the level and inherent lethality of the stressors, or on how earlier experience (or evolution) has shaped the organism’s relative abilities to cope with the two stressors physiologically. If both stressors can strongly reduce fitness, and if behavioural avoidance itself incurs a high cost (e.g., restriction to low-quality habitat), then organisms should not attempt small-scale avoidance but should, instead rely only on coping with the stressors via physiological responses - or on escape in space or time, if feasible (e.g., energetically affordable; trade-off 4).

Further complexities arise depending, for example, on the spatial scale of heterogeneity in stressor distributions relative to the organism’s movement capacity (Schmitz *et al.* 2017; Fey *et al.* 2019). Although numerous studies have examined behavioural avoidance of one stressor, there is a need for a better understanding of factors that explain when and why multiple stressors are negatively versus positively correlated, and for more studies examining how organisms respond behaviourally to conflicting (e.g., negatively correlated) stressors, particularly in the broader context of additional layers of trade-offs.

An alternative mechanism that results in trade-offs arises when increased energy devoted to coping physiologically with stressors results in *accelerating* fitness costs. The mechanism could involve increased stressor levels pushing organisms into homeostatic or allostatic overload (McEwen & Wingfield 2003; Romero *et al.* 2009), such that allocating energy to coping with any one stressor strains the organism’s ability to cope with other stressors. Additionally, and in a segue to the other major trade-offs in Figure 1, the increased fitness costs could arise via increased mortality risk associated with acquiring energy (trade-off 2) or via an energy allocation trade-off that reduces growth or reproduction (trade-off 3). Each of these mechanisms could result in ‘fitness cliffs’, or strong nonlinearities that can cause even a small change (in this case, an increase in the level of a stressor) to disproportionately reduce fitness. For example, Delnat *et al.* (2019) reported a synergistic increase in mosquito mortality when pesticides combined with high daily temperature variation (14 °C), but no such interaction was observed under lower (7 °C) or in the absence of daily temperature variation.

### **Trade-off 2: The energy acquisition trade-off: Balancing the needs and costs of obtaining energy**

To deal with stress, organisms require more energy to fuel metabolism, maintain homeostasis, and mount direct physiological responses to stressors (Romero *et al.* 2009). Balancing the needs and costs of obtaining energy and, in particular, the costs in terms of predation risk, is a core issue in behavioral ecology, where extensive theory and numerous empirical studies (Sih 1987; Lima 1998; Brown 1999; Houston & McNamara 1999) provide insights that we draw on to understand energy acquisition tradeoffs associated with responding to environmental stressors.

First, and perhaps most basic, is the fact that when physiological stress increases energy demands, the ability to meet those demands depends on food availability. When organisms have regular access to food and, thus, energy, the negative effects of stressors on organismal performance are typically weakened and, in some cases, entirely negated (Hettinger *et al.* 2013; Mayor *et al.* 2015; Tosi *et al.* 2017). Consequently, laboratory experiments that provide organisms with adequate/high food levels might underestimate multiple stressor impacts in nature, where animals are often food-limited (Martin 1995; McCue 2010). In some cases,

environmental stressors further exacerbate low food availability if stressor-induced higher energy demands cause consumers to deplete available resources more rapidly, or because the stressors themselves directly lower resource production and availability (Van der Putten *et al.* 2010; Bruder *et al.* 2017). When resources are low or there is heightened competition, acquiring energy becomes more energetically demanding.

Importantly, the increased energy demands associated with coping with stressors can require organisms to adopt riskier behaviours (e.g., higher activity, longer foraging bouts, increased time spent in patches with high food but high risk) (Lima 1998; Lienart *et al.* 2014). For instance, tadpoles have been shown to increase activity and reduce shelter use in response to higher concentrations of a pesticide and lower food availability (Rohr *et al.* 2004). Although organisms can partially counteract predation risk and buffer possible stressor synergisms by adopting additional vigilance, or social foraging strategies (Killen *et al.* 2016), ultimately, under natural conditions, the need to cope with stressors physiologically might often entail exposure to increased predation risk. Alternatively, because animals often respond to high predation risk by exhibiting antipredator behaviours that reduce energy intake this can constrain the ability of organisms to build and maintain the capacity to cope with stressors physiologically.

In the context of the classic risk-reward foraging tradeoff, a key under-studied topic is the spatial or temporal correlations among stressors, food levels and predation risk. Even if stressors are uncorrelated with food and predation risk, as noted above, the need to acquire more energy to cope with stressors physiologically can require increased exposure to predation risk. Thus, stressor exposure and predation risk can become indirectly correlated through the organism's behavior (see analogous phenomenon concerning behaviorally mediated stressor 'co-occurrence' in Box 4, Figure 4). If, instead, stressors are negatively correlated with predation risk (e.g., if avoiding stressors in space or time causes organisms to be more active in places or times when predation risk is particularly high), the cost of multiple stressors can be greatly amplified. To date, few studies have quantified these spatiotemporal correlations and how organisms might balance them adaptively (or not). Predation risk alone can induce physiological stress responses in prey (including elevated stress hormones and metabolic rate) and altered stoichiometry (Rinehart & Hawlena 2020). Although a meta-analysis found that the presence of a second stressor (most commonly food limitation or elevated temperature) did not generally influence prey stoichiometry beyond effects of predation risk, this result comes from relatively few studies that varied considerably in observed effects (Rinehart & Hawlena 2020).

In some cases, stressors interfere with an organism's sensory system and ability to avoid predators, leading to a synergistic negative effect of the stressor and background predation risk (Reeves *et al.* 2010; Hayden *et al.* 2015; Polo-Cavia *et al.* 2016; Martin *et al.* 2017; Sievers *et al.* 2018). For example, metal and pesticide contaminants indirectly increase mortality in frogs, because these contaminants can compromise predator recognition systems and avoidance behaviours, leading to higher predator attack rates and inflicted injuries (Reeves *et al.* 2010; Hayden *et al.* 2015). Similarly, fluoxetine exposure in mosquitofish, *Gambusia holbrooki*, inhibits neurotransmission pathways, leading to relaxed anti-predator behaviour and maladaptive responses to high predation risk (Martin *et al.* 2017).

If physiological stressors, foraging activity, and predation risk pose conflicting demands, the costs of stressors can then involve a mix of direct costs, where the stressors themselves cause harm (e.g., allostatic overload resulting in reduced fitness), and indirect costs (e.g., exacerbated hunger, higher predation risk) associated with the need to get energy to fuel physiological responses. When might we expect direct versus indirect costs to be larger? Parallel theory on balancing risks and foraging offers intuitive, qualitative predictions (Brown 1999; Houston & McNamara 1999). When food availability is high and predation risk is low, animals need not be very active to obtain sufficient energy to fuel physiological responses to stressors. As a result, the stressors' direct costs and their indirect fitness costs, in terms of predation risk, should be of similar, relatively small magnitude, so long as direct effects are mitigated via abundant energy (Hettinger *et al.* 2013; Mayor *et al.* 2015). In contrast, with low food levels, the activity needed to acquire sufficient energy to fuel physiological responses to stressors can require exposure to higher predation risk. The main cost of the stressors might then be increased predation risk and not mortality from the stressors per se. Notably, this indirect cost is not addressed in standard laboratory experiments, where focal organisms are not exposed to actual predation.

On the other hand, if the relationship between activity and predation risk accelerates (e.g., if foraging activity above a threshold level causes a pronounced increase in predation risk), then this can constrain activity (and energy intake) to be relatively low for safety, and, thus, constrain investment in physiological responses, resulting in greater direct costs of stressors. These intuitive qualitative predictions should be rigorously explored with quantitative models and empirical experiments to address stressor-foraging-risk trade-offs.

### **Trade-off 3: Energy allocation between stressors and life-history traits**

Stressors can not only directly reduce growth and reproduction of organisms (e.g. by disrupting endocrine systems (Rattan & Flaws 2019) or by shortening telomeres (Chatelain *et al.* 2020)), but they can also indirectly reduce fitness by demanding energy that could otherwise be allocated to growth and reproduction (Rohr *et al.* 2004; Portner & Knust 2007; Correa-Araneda *et al.* 2017). A fundamental tenet of basic life history theory is that adaptive allocation to competing demands depends on the marginal benefits versus costs of additional investment in each demand (Roff 2002). Nonlinearities involving accelerating costs or benefits of increased investment can also produce aforementioned fitness cliffs (threshold effects), where here, even a small reduction in investment in a given demand results in a large decrease in fitness. Life history studies suggest that, although there are exceptions, these nonlinearities are often associated with strong competition, or size/condition-dependent safety (Einum & Fleming 1999; Luttbegg & Sih 2010). Being near such a threshold could constrain organisms to allocate sufficient energy to a given demand to prevent falling over a fitness cliff. We next discuss some implications of this basic concept for how organisms might allocate energy to physiological responses to stressors versus competing life history demands. Intriguing insights come from acknowledging that adaptive allocation strategies involving multiple stressors can shift in non-intuitive ways that can be predicted by life history theory.

When energetic requirements for competing demands (e.g., for growth, reproduction, or other survival needs beyond coping with the focal stressors) are close to a fitness cliff, multiple stressors can have synergistic negative impacts through the combined energetic loads they place on an organism. That is, it is clear, through the lens of life-history theory, that stressors need not interact directly to drive strong synergistic effects on the organism; these can manifest through the co-occurrence of independent stressors at a sensitive level along the continuum of an organism's energetic state.

When physiological demands of stressors and life history demands are both near fitness cliffs, the need to divert energy to cope with stressors is particularly likely to produce strong indirect, negative impacts on fitness through reduced growth, development or reproduction. Life history stages that suffer higher marginal costs of reduced energy investment should be particularly vulnerable to suffering indirect costs of physiological demands of stressors. Life stages vary in their vulnerability to different combinations of stressors, and this varies across taxa (Stoks 2001; Rohr *et al.* 2011; Przeslawski *et al.* 2015; Watson *et al.* 2018; Tran *et al.* 2020). Yet, for many taxa, when juveniles divert energy to dealing with multiple stressors rather than development, this results in particularly strong negative effects, involving both increased sublethal effects and higher mortality (Byrne & Przeslawski 2013; Przeslawski *et al.* 2015; Lange *et al.* 2018; Miler *et al.* 2020). For example, echinoderm larvae can show elevated mortality, impaired development and signs of metabolic depression following exposure to heightened temperature and  $p$  CO<sub>2</sub> (Byrne & Przeslawski 2013; Przeslawski *et al.* 2015). Such costs of reduced growth and development can be particularly strong in systems with seasonal time horizons, where growing to a threshold size or stage or accumulating sufficient energy reserves in a given time period is crucial for survival (e.g., for migration, overwintering or metamorphosis when ephemeral habitats disappear).

Similarly, when reproduction requires an abundance of energy, females can suffer higher costs of coping with stressors during reproductive periods than during non-reproductive periods. French *et al.* (2007) experimentally manipulated reproductive investment in female tree lizards (*Urosaurus ornatus*) by stimulating vitellogenesis and found that lizards that had higher reproductive investment also had suppressed immune systems when resources were limited. In particular, if offspring fitness is a strongly nonlinear (e.g., sigmoidal) function of female parental investment, this can cause females to invest more into reproduction and less in coping with stressors, thus yielding larger direct costs of stressors. Alternatively, animals exposed to stress

sometimes reduce their investment per offspring (Domis *et al.* 2013; Jager *et al.* 2013). If this substantially reduces average offspring survival (e.g., if offspring survival falls over a fitness cliff), then adult exposure to stressors can result in a large indirect cost in terms of both offspring and adult fitness. For example, blue orchard bees (*Osmia lignaria*) exposed to resource limitation and the pesticide imidacloprid suffered an additive reduction in reproductive fitness via a lowered probability of successful nesting and a reduced number of offspring produced (Stuligross & Williams 2020). Additionally, offspring sex ratios became male biased, increasing the likelihood of further reductions in reproductive fitness in the future (Stuligross & Williams 2020).

For males, mating success often depends heavily on possessing either large relative size or ornaments (Andersson 1994); in these cases, males can suffer a fitness cliff where reduced investment in sexually selected traits can result in little or no mating success. Strong sexual selection can then favor males diverting their limited energy into sexually selected traits, even at the cost of reduced investment in physiological responses to stressors. Such scenarios would result in a strong direct cost (e.g. mortality due to the stressors) of exposure to stressors. Alternatively, if some sites have abundant food but high risk, sexual selection can favor taking greater risks (e.g., increasing exposure to predators or other stressors) to bring in the energy required to invest in both ornaments and in physiological responses to stressors to maintain condition; the increased exposure to predators would represent a large indirect cost of exposure to stressors.

#### **Trade-off 4: Larger-scale spatial or temporal escape from stressors**

As an alternative to coping with the suite of stressors an organism faces locally and immediately (the direct and indirect effects which are discussed in the preceding sections on trade-offs 1-3), some organisms can escape environmental stressors in space or time through long-distance dispersal or some form of substantial, relatively long-term reduction in metabolic demands. Escape in space (EIS) involves an organism, temporarily or permanently, relocating to a new environment. Seasonal migration, exhibited by various mammals, birds, and insects, is a common, cyclical form of temporary EIS, often tracking predictable large-scale variations in weather patterns and food availability. EIS can also be triggered by anthropogenic environmental stressors (Berg *et al.* 2010). For example, the onset of human hunting, rather than the onset of severe weather (e.g., snowfall), was a primary driver of autumn migration by red deer (Rivrud *et al.* 2016). Similarly, individual mule deer that undertake long migrations have been shown to dramatically reduce their risk of being harvested by human hunters relative to short- and moderate-distance migrants in the same population (Sawyer *et al.* 2016). Furthermore, non-migratory butterfly species have moved over vast areas of habitat made unsuitable by anthropogenic climate change to occupy new locations in Europe (Parmesan *et al.* 1999). Escape in time (EIT) involves reducing exposure and avoiding the costs of tolerance or dispersal by instead entering into torpor (Humphries *et al.* 2003; Geiser 2004), dormancy (including hibernation or estivation; (Danks 2000)), diapause (a special case of dormancy based on suspended development; (Chapman 1998)), or resting stages (Smirnov 2014). EIT is commonly used by animals to address extreme temperatures, drying conditions, and a limited food supply (Thomas *et al.* 1990; Danks 2000; Goto *et al.* 2001; Sarmaja-Korjonen 2003; Hairston Jr. & Fox 2009).

Theory on the evolution of adaptive dispersal and/or dormancy provides insights regarding factors that influence when organisms should attempt to escape in space or time (Levin *et al.* 1984; Snyder 2006; Bonte & de la Pena 2009; Bonte & Doherty 2017). Whether dispersal or dormancy is adaptive depends on the expected net fitness payoff, which depends on how organisms handle trade-offs 1-3 (Fig. 1) in both the current environment, and in alternative environments, as well as costs of escape in space or time (including mortality and the need for a substantial front-end investment in energy stores that increases escape success). Both dispersal and dormancy can involve substantial uncertainty about expected fitness. For long-distance dispersal, there is uncertainty about transit costs (that depend on both cost per unit of distance or time, and distance relative to mobility) and often great uncertainty over likely payoffs in prospective new environments. This might be especially true now, following the unprecedented human-induced rapid environmental change that is shaping natural habitats globally (Crowley *et al.* 2019; Van de Waal & Litchman 2020).

Importantly, when organisms disperse to a new habitat, they might face a different set of stressors that

require a different set of behavioral and physiological responses. Thus, the suitability of a new environment could hinge on the organism's plasticity in behaviour and physiology. The degree of dissimilarity between the suite of dominant stressors in an organism's former environment compared to its new environment can come with distinct costs; e.g., new stressors could require greater energetic investment in establishing appropriate physiological or behavioral responses. Furthermore, if, as is often the case, there are behavioural or physiological carryovers (i.e., earlier experiences with stressors influence later responses), then EIS can expand the scope of multiple stressors to include stressors that do not co-occur in space or time (see Box 4).

The benefit of escaping in time or space to a new environment is proportional to not just the increase in quality in the new environment but also to how long the new environment will remain of higher quality (i.e., the degree of temporal stability). If stressor levels fluctuate frequently or intensely over time, this can dilute the benefits of escape. In short, the key for adaptive dispersal or dormancy is not the spatiotemporal pattern of stressors per se; it is, instead, the spatiotemporal pattern of fitness adjusted for costs of dispersal or dormancy. In addition, because escaping to a new environment might also result in greater competition or predation risk (e.g., if competitors or predators make the same escape decision, or population demography yields this result), there is a game-theoretic aspect to this dynamic that can further complicate expectations.

Despite the various sources of complexity that can arise when considering whether an organism should stay and cope with stressors or, instead, attempt to escape them, simplified scenarios offer qualitative insights. Generally, we expect that the probability that an organism will attempt to escape stressors would scale with the potential for that escape to be possible: if stressors are highly localized in space or time, we would expect escape to be much more likely, relative to when stressors are widespread over space or time (i.e., chronic), and, thus, difficult or impossible to escape. If stressors are widespread in only one-dimension (i.e., time *or* space), we expect a threshold to exist for the other dimension, such that increasing the stressor's (or suite of stressors') presence over this dimension causes the organism to eventually shift from an optimal strategy of escape to one of tolerance (Figure 3A). In other words, when stressors occur at large enough scales in space and time, they become infeasible to avoid and tolerance becomes the sole strategy.

If we expand to consider animal behavior in the context of multiple stressors, the horizon of possibilities quickly becomes much more complex. For example, considering only two partially correlated stressors, expressed in time and space relative to the scales of these dimensions experienced by a focal organism, reveals that ten qualitatively distinct sets of possible behavioural responses emerge (Figure 3B). Generally, whenever one or more stressors is escapable in space or time, formulating quantitative predictions about when organisms will choose this strategy will hinge on the magnitude of effects of the escapable stressor(s) and the cost-benefit ratio of choosing to escape relative to choosing to tolerate the stressor(s).

### Interactions among trade-offs

Although we have discussed trade-offs one at a time, our approach, as summarized in Figure 1, emphasizes that these behaviours and allocation decisions are all part of an integrated response to stressors. The adaptive behaviour or allocation for each trade-off depends on options and decisions for the other trade-offs. In the short term and small scale, how much an animal should behaviourally avoid stressors (trade-off 1) depends on the costs of being exposed to the stressors, which depends on the organism's physiological coping capacity (tolerance) that, in turn, requires energy that often can only be acquired by taking risks (trade-off 2). In the longer term or larger scale, adaptive behaviour and physiological coping capacity depend on life history trade-offs (trade-off 3) and vice versa. Further, the decision to escape in space or time (trade-off 4) depends on the organism's expected fitness in each possible situation which depends on how the organism balances trade-offs 1-3. Furthermore, given that success in escape in space or time is often state or condition-dependent, the adaptive balance of trade-offs 1-3 must include the need to maintain energy stores to preserve the option to escape in space or time. While this overall integrated response is complex, we believe that it is a reality that can usefully guide our analyses of each component and, consequently our overall understanding of organismal responses to stressors.

The integration of behavioural, physiological and life history decisions highlight the importance of differences

between these types of plasticity in their relative speed and reversibility, relative to the rate of change in stressor levels. When should organisms escape versus stay and cope, using a mix of physiological and behavioral responses? If stressor levels increase slowly, organisms have time to both build higher physiological capacity and adjust behaviour, but if local stressor levels suddenly increase, this might exceed the speed of physiological plasticity. In that case, the notion of taking more risks to get more energy (trade-off 2) might not come into play, because even with more energy, organisms simply cannot mount the necessary physiological response quickly enough. Organisms can potentially still compensate behaviourally (avoid in space or time in the short term; trade-off 1), but if they cannot do that, they may be ‘forced’ to escape in space or time at a larger scale (trade-off 4).

### Future research directions

Here, we have focused primarily on ecological scenarios where organisms are exposed to two primary stressors, with a third stressor (predation risk) possibly arising as a consequence of increased energy acquisition behaviour (trade-off 2). However, to develop a deeper understanding, including means of accurately predicting the nature and strength of interactive effects of multiple stressors, we must extend our focus to scenarios involving more than two primary stressors, where higher-order interactions can occur. While empiricists are incorporating increasingly larger numbers of stressors into experiments (e.g. Beermann *et al.* (2018)), and fields outside of ecology have developed conceptual models to define higher-order interactions among three or more stressors (e.g. interactions among pharmaceutical drugs, Beppler *et al.*(2016)), our current framework suggests that explicitly considering animal behavior in these efforts will generate novel insights relevant to ecology and conservation. Furthermore, in light of recent advances in simultaneously collecting large volumes of data on animal behavior and multiple environmental variables *in situ*, such an integration is both timely and likely to illuminate additional stressor-related trade-offs and alternative behavioral responses used by organisms to navigate such tradeoffs.

With regard to understanding variation in how organisms respond to multiple environmental factors, for over a decade, there has been mounting interest in the importance of consistent individual differences in animal personalities or behavioural syndromes (e.g., in aggressiveness, boldness or exploratory tendency; (Sih *et al.*2004; Reale *et al.* 2007; Sih *et al.* 2012) including dispersal tendency (Cote *et al.* 2010), physiology (Biro & Stamps 2008) and life histories (Reale *et al.* 2010). Promising topics that remain understudied include how individual differences in suites of phenotypic traits relate to variation in how organisms balance the four trade-offs discussed here.

Another fruitful direction for future studies would be to examine the influence of a mix of genetic adaptation and transgenerational and within-generation developmental plasticity (including learning) in shaping an integrated response to multiple stressors. Examining ecological and social factors that, in the past or present, shaped the overall integrated response to multiple stressors could help identify genetic or developmental constraints that affect the speed or trajectory of adaptation to multiple stressors (De Coninck *et al.* 2013; Cambronero *et al.* 2018). In particular, understanding epigenetic or developmental effects can reveal otherwise hidden mechanisms of multiple stressor effects discussed in Box 4. With multi-generational transgenerational plasticity, behavioural responses to stressors in one generation can influence impacts of those stressors on others generations into the future (Bell & Hellmann 2019).

Finally, while we have focused primarily on individual responses to multiple stressors, in Box 5 and Figure 5 we expand our scope to consider stressors, and their physiological and behavioral effects, in the context of natural communities. Specifically, we outline how stressors can affect species interactions and how the nature, strength, and trophic position of these affected interactions can determine qualitatively distinct outcomes for communities and ecosystems. Further theoretical and empirical investigations of how our comprehensive framework on stressor effects (Figure 1) could help explain the structure and dynamics of natural communities offer a timely and promising avenue for future study.

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### Box 1: Glossary of terms

**Additive effect:** the combined effect of stressors is equal to the sum of each stressor alone (i.e. no statistical interaction)

**Antagonistic effect:** the combined effect of stressors is less than what would be predicted under an additive model

**Cross-susceptibility:** where the physiological response to/effect of one stressor increases the susceptibility to another stressor

**Cross-tolerance:** where the physiological response to/effect of one stressor increases the tolerance to another stressor

**Co-tolerance:** arises when species display correlated tolerances to multiple stressors at the community level (negative co-tolerance when tolerances are not correlated).

**Cue :** sensory information in the environment that indicates the presence or strength of a particular stressor.

**Escape:** A discrete, costly means by which to reduce stressor exposure. Draws energy from a reserve pool.

**Escape in Time:** (EIT) Accomplishes escape by substantially reducing activity, metabolism and energy assimilation.

**Escape in Space:** (EIS) Accomplishes escape by means of dispersal to a new location.

**Physiological Response:** A short-term response to one or more stressors involving immediate energy allocation to physiological functions.

**Stressor:** any environmental factor that has a negative effect on an organism's fitness through reduced growth, survivorship or reproduction

**Synergistic effect:** the combined effect of stressors is greater than what would be predicted under an additive model

### Box 2. Classification of multiple stressor combinations

Organisms can influence some stressors (that is, modify the strength or presence of the stressor) but not others. For example, an organism's avoidance behaviours can modify predator behaviour. In contrast, while ectotherms typically increase their foraging rates to cope with the energetic costs of increased metabolic rates resulting from elevated temperature (Portner and Kust 2007), this behavioural response does not alter the temperature itself. Here, we classify multiple stressor combinations into three forms depending on whether: A) the focal organism cannot modify either stressor (i.e. no feedback between the focal organism and the stressors); B) the organism can modify one stressor only (bi-directional feedback between a single stressor and the organism) or C) the organism can modify both stressors (bi-directional feedbacks between both stressors and the organism) (Figure 2). Stressor interactions and impacts on organisms can hinge on these categories.

In a Type A stressor combination, an organism can employ mechanisms to cope with stressor exposure, but it is unable to directly alter the strength or presence of either stressor, except via avoidance or escape in space or time. In a Type B stressor combination, an organism can modify one stressor but not the other. Notably, the stressor that the organism can modify could also be modified (e.g., its effect amplified or reduced) by the other stressor, meaning a biotic stressor such as a predator may be differently impacted by the abiotic

stressor than the prey (focal individual) (Allan *et al.* 2013; Allan *et al.* 2015). For example, crayfish predators were more negatively affected by the pesticide carbaryl than were their snail prey, which resulted in lower predation rates by crayfish upon snails (Reylea 2003). Finally, Type C depicts a combination of two stressors that an organism can modify through its behavior. Additionally, the stressors may directly (or indirectly) influence one another; e.g., interactions between predators (e.g. intraguild predation) can determine whether their combined effects on prey are additive, antagonistic or synergistic (also known as independent, risk reducing or risk enhancing effects) (Sih *et al.* 1998; Schmitz 2007).

### **Box 3: Multiple cues drive behavioral responses to multiple stressors**

Responses to dangers (e.g., running from predators) are typically elicited by sensory cues relating to that danger (e.g., seeing or hearing a predator). Thus, at a detailed level, it is the *cue* of the danger that really acts as the stressor (in terms of eliciting a response) in trade-offs 1-4, rather than the danger per se, though these are sometimes confounded when it comes to automatic physiological responses because the danger itself can also directly act as the cue (e.g., the physiological response of a fish following an increase in water temperature or salinity). Here, we consider the case of responses to possible predators, where it is the cues that drive responses, rather than the danger directly. This may initially seem very simple; however, unlike the physiological case of heat/salinity, we consider cases where multiple cues are present and no cue is perfectly reliable.

In many cases, action should be taken before an organism is certain of their situation. There are three cases relating to the source of the cues:

A common cause, so one best action (Fig. 3A)

Multiple cues may be produced by a single danger (e.g., a glimpse of a predator, combined with a faint whiff of its scent) (Hale *et al.* 2017) Such cases are relatively simple in that there is typically a single best response to such a danger, and the cues correlate positively with that danger, so the best response also correlates positively with the overall probability given by those cues.

Different causes, but one best action (Fig. 3B)

In some cases, there may be multiple uncertain cues of danger, each of which, alone, does not tell an organism to take evasive action, but together they do. For instance, a vole emerging from its hole may get the faint whiff of a cat (which may not be enough on its own to trigger a response of fleeing back to its hole), and a glimpse of a bird overhead (which alone, may not be sufficiently indicative of an aerial predator). Because the best response to each danger is the same (although the cues come from different sources), they can be combined to govern a stress response of fleeing (or of increasing one's physiological readiness to flee).

Different causes, with different best actions (Fig. 3C)

The more complex case is one where the best response to one danger (e.g., running from a terrestrial predator) conflicts with the best response to another danger (e.g., an aerial predator may be more likely to spot moving prey). In this case, the uncertainties relating to the cues interact with the expected payoffs for each possible action in each situation (Brilot *et al.* 2012). This can often mean that an action which is not optimal in either actual situation (terrestrial or aerial danger present) is the best while gathering more information. For instance, it may be best to freeze for a short time while gathering more information, even if climbing a tree would be the best defense against one danger, whilst running back toward one's burrow is best against another danger.

Cases (1) and (2) can usually be represented using simple (one dimensional) signal detection theory but, in general, the number of dimensions (required for a signal detection approach) increases with the number of possible dangers (even when there are only two possible actions). Thus, signal detection theory provides a robust framework that can be applied to systematically evaluate expectations for behavioral responses to the multiple- (often many-) stressor scenarios that abound in nature.

### **Box 4. Animal behavior can redefine 'multiple stressors'**

The concept of ‘multiple stressors’ traditionally deals with stressors that co-occur in time and space, and, thus, the affected organism is exposed to these stressors simultaneously. However, multiple stressors need not co-occur in time or space or affect a focal organism simultaneously to have interactive, potentially synergistic effects that determine the organism’s survival and fitness. A prime driver of such unexpected potential stressor interactions is animal behavior. By moving across natural landscapes that can exhibit extensive heterogeneity in the spatial distributions of stressors (e.g., involving variation in elevation, moisture, salinity, turbidity, pollution, natural and foreign predators), animals can determine the suite, relative exposure, sequence, and spatiotemporal overlap of stressors they will face. Thus, stressors separated in time or space or both (Fig. 5) can interact with one another indirectly at the organismal level, akin to analogous indirect interactions, such as apparent competition (Holt 1977) and apparent mutualism (Abrams *et al.* 1998; Rudolf 2008). Interactive effects of multiple stressors that do not co-occur over space and/or time expand the concept of multiple stressors and are candidate drivers of population declines in natural systems (Fig. 5).

For non-co-occurring stressors to interact at the organismal level requires that at least one stressor involved imposes at least one carryover effect: a physiological and/or behavioral effect of a stressor(s) that lingers after direct exposure ceases, allowing this stressor’s effect to interact with effects of future stressors. Carryover effects on physiological stressor responses have been observed in many systems; for example, bivalves have decreased immune response following temperature stress, which makes them more susceptible to disease-based stressors (Rahman *et al.* 2019). Damsel fly larvae previously exposed to food limitation and heat waves suffered considerably lower growth rates and higher mortality when later exposed to an agricultural pesticide (Dinh *et al.* 2016). Behavioral carryover effects have also been observed: e.g., tadpoles from high-risk environments are generally more active, which increased survival in response to pursuit predators in the future (Ferrari *et al.* 2015).

Carryover effects may be particularly pronounced for stressors experienced during development. Experience with a stressor can lead to acclimation via phenotypic (either physiological or behavioral) plasticity such that the effect of experience with that stressor in the future is altered. Indeed, such developmental experience can lead to permanent changes in behaviour or physiology, resulting in improved performance in the presence of the stressor(s) later in life (Schnurr *et al.* 2014). For example, the keystone sea hare species, *Stylochelium striatus*, significantly reduced its locomotion speed and rate of correct foraging decisions following exposure to elevated temperature and  $p$  CO<sub>2</sub>. While exposure to these stressors during development still resulted in decreased performance in adults, developmental exposure lessened the severity of the impacts, suggesting beneficial phenotypic plasticity (Horwitz *et al.* 2020).

The carryover effects of developmental exposure to a single stressor on responses to different, future stressors is less well understood despite the potentially impactful changes to organisms as a result of acclimation. For instance, warm-acclimated common minnows (*Phoxinus phoxinus*) had larger brains compared to cool-acclimated fish but made more errors in exploring a maze, suggesting that maintaining physiological function under stress can result in cognitive impairments (Zavoroka *et al.* 2020). Developmental stress has been shown to affect a variety of behaviors including foraging (Crino *et al.* 2014; Chaby *et al.* 2015), learning (Brust *et al.* 2014; Kriengwatana *et al.* 2015), social network position (Boogert *et al.* 2014) and the development of behavioral syndromes (Edenbrow & Croft 2013; Hope *et al.* 2020) that may interact with the ability to respond to future challenges.

Though far less studied, carryover effects can also manifest over much shorter timescales, with the sequence and relative magnitude of stressor exposure determined not by temporal variation in the stressors themselves, but instead by temporal variation in spatial patch use by the focal animal. By simply moving through its home range or migrating between distant locations, an animal can be affected by spatially or temporally separate stressors at sufficiently close points in time for interactions to manifest. For example, rainbow trout (*Oncorhynchus mykiss*) use shelters to avoid predators, however, when they compete for shelters they are at an increased risk of contracting trematode parasites from outside habitat patches (Mikheev *et al.* 2020).

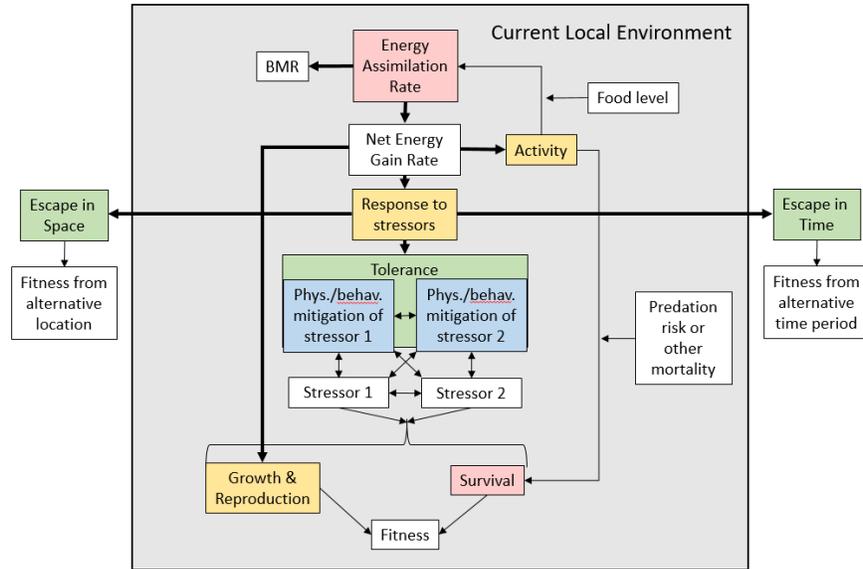
### **Box 5: How behavior can shape stressor effects on communities**

Behavioural responses to stressors can have important indirect implications for community structure and function (Figure 5). Adaptive responses to stressors often involve shifts in foraging or antipredator behaviour that change the functional role of organisms within the food-web. For instance, in response to stress, herbivores may shift their diet preference to select plants with higher rich, digestible carbohydrates to achieve nutritional and homeostatic balance. This selective herbivory not only changes the plant community composition, but has consequences for nutrient cycling and energy flow, because it alters the elemental composition and non-processed plant litter reaching the detrital pool (Hawlena & Schmitz 2010). Importantly, however, such behavioural responses to environmental stressors, and the corresponding ramifications for communities, are largely mediated by how these stressors alter species interactions, such as predator-prey dynamics, competition and mutualisms (Miller *et al.* 2014; Thompson *et al.* 2018). Understanding how stressors impact behaviorally mediated species interactions is essential for predicting when synergistic interactions will arise, but this fundamental aspect of ecology is often absent from multiple stressor studies (Tylianakis *et al.* 2008; Thompson *et al.* 2018).

If stressors hit predators harder than prey, stressors can benefit prey and moderate both the individual and combined effects of stressors by allowing prey to feed with reduced risk, and divert energy into other life-history and physiological processes (Francis *et al.* 2009; White *et al.* 2018). If stressors specifically inhibit keystone predators, however, this can lead to the restructuring or collapse of entire ecosystems (Breitburg *et al.* 1998; Rumschlag *et al.* 2019). For example, the combination of organophosphate insecticides and triazine herbicides dramatically increased trematode pathogens in pond mesocosms, because these conditions favoured populations of the intermediate host (snails) by reducing the top-down behaviorally- and density-mediated effects of their predators and increasing periphyton food abundance (Rumschlag *et al.* 2019). In contrast, if stressors disproportionately change the behavior and feeding ecology of prey, for instance, by increasing their foraging activity or reducing antipredator responses, predation rates are likely to increase, leading to stronger top-down effects on intermediate consumers (Shears & Ross 2010; Miller *et al.* 2014).

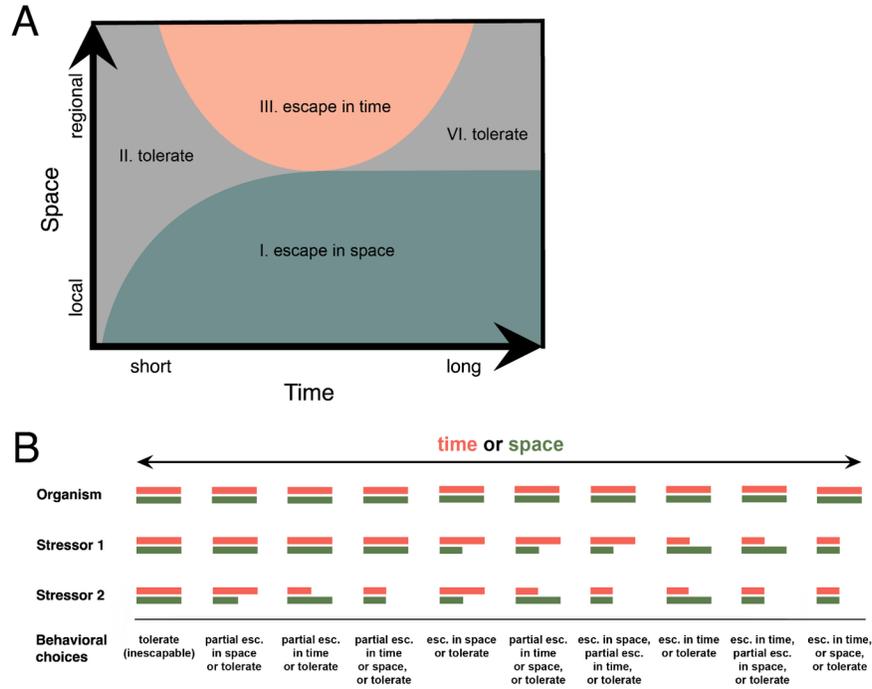
Single and multiple stressors can also directly and indirectly disrupt mutualisms (Hegland *et al.* 2009; Schweiger *et al.* 2010). Changes in the timing and spatial synchronicity of species behavioural patterns in response to stress may lower species co-occurrence rates leading to the deterioration of mutualistic interactions (Hegland *et al.* 2009, Schweiger *et al.* 2010, Figure III). Furthermore, negative impacts of stressors on a single member of a mutualism can have large costs for other members, including indirect beneficiaries of the mutualism (Hegland *et al.* 2009; Schweiger *et al.* 2010; Barton & Ives 2014). For example, the negative impact of agricultural pesticides on honeybee foraging behaviour and colony health can reduce plant numbers (via reduced pollination) and, in turn, have negative effects on herbivores (Goulson *et al.* 2015; Tosi *et al.* 2017). Alternatively, mutualisms can help buffer ecosystems against negative effects of environmental stress (Thompson *et al.* 2018). For instance, an ant-aphid mutualism can protect plants from indirect effects of increasing temperatures by limiting positive-effects of rising temperatures on the abundance of pest predator species (Marquis *et al.* 2014).

Multiple stressor effects on communities are difficult to predict but are likely contingent upon the degree of tolerance and co-tolerance of species and functional groups to those stressors (Vinebrooke *et al.* 2004), as well as the trophic level(s) upon which these stressors have the greatest impact. In situations when key functional groups or species are particularly sensitive to stressors and are subsequently reduced or eliminated from the community pool, pronounced behavioural and numerical effects can propagate across trophic levels if the ecosystem functionality of those groups is not replaced (Galic *et al.* 2018; Dib *et al.* 2020). On the other hand, when remaining species can compensate functionally for this loss, stressor effects tend to be weakened across trophic levels, leading to more resistant communities (Jackson *et al.* 2016).

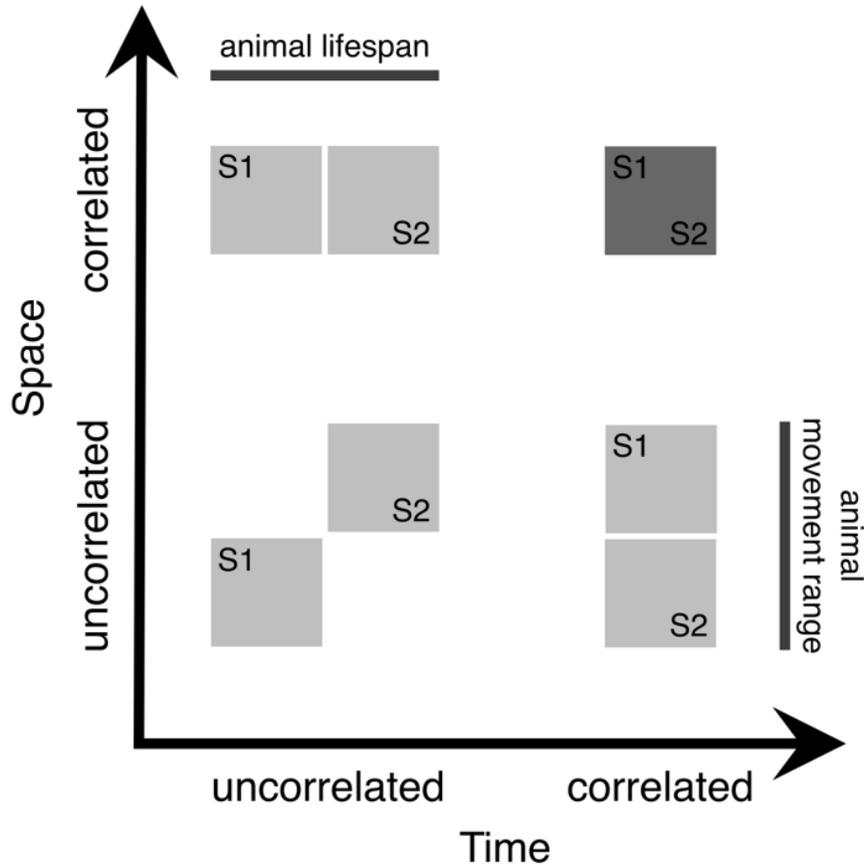


**Figure 1.** Conceptual Framework: integrating the behavior, physiology, and bioenergetics of coping with multiple stressors. Energy is allocated among key components (thick arrows) leading ultimately to fitness effects; the 4 key trade-offs are color-coded. Assimilated Energy pays the energy cost of basal metabolism (BMR), and the remaining Net Energy Gain Rate is subdivided into three competing energy sinks (yellow rectangles, trade-off 3). The energy flow into response to stressors powers two types of escape plus tolerance (green rectangles, trade-off 4). Stressor Tolerance provides energy for the mechanisms to avoid when possible or otherwise to mitigate the stressor effects. These mechanisms may be behavioral or physiological or both (blue rectangles, trade-off 1); they are triggered by the Stressors and ameliorate them while potentially interacting with each other. Activity creates a trade-off between Energy Assimilation Rate and Survival (pink rectangles, trade-off 2). Food Availability and Risk of Predation or Other Mortality sources potentially increased by activity act on these linkages. Survival and Growth/Reproduction are influenced by the Stressors and Coping Mechanisms, jointly yielding Fitness.

**Figure 2 .** Categories of multiple stressor combination types according to degrees of feedback between stressor(s) and focal organisms from A) no feedback, B) uni-directional feedback and C) bi-directional feedback.



**Figure 3.** Trade-offs and choices associated with stressors in time and space. (A) When a single stressor, or a combination of multiple stressors that co-occur in time and space, is highly constrained in space (e.g., it affects a small patch of habitat), costs of avoidance in space are low, and, thus, escape in space should be the optimal choice (I). If the stressor duration is very short and its spatial scale is not very local, it should generally be optimal to tolerate the stressor (II), rather than invest in escape in time. However, as stressor duration increases, it can become optimal to escape in time (III), and this choice is more likely to be optimal when the stressor occurs over a greater spatial scale (i.e., the stressor is experienced more by the organism in space). However, when the stressor duration is very long (and it is large-scale), escape in time is impractical (as is escape in space), and so tolerance is the optimal choice (IV). (B) The relative spatial (pink [light] bars) and temporal (green [dark] bars) scales over which an organism and each of two stressors operate determine the set of behavioral choices available to the organism. When the spatial or temporal extent of a stressor overlaps with but is less than that of the organism (i.e., the time or space bar is shorter than that of the organism), the organism can choose to avoid the stressor in space or time, respectively. The optimal choice will depend on the relative costs of escape and tolerance. If, instead, the spatial or temporal extent of either stressor matches or exceeds that of the organism, it is left with fewer behavioral choices. Note: this is a subset of qualitatively distinct scenarios in which an organism can experience effects of multiple stressors that are at least partially correlated in space and time; allowing the pair of stressors to be completely uncorrelated greatly expands the number of possible unique scenarios.



**Figure 4.** Animal behaviour can redefine ‘multiple stressor’ scenarios: When effects of stressors carry over into periods of time when the stressors are not present, this allows multiple stressors that are not correlated in time and/or space to nonetheless have ‘co-occurring effects’ on mobile organisms. Here, stressor 1 (S1) and stressor 2 (S2) co-occur in time and space (top right), co-occur in space only (top right), co-occur in time only (bottom right), or neither co-occur in time or space (bottom left). In these latter two scenarios, animal movement and space-use decisions can cause ‘multiple stressor effects’ if at least the first stressor experienced has carryover effects. The optimal decision (e.g., be active vs. inactive, move to an area with one stressor or an area with the other) in each of these scenarios depends on costs of avoidance in space or time and the relative strengths of stressor effects.

#### Hosted file

image4.emf available at <https://authorea.com/users/393011/articles/506749-integrating-animal-behaviour-into-research-on-multiple-environmental-stressors-a-conceptual-framework>

**Figure 5.** Two hypothetical scenarios of how stressor effects can propagate across trophic levels leading to complex community outcomes and disruption of species interactions. (**Scenario A**) Stressor A may disproportionately affect a single functional level (e.g. a keystone predator) which has positive indirect benefits for a consumer and negative

indirect benefits on a producer. Stressor A, for example, may cause high physiological stress in the predator leading to reduced activity and hunting, thus releasing the consumer from density and trait mediated effects of the predator. Even though stressor A also has a physiological cost on the consumer, this cost is exceeded by the benefits associated with lower predation risk and increased foraging opportunities. Conversely, the

direct negative effects of stressor A combined with increased top-down effects from consumers, may lead to negative synergistic effects on producers. (**Scenario B**) Stressor B disrupts the sensory capability of a specialist pollinator leading to decreased foraging activity and pollination of ‘plant A’. A key seed disperser which prefers a diet of ‘plant A’, switches their primary diet to fruits of ‘plant B’ due to a reduction in the availability of ‘plant A’. ‘Plant B’ now benefits both from increased seed dispersal and decreased space competition from ‘plant A’ leading to a fundamental shift in the composition of the plant community. Line thickness denotes size of the stressor effect. Positive/negative symbols represent stressor net effects on each trophic node.

## REFERENCES

- Abrams, P.A., Holt, R.D. & Roth, J.D. (1998). Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology* , 79, 201-212.
- Allan, B.J.M., Domenici, P., McCormick, M.I., Watson, S.A. & Munday, P.L. (2013). Elevated CO<sub>2</sub> Affects Predator-Prey Interactions through Altered Performance. *Plos One* , 8.
- Allan, B.J.M., Domenici, P., Munday, P.L. & McCormick, M.I. (2015). Feeling the heat: the effect of acute temperature changes on predator-prey interactions in coral reef fish. *Conserv. Physiol.* , 3.
- Andersson, M. (1994). *Sexual Selection* . Princeton University Press.
- Barton, B.T. & Ives, A.R. (2014). Direct and indirect effects of warming on aphids, their predators, and ant mutualists. *Ecology* , 95, 1479-1484.
- Beermann, A.J., Elbrecht, V., Karnatz, S., Ma, L., Matthaei, C.D., Piggott, J.J. *et al.* (2018). Multiple-stressor effects on stream macroinvertebrate communities: A mesocosm experiment manipulating salinity, fine sediment and flow velocity. *Sci. Total Environ.* , 610-611, 961-971.
- Bell, A.M. & Hellmann, J.K. (2019). An Integrative Framework for Understanding the Mechanisms and Multigenerational Consequences of Transgenerational Plasticity. In: *Annual Review of Ecology, Evolution, and Systematics, Vol 50* (ed. Futuyama, DJ), pp. 97-118.
- Beppler, C., Tekin, E., Mao, Z.Y., White, C., McDiarmid, C., Vargas, E. *et al.* (2016). Uncovering emergent interactions in three-way combinations of stressors. *Journal of the Royal Society Interface* , 13, 1-11.
- Berg, M.P., Kiers, E.T., Driessen, G., van der Heijden, M., Kooi, B.W., Kuenen, F. *et al.* (2010). Adapt or disperse: understanding species persistence in a changing world. *Glob. Change Biol.* , 16, 587-598.
- Biro, P.A. & Stamps, J.A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution* , 23, 361-368.
- Bonte, D. & Doherty, M. (2017). Dispersal: a central and independent trait in life history. *Oikos* , 126, 472-479.
- Bonte, D. & de la Pena, E. (2009). Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology* , 22, 1242-1251.
- Boogert, N.J., Farine, D.R. & Spencer, K.A. (2014). Developmental stress predicts social network position. *Biology Letters* , 10.
- Boone, M.D., Semlitsch, R.D., Little, E.E. & Doyle, M.C. (2007). Multiple stressors in amphibian communities: effects of chemical contamination, bullfrogs, and fish. *Ecological Applications* , 17, 291-301.
- Breitburg, D.L., Baxter, J.W., Hatfield, C.A., Howarth, R.W., Jones, C.G., Lovett, G.M. *et al.* (1998). Understanding effects of multiple stressors: ideas and challenges. In: *Successes, limitations, and frontiers in ecosystem science.* (eds. M.L., P & P.M., G). Springer New York, NY, pp. 416-431.
- Brilot, B.O., Bateson, M., Nettle, D., Whittingham, M.J. & Read, J.C.A. (2012). When is general wariness favored in avoiding multiple predator types? *The American Naturalist* 179, 180-195.

- Brown, J.S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. . *Evolutionary Ecology Research* , 1, 49-71.
- Bruder, A., Salis, R.K., Jones, P.E. & Matthaei, C.D. (2017). Biotic interactions modify multiple-stressor effects on juvenile brown trout in an experimental stream food web. *Glob. Change Biol.* , 23, 3882-3894.
- Brust, V., Kruger, O., Naguib, M. & Krause, E.T. (2014). Lifelong consequences of early nutritional conditions on learning performance in zebra finches (*Taeniopygia guttata* ). *Behav. Processes* , 103, 320-326.
- Byrne, M. & Przeslawski, R. (2013). Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. *Integrative and Comparative Biology* , 53, 582-596.
- Cambronero, M.C., Marshall, H., De Meester, L., Davidson, T.A., Beckerman, A.P. & Orsini, L. (2018). Predictability of the impact of multiple stressors on the keystone species *Daphnia*. *Scientific Reports* , 8, 11.
- Chaby, L.E., Sheriff, M.J., Hirrlinger, A.M. & Braithwaite, V.A. (2015). Does early stress prepare individuals for a stressful future? Stress during adolescence improves foraging under threat. *Animal Behaviour* , 105, 37-45.
- Chapman, R.F. (1998). *The Insects: Structure and Function*, . Cambridge University Press.
- Chatelain, M., Drobniak, S.M. & Szulkin, M. (2020). The association between stressors and telomeres in non-human vertebrates: a meta-analysis. *Ecology Letters* , 23, 381-398.
- Clusella-Trullas, S. & Chown, S.L. (2014). Lizard thermal trait variation at multiple scales: a review. *Journal of Comparative Physiology B-Biochemical Systems and Environmental Physiology* , 184, 5-21.
- Correa-Araneda, F., Basaguren, A., Abdala-Diaz, R.T., Tonin, A.M. & Boyero, L. (2017). Resource-allocation trade-offs in caddisflies facing multiple stressors. *Ecology and Evolution* , 7, 5103-5110.
- Cote, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B-Biological Sciences* , 283.
- Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B-Biological Sciences* , 365, 4065-4076.
- Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* , 11, 1304-1315.
- Crino, O.L., Driscoll, S.C., Ton, R. & Breuner, C.W. (2014). Corticosterone exposure during development improves performance on a novel foraging task in zebra finches. *Animal Behaviour* , 91, 27-32.
- Crowley, P.H., Trimmer, P.C., Spiegel, O., Ehlman, S.M., Cuello, W.S. & Sih, A. (2019). Predicting habitat choice after rapid environmental change. *The American Naturalist* , 193, 619-632.
- Danks, H.V. (2000). Dehydration in dormant insects. *Journal of Insect Physiology* , 46, 837-852.
- De Coninck, D.I.M., De Schampelaere, K.A.C., Jansen, M., De Meester, L. & Janssen, C.R. (2013). Interactive effects of a bacterial parasite and the insecticide carbaryl to life-history and physiology of two *Daphnia magna* clones differing in carbaryl sensitivity. *Aquatic Toxicology* , 130, 149-159.
- Delnat, V., Tran, T.T., Janssens, L. & Stoks, R. (2019). Daily temperature variation magnifies the toxicity of a mixture consisting of a chemical pesticide and a biopesticide in a vector mosquito. *Sci. Total Environ.* , 659, 33-40.
- Dib, V., Pires, A.P.F., Nova, C.C., Bozelli, R.L. & Farjalla, V.F. (2020). Biodiversity-mediated effects on ecosystem functioning depend on the type and intensity of environmental disturbances. *Oikos* , 129, 433-443.

- Dieleman, W.I.J., Vicca, S., Dijkstra, F.A., Hagedorn, F., Hovenden, M.J., Larsen, K.S. *et al.* (2012). Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO<sub>2</sub> and temperature. *Glob. Change Biol.* , 18, 2681-2693.
- Dinh, K.V., Janssens, L. & Stoks, R. (2016). Exposure to a heat wave under food limitation makes an agricultural insecticide lethal: a mechanistic laboratory experiment. *Glob. Change Biol.* , 22, 3361-3372.
- Domis, L.N.D., Elser, J.J., Gsell, A.S., Huszar, V.L.M., Ibelings, B.W., Jeppesen, E. *et al.* (2013). Plankton dynamics under different climate conditions in tropical freshwater systems (a reply to the comment by Sarmiento, Amado & Descy, 2013). *Freshwater Biology* , 58, 2211-2213.
- Edenbrow, M. & Croft, D.P. (2013). Environmental and genetic effects shape the development of personality traits in the mangrove killifish *Kryptolebias marmoratus* . *Oikos* , 122, 667-681.
- Einum, S. & Fleming, I.A. (1999). Maternal effects of egg size in brown trout (*Salmo trutta* ): norms of reaction to environmental quality. *Proceedings of the Royal Society B-Biological Sciences* , 266, 2095-2100.
- Ferrari, M.C.O., Munday, P.L., Rummer, J.L., McCormick, M.I., Corkill, K., Watson, S.A. *et al.* (2015). Interactive effects of ocean acidification and rising sea temperatures alter predation rate and predator selectivity in reef fish communities. *Glob. Change Biol.* , 21, 1848-1855.
- Fey, S.B., Vasseur, D.A., Alujevic, K., Kroeker, K.J., Logan, M.L., O'Connor, M.I. *et al.* (2019). Opportunities for behavioral rescue under rapid environmental change. *Glob. Change Biol.* , 25, 3110-3120.
- Francis, C.D., Ortega, C.P. & Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Current Biology* , 19, 1415-1419.
- Galic, N., Sullivan, L.L., Grimm, V. & Forbes, V.E. (2018). When things don't add up: quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. *Ecology Letters* , 21, 568-577.
- Garcia, T.S., Stacy, J. & Sih, A. (2004). Larval salamander response to uv radiation and predation risk: Color change and microhabitat use. *Ecological Applications* , 14, 1055-1064.
- Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* , 360, 1232-1235.
- Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Review of Physiology* , 66, 239-274.
- Goto, M., Sekine, Y., Outa, H., Hujikura, M. & Suzuki, K. (2001). Relationships between cold hardiness and diapause, and between glycerol and free amino acid contents in overwintering larvae of the oriental corn borer, *Ostrinia furnacalis*. *Journal of Insect Physiology* , 47, 157-165.
- Goulson, D., Nicholls, E., Botias, C. & Rotheray, E.L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* , 347, 10.
- Hairston Jr., N.G. & Fox, J.A. (2009). Egg Banks. In: *Encyclopedia of Inland Waters* (ed. Likens, GE). Academic Press New York.
- Hale, R., Piggott, J.J. & Swearer, S.E. (2017). Describing and understanding behavioral responses to multiple stressors and multiple stimuli. *Ecology and Evolution* , 7, 38-47.
- Hawlena, D. & Schmitz, O.J. (2010). Physiological Stress as a Fundamental Mechanism Linking Predation to Ecosystem Functioning. *American Naturalist* , 176, 537-556.
- Hayden, M.T., Reeves, M.K., Holyoak, M., Perdue, M., King, A.L. & Tobin, S.C. (2015). Thrive as easy to catch! Copper and temperature modulate predator-prey interactions in larval dragonflies and anurans. *Ecosphere* , 6.

- Hegland, S.J., Nielsen, A., Lazaro, A., Bjercknes, A.L. & Totland, O. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters* , 12, 184-195.
- Hettinger, A., Sanford, E., Hill, T.M., Hosfelt, J.D., Russell, A.D. & Gaylord, B. (2013). The influence of food supply on the response of *Olympia* oyster larvae to ocean acidification. *Biogeosciences* , 10, 6629-6638.
- Hintz, W.D., Jones, D.K. & Relyea, R.A. (2019). Evolved tolerance to freshwater salinization in zooplankton: life-history trade-offs, cross-tolerance and reducing cascading effects. *Philosophical Transactions of the Royal Society B-Biological Sciences* , 374, 10.
- Holmstrup, M., Bindesbol, A.M., Oostingh, G.J., Duschl, A., Scheil, V., Kohler, H.R. *et al.* (2010). Interactions between effects of environmental chemicals and natural stressors: A review. *Sci. Total Environ.* , 408, 3746-3762.
- Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* , 12, 197-229.
- Hope, B.V., Fjellner, K.L., Renn, S.C.P. & Hurd, P.L. (2020). Juvenile stress disrupts the development of an exploration-boldness behavioural syndrome in convict cichlid fish. *Animal Behaviour* , 161, 95-102.
- Horwitz, R., Norin, T., Watson, S.A., Pistevos, J.C.A., Beldade, R., Hacquart, S. *et al.* (2020). Near-future ocean warming and acidification alter foraging behaviour, locomotion, and metabolic rate in a keystone marine mollusc. *Scientific Reports* , 10.
- Houston, A.I. & McNamara, J.M. (1999). *Models of adaptive behaviour, an approach based on state*. Cambridge University Press, Cambridge, UK.
- Humphries, M.M., Thomas, D.W. & Kramer, D.L. (2003). The role of energy availability in mammalian hibernation: A cost-benefit approach. *Physiological and Biochemical Zoology* , 76, 165-179.
- Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Glob. Change Biol.* , 22, 180-189.
- Jager, T., Barsi, A. & Ducrot, V. (2013). Hormesis on life-history traits: is there such thing as a free lunch? *Ecotoxicology* , 22, 263-270.
- Killen, S.S., Fu, C., Wu, Q.Y., Wang, Y.X. & Fu, S.J. (2016). The relationship between metabolic rate and sociability is altered by food deprivation. *Functional Ecology* , 30, 1358-1365.
- Killen, S.S., Marras, S., Metcalfe, N.B., McKenzie, D.J. & Domenici, P. (2013). Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology & Evolution* , 28, 651-658.
- Kriengwatana, B., Farrell, T.M., Aitken, S.D.T., Garcia, L. & MacDougall-Shackleton, S.A. (2015). Early-life nutritional stress affects associative learning and spatial memory but not performance on a novel object test. *Behaviour* , 152, 195-218.
- Lange, K., Bruder, A., Matthaei, C.D., Brodersen, J. & Paterson, R.A. (2018). Multiple-stressor effects on freshwater fish: Importance of taxonomy and life stage. *Fish and Fisheries* , 19, 974-983.
- Levin, S.A., Cohen, D. & Hastings, A. (1984). Dispersal strategies in patchy environments. *Theoretical Population Biology* , 26, 165-191.
- Lienart, G.D.H., Mitchell, M.D., Ferrari, M.C.O. & McCormick, M.I. (2014). Temperature and food availability affect risk assessment in an ectotherm. *Animal Behaviour* , 89, 199-204.
- Lima, S.L. (1998). Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. In: *Stress and Behavior* (eds. Moller, AP, Milinski, M & Slater, PJB), pp. 215-290.

- Luttbeg, B. & Sih, A. (2010). Risk, resources and state- dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B-Biological Sciences* , 365, 3977-3990.
- MacMillan, H.A., Walsh, J.P. & Sinclair, B.J. (2009). The effects of selection for cold tolerance on cross-tolerance to other environmental stressors in *Drosophila melanogaster*. *Insect Science* , 16, 263-276.
- Marquis, M., Del Toro, I. & Pelini, S.L. (2014). Insect mutualisms buffer warming effects on multiple trophic levels. *Ecology* , 95, 9-13.
- Martin, J.M., Saaristo, M., Bertram, M.G., Lewis, P.J., Coggan, T.L., Clarke, B.O. *et al.* (2017). The psychoactive pollutant fluoxetine compromises antipredator behaviour in fish. *Environ. Pollut.* , 222, 592-599.
- Martin, T.E. (1995). Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* , 65, 101-127.
- Mayor, D.J., Sommer, U., Cook, K.B. & Viant, M.R. (2015). The metabolic response of marine copepods to environmental warming and ocean acidification in the absence of food. *Scientific Reports* , 5.
- McCue, M.D. (2010). Starvation physiology: Reviewing the different strategies animals use to survive a common challenge. *Comp. Biochem. Physiol. A-Mol. Integr. Physiol.* , 156, 1-18.
- McEwen, B.S. & Wingfield, J.C. (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior* , 43, 2-15.
- Mikheev, V.N., Pasternak, A.F., Morozov, A.Y. & Taskinen, J. (2020). Innate antipredator behavior can promote infection in fish even in the absence of predators. *Behavioral Ecology* , 31, 267-276.
- Miler, K., Stec, D. & Czarnoleski, M. (2020). Heat wave effects on the behavior and life-history traits of sedentary antlions. *Behavioral Ecology* .
- Miller, L.P., Matassa, C.M. & Trussell, G.C. (2014). Climate change enhances the negative effects of predation risk on an intermediate consumer. *Glob. Change Biol.* , 20, 3834-3844.
- Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C. *et al.* (2020). Towards a unified study of multiple stressors: divisions and common goals across research disciplines. *Proceedings of the Royal Society B-Biological Sciences* , 287.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H. *et al.* (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* , 399, 579-583.
- Petitjean, Q., Jean, S., Gandar, A., Cote, J., Laffaille, P. & Jacquin, L. (2019). Stress responses in fish: From molecular to evolutionary processes. *Sci. Total Environ.* , 684, 371-380.
- Pincebourde, S., Sanford, E., Casas, J. & Helmuth, B. (2012). Temporal coincidence of environmental stress events modulates predation rates. *Ecology Letters* , 15, 680-688.
- Polo-Cavia, N., Burraco, P. & Gomez-Mestre, I. (2016). Low levels of chemical anthropogenic pollution may threaten amphibians by impairing predator recognition. *Aquatic Toxicology* , 172, 30-35.
- Portner, H.O. & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* , 315, 95-97.
- Przeslawski, R., Byrne, M. & Mellin, C. (2015). A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. *Glob. Change Biol.* , 21, 2122-2140.
- Rahman, M.A., Henderson, S., Miller-Ezzy, P., Li, X.X. & Qin, J.G. (2019). Immune response to temperature stress in three bivalve species: Pacific oyster *Crassostrea gigas* , Mediterranean mussel *Mytilus galloprovincialis* and mud cockle *Katelysia rhytiphora* . *Fish & Shellfish Immunology* , 86, 868-874.

- Rattan, S. & Flaws, J.A. (2019). The epigenetic impacts of endocrine disruptors on female reproduction across generations. *Biology of Reproduction* , 101, 635-644.
- Reale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B-Biological Sciences* , 365, 4051-4063.
- Reale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews* , 82, 291-318.
- Reeves, M.K., Jensen, P., Dolph, C.L., Holyoak, M. & Trust, K.A. (2010). Multiple stressors and the cause of amphibian abnormalities. *Ecological Monographs* , 80, 423-440.
- Rinehart, S. & Hawlena, D. (2020). The effects of predation risk on prey stoichiometry: a meta-analysis. *Ecology* , 101.
- Rivrud, I.M., Bischof, R., Meisingset, E.L., Zimmermann, B., Loe, L.E. & Mysterud, A. (2016). Leave before it's too late: anthropogenic and environmental triggers of autumn migration in a hunted ungulate population. *Ecology* , 97, 1058-1068.
- Roff, D. (2002). *Life History Evolution*. Oxford University Press, Oxford, UK.
- Rohr, J.R., Elskus, A.A., Shepherd, B.S., Crowley, P.H., McCarthy, T.M., Niedzwiecki, J.H. *et al.* (2004). Multiple stressors and salamanders: Effects of an herbicide, food limitation, and hydroperiod. *Ecological Applications* , 14, 1028-1040.
- Rohr, J.R., Sesterhenn, T.M. & Stieha, C. (2011). Will climate change reduce the effects of a pesticide on amphibians?: partitioning effects on exposure and susceptibility to contaminants. *Glob. Change Biol.* , 17, 657-666.
- Romero, L.M., Dickens, M.J. & Cyr, N.E. (2009). The reactive scope model - A new model integrating homeostasis, allostasis, and stress. *Hormones and Behavior* , 55, 375-389.
- Rudolf, V.H.W. (2008). Impact of cannibalism on predator-prey dynamics: Size-structured interactions and apparent mutualism. *Ecology* , 89, 1650-1660.
- Rumschlag, S.L., Halstead, N.T., Hoverman, J.T., Raffel, T.R., Carrick, H.J., Hudson, P.J. *et al.* (2019). Effects of pesticides on exposure and susceptibility to parasites can be generalised to pesticide class and type in aquatic communities. *Ecology Letters* , 22, 962-972.
- Sarmaja-Korjonen, K. (2003). Chydorid ephippia as indicators of environmental change - biostratigraphical evidence from two lakes in southern Finland. *Holocene* , 13, 691-700.
- Sawyer, H., Middleton, A.D., Hayes, M.M., Kauffman, M.J. & Monteith, K.L. (2016). The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. *Ecosphere* , 7.
- Schmitz, O.J. (2007). Predator diversity and trophic interactions. *Ecology* , 88, 2415-2426.
- Schmitz, O.J., Miller, J.R.B., Trainor, A.M. & Abrahms, B. (2017). Toward a community ecology of landscapes: predicting multiple predator-prey interactions across geographic space. *Ecology* , 98, 2281-2292.
- Schnurr, M.E., Yin, Y. & Scott, G.R. (2014). Temperature during embryonic development has persistent effects on metabolic enzymes in the muscle of zebrafish. *Journal of Experimental Biology* , 217, 1370-1380.
- Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S. *et al.* (2010). Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews* , 85, 777-795.

- Sears, M.W., Angilletta, M.J., Schuler, M.S., Borchert, J., Dilliplane, K.F., Stegman, M. *et al.* (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences of the United States of America* , 113, 10595-10600.
- Shears, N.T. & Ross, P.M. (2010). Toxic cascades: multiple anthropogenic stressors have complex and unanticipated interactive effects on temperate reefs. *Ecology Letters* , 13, 1149-1159.
- Sievers, M., Hale, R., Swearer, S.E. & Parris, K.M. (2018). Contaminant mixtures interact to impair predator-avoidance behaviours and survival in a larval amphibian. *Ecotoxicology and Environmental Safety* , 161, 482-488.
- Sih, A. (1987). Predators and prey lifestyles: an evolutionary and ecological overview. In: *Predation: direct and indirect impacts on aquatic communities*. (eds. Kerfoot, WC & Sih, A). University Press of New England Hanover, NH, pp. 203-224.
- Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology* , 79, 241-277.
- Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters* , 15, 278-289.
- Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution* , 13, 350-355.
- Sinclair, B.J., Ferguson, L.V., Salehipour-shirazi, G. & MacMillan, H.A. (2013). Cross-tolerance and cross-talk in the cold: relating low temperatures to desiccation and immune stress in insects. *Integrative and Comparative Biology* , 53, 545-556.
- Smirnov, N.N. (2014). *The physiology of Cladocera* . Academic Press, Amsterdam.
- Snyder, R.E. (2006). Multiple risk reduction mechanisms: can dormancy substitute for dispersal? *Ecology Letters* , 9, 1106-1114.
- Stoks, R. (2001). Food stress and predator-induced stress shape developmental performance in a damselfly. *Oecologia* , 127, 222-229.
- Stuligross, C. & Williams, N.M. (2020). Pesticide and resource stressors additively impair wild bee reproduction. *Proceedings. Biological sciences* , 287, 20201390.
- Thomas, D.W., Dorais, M. & Bergeron, J.M. (1990). Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus* . *Journal of Mammalogy* , 71, 475-479.
- Thompson, P.L., MacLennan, M.M. & Vinebrooke, R.D. (2018). Species interactions cause non-additive effects of multiple environmental stressors on communities. *Ecosphere* , 9.
- Todgham, A.E., Schulte, P.M. & Iwama, G.K. (2005). Cross-tolerance in the tidepool sculpin: The role of heat shock proteins. *Physiological and Biochemical Zoology* , 78, 133-144.
- Tosi, S., Nieh, J.C., Sgolastra, F., Cabbri, R. & Medrzycki, P. (2017). Neonicotinoid pesticides and nutritional stress synergistically reduce survival in honey bees. *Proceedings of the Royal Society B-Biological Sciences* , 284.
- Tran, T.T., Van, K.D., Janssens, L. & Stoks, R. (2020). The effect of warming on pesticide toxicity is reversed between developmental stages in the mosquito *Culex pipiens*. *Sci. Total Environ.* , 717, 10.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters* , 11, 1351-1363.
- Van de Waal, D.B. & Litchman, E. (2020). Multiple global change stressor effects on phytoplankton nutrient acquisition in a future ocean. *Philosophical Transactions of the Royal Society B-Biological Sciences* , 375, 8.

- Van der Putten, W.H., Macel, M. & Visser, M.E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B-Biological Sciences* , 365, 2025-2034.
- van der Vinne, V., Tachinardi, P., Riede, S.J., Akkerman, J., Scheepe, J., Daan, S. *et al.* (2019). Maximising survival by shifting the daily timing of activity. *Ecology Letters* , 22, 2097-2102.
- Vinebrooke, R.D., Cottingham, K.L., Norberg, J., Scheffer, M., Dodson, S.I., Maberly, S.C. *et al.* (2004). Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos* , 104, 451-457.
- Watson, S.A., Allan, B.J.M., McQueen, D.E., Nicol, S., Parsons, D.M., Pether, S.M.J. *et al.* (2018). Ocean warming has a greater effect than acidification on the early life history development and swimming performance of a large circumglobal pelagic fish. *Glob. Change Biol.* , 24, 4368-4385.
- White, L., Donohue, I., Emmerson, M.C. & O'Connor, N.E. (2018). Combined effects of warming and nutrients on marine communities are moderated by predators and vary across functional groups. *Glob. Change Biol.* , 24, 5853-5866.
- Wingfield, J.C. (2013). Ecological processes and the ecology of stress: the impacts of abiotic environmental factors. *Functional Ecology* , 27, 37-44.
- Yue, K., Fornara, D.A., Yang, W.Q., Peng, Y., Li, Z.J., Wu, F.Z. *et al.* (2017). Effects of three global change drivers on terrestrial C:N:P stoichiometry: a global synthesis. *Glob. Change Biol.* , 23, 2450-2463.
- Zavorka, L., Koeck, B., Armstrong, T.A., Soganci, M., Crespel, A. & Killen, S.S. (2020). Reduced exploration capacity despite brain volume increase in warm-acclimated common minnow. *Journal of Experimental Biology* , 223.