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, how behavioural and life-history plasticity mediate multiple-stressor effects remains underexplored. Behavioural plasticity can not only drive organism-level responses to stressors directly but can also mediate physiological responses. Here, we provide a conceptual framework incorporating four fundamental trade-offs that explicitly link 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 either mediate or 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* large-scale movement or dormancy. Finally, we outline how these trade-offs interactively affect fitness and qualitative ecological outcomes resulting from multiple stressors. Our framework suggests that explicitly considering animal behaviour should enrich our mechanistic understanding of stressor effects, help explain extensive context dependence observed in these effects, and highlight promising avenues for future empirical and theoretical research.

Key words: climate change, HIREC, predator–prey dynamics, chemical pollution, animal behaviour, animal movement, environmental change, phenotypic plasticity, trade-off, anthropogenic.

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I. INTRODUCTION

Physiologists and ecologists have long studied environmental stressors, which we define broadly as abiotic (e.g. chemical pollutant, low oxygen, ocean acidification, temperature) or biotic factors (e.g. disease, predation risk, food scarcity) 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) (see Table 1 for definitions of key terms). Importantly, stressors rarely act in isolation, stimulating a recent focus on multiple stressors and their potential for synergistic impacts (Przeslawski, Byrne & Mellin, 2015; Cote, Darling & Brown, 2016; Cambronero *et al.*, 2018; Petitjean *et al.*, 2019). Despite this effort, Orr *et al.* (2020, p. 8) concluded that when it comes to addressing the effects of stressor combinations, 'over the past 20 years [...] very few, if any, general patterns have emerged from meta-analyses'. Our thesis is that a clear theoretical understanding of behavioural and life-history plasticity in response to multiple stressors can facilitate a more mechanistic understanding of stressor effects, including generalities regarding their context dependence and how they manifest in the wild. At a broad level, we build on Arnold's (1983) conceptual framework linking traits (here, behavioural and life-history plasticity) to fitness *via* effects of traits on performance in fitness-related tasks.

Conceptual models of how organisms respond physiologically to environmental variation [e.g. the Allostatic Load Model (McEwen & Wingfield, 2003; Wingfield, 2013) and Reactive Scope Model (Romero, Dickens & Cyr, 2009)] provide frameworks for understanding how stressors affect fitness (or performance). Dynamic energy budget models (Kooijman, 2009) have also been used in combination with oxygen- and capacity-limited thermal tolerance models (Pörtner, 2010) to create a framework that uses key parameters of energy balance (e.g. aerobic scope) to integrate the effects of multiple stressors and predict the consequences of exposure to stressors (Sokolova *et al.*, 2012). These effects are expressed through physiological mediators, both within a range that does not reduce fitness (the reactive scope/'pejus range') and in scenarios that push organisms into an overload that reduces survival (the 'pessimum range') (Sokolova *et al.*, 2012; Sokolova, 2013).

Behaviour (e.g. feeding, locomotion, aggression, fleeing, vigilance, and migration; see Table 1 in Romero *et al.*, 2009) plays a role in these general frameworks in mediating

Table 1. Definition of key 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.
Direct stressor effect	The effect of a stressor on an organism's physiology, behaviour and life-history traits.
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.
Indirect stressor effect	Stressor effects that arise as a result of organism responses to mitigate the effects of stressors, e.g. including large-scale space use *via* migration.
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.

physiological responses, but the integration of physiology and behaviour is not developed in detail.

An alternative physiologically based approach examines specific stressors in detail. For example, thermodynamic niche models have analysed thermal, mass and water balance demand by combining biophysical models that account for microclimatic variation (in space and time) and the organism's morphology, physiology and behavioural repertoire. These include models of multiple nutrient needs (e.g. energy, protein, minerals), dynamic energy budget models (Kooijman, 2009) of overall energy balance and allocation over a lifetime, and biomechanic models of the exchange of heat, mass, and momentum between an organism and its environment (Denny & Helmuth, 2009). These approaches have been used to predict behaviour (e.g. patterns of activity and microhabitat use), physiology, life histories, fitness and even population persistence with climate change (Denny & Gaylord, 2010; Kearney *et al.*, 2013, 2018; Kearney & Porter, 2020). While these models are detailed and comprehensive in many dimensions, their

analyses have largely ignored some key behavioural trade-offs (e.g. between predation risk and feeding, growth and mating demands) that have major impacts on energy intake and/or allocation that can feed back to affect behavioural and physiological states and ultimately fitness (Lima, 1998; Peacor *et al.*, 2020; Wirsing *et al.*, 2021).

Here, we propose 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 (Fig. 1). We draw conceptually from the literature on multiple-predator effects (MPEs). Indeed, we provide a generalised framework in which MPEs are nested but, importantly, can combine and potentially interact with any other biotic or abiotic stressor(s), including those that, unlike predators, do not react to the behaviour of the focal organism. Our framework is outlined in terms of four trade-offs. 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
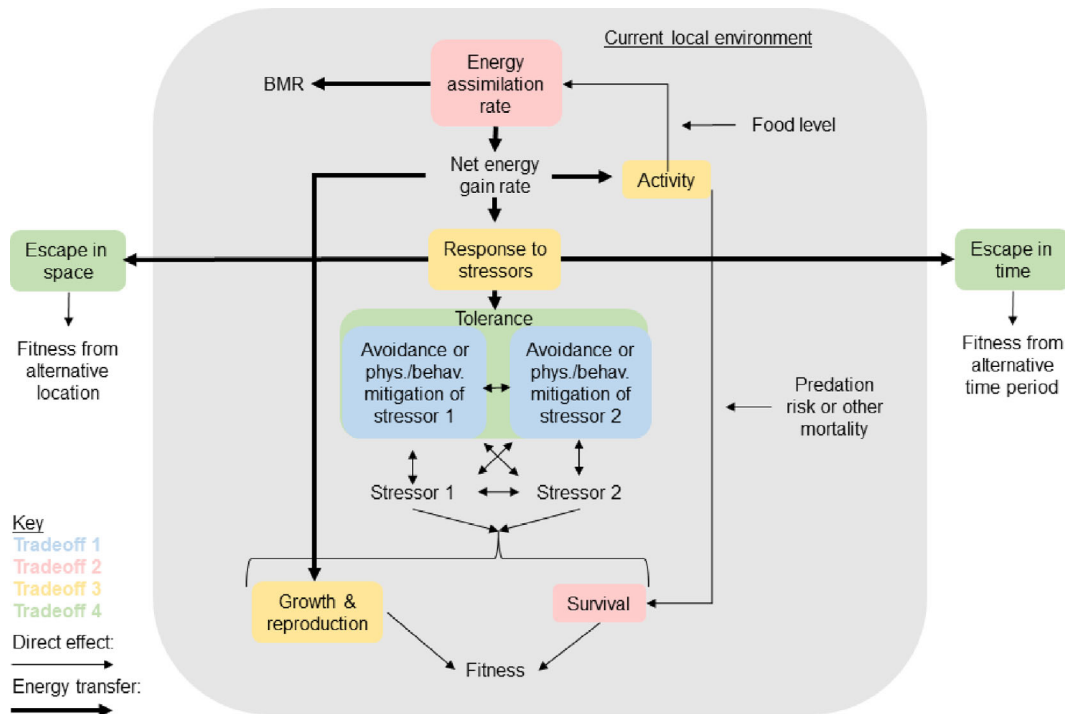
Fig. 1. Conceptual framework. Integrating the behaviour, physiology, and bioenergetics of coping with multiple stressors reveals four fundamental trade-offs. Energy is allocated among key components (thick arrows) leading ultimately to fitness effects; the four key trade-offs are colour-coded. Energy assimilation rate pays the energy cost of basal metabolic rate (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 behavioural or physiological or both (blue rectangles, trade-off 1); they are triggered by the stressors, which they can ameliorate 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 tolerance mechanisms, jointly yielding fitness. Note that while stressors can directly affect an organism (diagonal arrows below stressors), various indirect stressor effects can also manifest *via* animal behaviour and life-history characteristics (e.g. activity and consequent predation risk can be driven by energetic demands imposed by stressors, ultimately shaping fitness).

organism's vulnerability to the effects of a second stressor, or alter the magnitude of these effects on fitness (Fig. 1, trade-off 1). Second, because responding physiologically to stressors often requires energy, this can favour increased foraging activity which often increases exposure to additional risks, e.g. predation (trade-off 2). If the organism has obtained the energy it requires, it will then 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 emphasise 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 movements) or time (e.g. *via* dormancy or diapause). Escape in space or time typically incurs other costs (trade-off 4).

Our integrated framework, using energy as the common currency, highlights: (1) that stressor effects can go far beyond direct effects, whereby stressors directly cause physical harm, but can give rise to a suite of indirect effects; e.g. the indirect costs of an abiotic stressor might include increased predation risk or reduced mating success; (2) the fundamental role that scales of spatial and temporal correlations between stressors, resources and other risks can play; and (3) the need to 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 first classify multiple stressor interactions within our framework and briefly describe how animal behaviour can 'redefine' these interactions. We then provide a detailed description of each of the four fundamental and interrelated trade-offs (Fig. 1) in our framework and outline the broad insights they offer.

II. 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 cause its predators to modify their behaviour (e.g. hunting in different habitats). On the other hand, while ectotherms typically increase their foraging rates to cope with the energetic costs of increased metabolic rates resulting from elevated temperature (Pörtner & Knust, 2007), this behavioural response does not alter the temperature itself. Here, we classify multiple-stressor combinations into three forms (Fig. 2):

AA: the focal organism cannot modify either stressor (i.e. no feedback between the focal organism and the stressors), except *via* avoidance or escape in space or time.
AB: the organism can modify only one stressor (bi-directional feedback between a single stressor and the organism). Notably, here, a responsive biotic stressor (e.g. a predator) can often also be impacted by the non-responsive stressor. (e.g. a chemical contaminant).
BB: The organism can modify both stressors (bi-directional feedbacks between both stressors and the organism – it is within this category that multiple-predator effects reside).

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, Englund & Wooster, 1998; Schmitz, 2007) (Fig. 2). Stressor interactions and impacts on organisms can hinge on these categories.

III. ANIMAL BEHAVIOUR 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
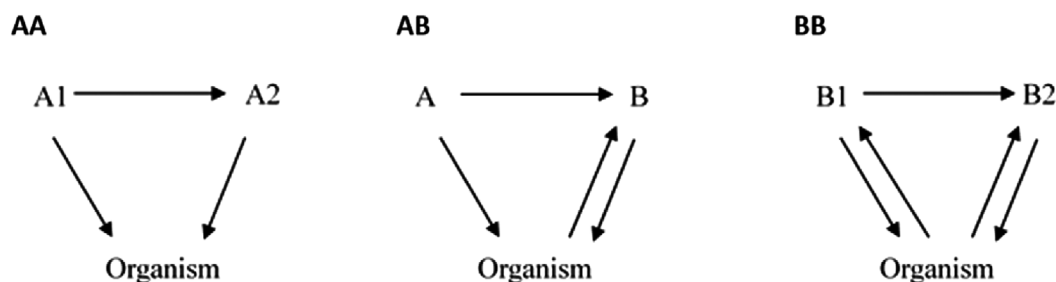
Fig. 2. Categories of multiple-stressor combination types according to degrees of feedback between stressors (abiotic, A, and/or biotic, B) and the focal organism. Stressor combination AA shows a combination with no feedback between stressors; for stressor combination AB there is unidirectional feedback and stressor combination BB there is bi-directional feedback [multiple-predator effects (MPEs) are an example of this interaction]. Feedbacks occur when the organism affected by a stressor, in turn, affects that stressor (e.g. a shift in the behaviour of a prey species can affect the behaviour of its potential predator).

such unexpected potential stressor interactions is animal behaviour. 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, and natural and exotic 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. 3) can interact with one another indirectly at the organismal level, akin to analogous species indirect interactions, such as apparent competition (Holt, 1977) and apparent mutualism (Abrams, Holt & Roth, 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.

Stressors that do not overlap in time can still have non-additive effects, through physiological changes or due to behavioural responses to the first stressors. Physiological carryover effects of stressors have been observed in many
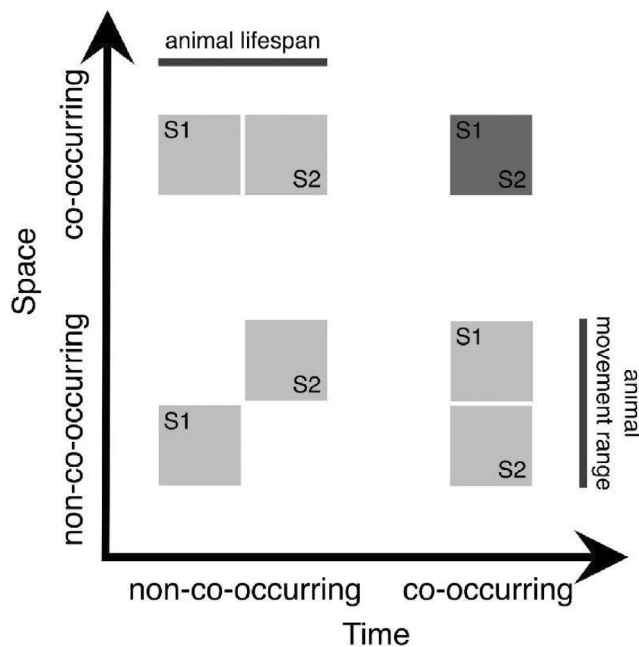
Fig. 3. Animal behaviour can redefine 'multiple-stressor' scenarios. When effects of stressors carry over into periods of time when the stressors are not present, this allows multiple stressors that do not co-occur in time and/or space nonetheless to have 'co-occurring effects' on mobile organisms. Here, stressor 1 (S1) and stressor 2 (S2) co-occur in time and space (top right), co-occur in space only (top left), co-occur in time only (bottom right), or co-occur neither in time nor 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 *versus* inactive, move to an area with one stressor or an area with the other) in each of these scenarios depends on the costs of avoidance in space or time and the relative strengths of stressor effects.

systems. For example, bivalves have decreased immune response following temperature stress, which makes them more susceptible to disease-based stressors (Rahman *et al.*, 2019). Similarly, damselfly 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, Janssens & Stoks, 2016). Indeed, broadly speaking, if a stressor simply causes reduced net energy gain (e.g. *via* a taxing physiological load), this could manifest as a carryover effect that could interact with other stressors down the line. Behavioural carryover effects have also been observed. For instance, tadpoles from high-risk environments are generally more active, which increases 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 behavioural) 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 (Dinh *et al.*, 2022; Schnurr, Yin & Scott, 2014). For example, the keystone sea hare species *Stylochelius striatus* significantly reduced its locomotion speed and rate of correct foraging decisions following exposure to elevated temperature and pCO_2. 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 (Zavorka *et al.*, 2020). Developmental stress has been shown to affect a variety of behaviours including foraging (Crino *et al.*, 2014; Chaby *et al.*, 2015), learning (Brust *et al.*, 2014; Kriengwatana *et al.*, 2015), social network position (Boogert, Farine & Spencer, 2014) and the development of behavioural 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 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). Generally, landscape heterogeneity and large home ranges or migration ranges increase the likelihood that stressors that do not co-occur in time or space can, nonetheless, have interactive effects on an animal *via* the sequence of exposure it experiences through its movement decisions (Shepard *et al.*, 2013; Jachowski *et al.*, 2018).

(1) Multiple cues drive behavioural responses to multiple stressors

Behavioural 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*, although 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:

(1) A common cause, so one best action. 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, Piggott & Swearer, 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;

(2) Different causes, but one best action. 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);

(3) Different causes, with different best actions. 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 that 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 defence 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 systematically to evaluate expectations for behavioural responses to the multiple- (often many)-stressor scenarios that abound in nature.

IV. TRADE-OFFS UNDER MULTIPLE STRESSORS

(1) Trade-off 1: small-scale energetic and behavioural trade-offs

Organisms informed by cues can respond to one or more stressors in various, potentially interactive, ways. Physiologists have rigorously investigated physiological trade-offs – where the physiological portion of an organism's response to stressor X either enhances (cross-tolerance) or interferes with (cross-susceptibility) the physiological portion of its response to stressor Y (Todgham, Schulte & Iwama, 2005; MacMillan, Walsh & Sinclair, 2009; Sinclair *et al.*, 2013; Hintz, Jones & Relyea, 2019). Here, we focus on additional, less-studied behavioural and energetic responses, whereby exposure to stressor X changes either the exposure to or fitness costs of stressor Y.

Many organisms respond to environmental stressors by adjusting their space use or temporal activity patterns (Porter *et al.*, 1973; Stevenson, 1985; Clusella-Trullas & Chown, 2014; Araújo, Moreira-Santos & Ribeiro, 2016; Sears *et al.*, 2016; 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, migration or dormancy, trade-off 4, which we discuss in Section IV.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. It is important to note that the degree to which small-scale avoidance *versus* large-scale escape confers a greater fitness advantage could hinge on the presence of feedbacks from stressors to the focal organism (Fig. 2); e.g. the efficacy of prey avoidance or escape will depend on the tendency and ability of multiple predators to track prey actively in space or time.

Behavioural 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, i.e. where the response to either stressor increases exposure to the other, the negative impact of the stressor pair can be enhanced. For example, rising water temperatures can increase the exposure of fish to chemical pollutants by increasing activity and consumption of contaminated prey (Brodin *et al.*, 2014; Saaristo *et al.*, 2018). 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 (Gunderson, Armstrong & Stillman, 2016; Rozen-Rechels *et al.*, 2019) (see Section III 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 also to 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 moving to deeper water, but doing so exposes them to higher predation risk from fish (Garcia, Stacy & Sih, 2004).

Invoking parallel theory on avoidance of multiple predators (Lima, 1992; Matsuda, Hori & 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 weight avoidance of the more detrimental stressor(s) more heavily. 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. Instead, they should cope with the stressors *via* physiological responses (if feasible), or escape in space or time (if 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 (Sears *et al.*, 2016; 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. In some cases, clear mechanisms underlie a correlation between stressors. For example, in terrestrial systems, heat stress and water loss are correlated physiologically through evaporation, which depends on wind speed, humidity and air temperature (Mitchell *et al.*, 2018; Rozen-Rechels *et al.*, 2019; Kearney & Porter, 2020). Stress associated with hot, dry conditions can then be correlated spatially *via* landscape structure and microhabitat variation (e.g. vegetation, shade; Sears *et al.*, 2016). In coastal marine

systems, seasonal upwelling brings up cold, low-oxygen, high CO_2 waters, thus generating a temporal correlation between ocean acidification and hypoxia (Davis *et al.*, 2018; Chan *et al.*, 2019).

In other cases, spatiotemporal correlations between stressors are less clear, but could be deduced from known stressor–organism relationships. For prey, the relationship between predation risk and various abiotic stressors likely depends on whether focal prey or their predators are more susceptible to those abiotic stressors (Ferrari *et al.*, 2011; Kroeker *et al.*, 2014). If predators are more negatively affected than prey by an abiotic stressor, then situations with high abiotic stress can be 'safe sites' for prey (Relyea, Schoeppner & Hoverman, 2005). For example, predation rates of northern pike (*Esox lucius*) upon brown trout (*Salmo trutta*) fell drastically when exposed to temperatures below 11 °C. Below this thermal threshold the maximum attack speed of the predator decreased while the prey's swimming speed was less affected (Ohlund *et al.*, 2015). This is a version of the 'enemy of my enemy is my friend' effect that is well studied in systems where prey do better in, and in some cases, prefer places where top predators (including humans) reduce risk from intermediate predators (Berger, 2007; Bestion *et al.*, 2015; Suraci *et al.*, 2019; Culshaw-Maurer, Sih & Rosenheim, 2020).

Importantly, when stressors are commonly correlated for systematic reasons, organisms can evolve or learn to account for that correlation in their behavioural and/or physiological response. By contrast, if the correlations vary unpredictably, a lack of reliable information can constrain the animal's ability to balance needs adaptively to avoid the different stressors. This is an example of the general point that cue reliability and how cues interact can have major effects on whether and how organisms respond (with changes in behaviour and/or physiology), and the effectiveness of their responses [(Trimmer *et al.*, 2017), see also Section III.1]. Overall, more studies are needed to examine 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, whereby fitness costs increase non-linearly with greater stressor levels. 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 suddenly strains the organism's ability to cope with other stressors. Additionally, as a pathway to the other major trade-offs (Fig. 1), 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 non-linearities (steep thresholds in effect size) that can cause even a small change (in this case, an increase in the level of a stressor) to reduce fitness

disproportionately. For example, Delnat, Janssens & Stoks (2019) exposed mosquito larvae to warming (20 °C *versus* 24 °C) and three different concentrations of the pesticide chlorpyrifos. The synergistic impact of these stressors on survival depended on chlorpyrifos concentration; survival was drastically decreased following exposure to warming and 0.44 μg/l chlorpyrifos but not 0.37 μg/l chlorpyrifos.

(2) 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). Although these costs are not always well understood (but see Feder & Burggren, 1992), balancing the needs and costs of obtaining energy and, in particular, the costs in terms of predation risk, is a core issue in behavioural ecology. 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 trade-offs associated with responding to environmental stressors.

Most fundamentally, when physiological responses to stressors increase 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). Honeybees, for instance, are not significantly impaired by neonicotinoid pesticides if they are not faced with nutritional stress (Tosi *et al.*, 2017). Consequently, laboratory experiments that provide organisms with *ad libitum* and/or high food levels might underestimate multiple-stressor impacts in nature, where animals may often be 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, Macel & Visser, 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; Goldenberg *et al.*, 2018). 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, which requires increased energy intake, might often entail exposure to higher 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. For example, when faced with perceived predation risk, Iberian rock lizards, *Lacerta monticola*, face a trade-off over how long to 'pay' the thermal costs of remaining in a relatively cool refuge *versus* emerging (Martín & López, 1999).

In the context of the classic risk–reward foraging trade-off, a key understudied topic is the spatial or temporal correlations among stressors, food levels and predation risk. Even if stressors are uncorrelated with food and predation risk, 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 behaviour (see analogous phenomenon concerning behaviourally mediated stressor 'co-occurrence' in Section III and Fig. 3). If avoiding stressors in space and time causes organisms to be more active in places or times when predation risk is particularly high, the cost of multiple stressors can be 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 (Clinchy, Sheriff & Zanette, 2013), 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 came 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 detect and avoid predators, leading to synergistic negative interactions between the stressor and background predation risk (Reeves *et al.*, 2010; Hayden *et al.*, 2015; Polo-Cavia, Burraco & Gomez-Mestre, 2016; 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).

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 obtain energy to fuel physiological responses, as well as the costs of mounting a defence. Disentangling the relative importance of direct and indirect costs on organisms will likely require an integrative approach that couples measurements of bioenergetic responses at the individual and cellular level, life-history traits and key behaviours. In principle, data on how exposure to stressors reduces net energy budgets *via* reduced energy inputs and reserves and increased consumption rates provides a quantitative window into these alternative

components of indirect costs of these stressors. For example, recent studies into the effects of warming and pesticides on aquatic insects have demonstrated the value of measuring cellular energy allocation – an estimation of an organism's net energy budget derived from measures of available energy reserves (protein, sugar and fat) and energy consumption (based on activity of the electron transport system) – that has been shown to correlate positively with organism growth rate (Van Dievel, Janssens & Stoks, 2019; Verheyen & Stoks, 2020; Meng *et al.*, 2022). Meng *et al.* (2022) showed that exposure to acute periods of warming and chlorpyrifos (a pesticide) increased mortality in mosquito larvae (*Culex pipiens molestus*). Acute warming resulted in lower energy availability, which reduced the net energy budget for physiological coping mechanisms for detoxifying chlorpyrifos [i.e. heat shock protein 70 (Hsp70) and the enzyme cytochrome P450 monooxygenase (Janssens, Dinh & Stoks, 2014)]. Field and mesocosm experiments that manipulate predator presence and food availability, paired with assessments of bioenergetic and behavioural responses, should be useful in understanding when stressors have indirect effects *via* challenges to energy acquisition and changes in predation risk associated with increased foraging.

Theory on balancing risks and foraging needs offers additional intuitive, qualitative predictions (Brown, 1999; Houston & McNamara, 1999) on when we might expect direct *versus* indirect costs to be larger. When food availability is high and predation risk is low, animals may not need to be very active to obtain sufficient energy to fuel physiological responses to stressors. As a result, the stressors' direct costs and their indirect 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). By contrast, during food shortages, the activity needed to acquire sufficient energy to fuel physiological responses to stressors may lead to higher exposure to predation risk. The main cost of the stressors might then be indirect; that is, increased predation risk and not direct damage or mortality from the stressors *per se*. Notably, most indirect costs are not addressed in standard laboratory experiments, where focal organisms are typically not exposed to predation. On the other hand, if increased activity causes a sharp, accelerating 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 on stressor–foraging risk trade-offs remain to be rigorously explored with quantitative models and empirical experiments in the laboratory and the field.

(3) Trade-off 3: energy allocation between stressors and life-history traits

Stressors not only directly reduce growth and reproduction of organisms [e.g. by disrupting endocrine systems (Rattan & Flaws, 2019) or by shortening telomeres (Chatelain, Drobniak & Szulkin, 2020)], they can also indirectly reduce fitness by demanding energy that could otherwise be allocated to growth and reproduction (Rohr *et al.*, 2004; Pörtner & Knust, 2007; Correa-Araneda *et al.*, 2017). While in most cases, studies have not quantified how much the physiological impacts of stressors increase energy demands, work on the energetic costs of mounting immune responses suggests that this effect depends on context but can be substantial (Bonneaud *et al.*, 2003).

To predict how much organisms should invest adaptively in physiological mechanisms to cope with stressors, despite the accompanying trade-off of reduced growth or reproduction, we draw on a fundamental tenet of basic life-history theory: that adaptive allocation to competing demands depends on the marginal benefits *versus* costs of additional investment in each demand (Roff, 2002). Non-linearities involving accelerating costs or benefits of increased investment can also produce the aforementioned fitness cliffs (threshold effects), where 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 non-linearities are often associated with strong competition, or size/condition-dependent safety (Einum & Fleming, 1999; Luttbeg & 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.

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. In other words, through the lens of life-history theory, stressors need not interact directly to drive strong synergistic effects on the organism. Instead, these effects can manifest through the combined effects of independent stressors on energy demands when organisms are close to an energetic threshold (e.g. a starvation threshold).

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, Sesterhenn & Stieha, 2011; Przeslawski *et al.*, 2015; Watson *et al.*, 2018; Dahlke *et al.*, 2020; 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; Byrne *et al.*, 2020; Miler, Stec & Czarnoleski, 2020). For example, echinoderm larvae can show elevated mortality, impaired development and signs of metabolic depression following exposure to heightened temperature and CO_2 partial pressure (pCO_2) (Byrne & Przeslawski, 2013; Przeslawski *et al.*, 2015). Negative effects of multiple stressors on juvenile stages may be ameliorated by increased energy uptake. For example, larvae of the barnacle *Balanus amphitrite* significantly increased their feeding rate under hypoxia and ocean acidification, and had similar survival and settlement rates to larvae exposed to each stressor individually or to no stressors at all (Campanati *et al.*, 2016). Nevertheless, 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). For some taxa, tolerance to stressors can increase with age as energy reserves are built and physiological regulatory mechanisms develop (Pörtner, Lagenbuch & Reipschläger, 2004; Vetter, Franke & Bulchholz, 1999). However, the high vulnerability of certain life cycle stages to multiple stressors may represent a 'weak link' and have significant repercussions on population dynamics, even if adult life stages experience lower mortality and impairment than juveniles (Russell *et al.*, 2012).

Similarly, when reproduction requires an abundance of energy, females can suffer higher costs of coping with stressors during reproductive periods than during nonreproductive periods. French, DeNardo & Moore (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 non-linear (e.g. sigmoidal) function of female parental investment, this can cause females to invest more into reproduction and less into coping with stressors, thus yielding larger direct costs of stressors. Alternatively, animals exposed to stress sometimes reduce their investment per offspring (Rasanen *et al.*, 2008; Freuchet, Flores & Tremblay, 2015). 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, *Daphnia pulicaria* adults exposed to the pesticide carbaryl and toxic cyanobacteria *Microcystis aeruginosa* produced significantly fewer eggs and more frequent premature delivery of offspring (Cerbin *et al.*, 2010). Additionally, more body deformations were observed in offspring whose mothers had been exposed to both stressors (Cerbin *et al.*, 2010).

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 (e.g. *via* reduced apparency to females and/or reduced competitiveness with other

males). Strong sexual selection could then favour 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. In a study of 28 species of North American passerine birds, male (but not female) mortality was related to sexual size dimorphism and female (but not male) mortality was negatively correlated with male brightness, which suggests that sexually selected traits are costly and constrained by the background mortality costs of other stressors (Promislow, Montgomerie & Martin, 1992). In mammals, the relationship between male-biased mortality and sexual size dimorphism was found to be partially due to male-biased parasitism rates (Moore & Wilson, 2002). Investing in sexually selected traits, like increased size, may thus make males more vulnerable to other stressors (i.e. parasites). Alternatively, if some sites have abundant food but high risk, sexual selection can favour taking greater risks (e.g. increasing exposure to predators, aggressive competitors, or other stressors) to bring in the energy required to invest in both ornaments and in physiological responses to stressors to maintain condition.

Trade-off 3 – balancing investment in stressor response, life-history traits, and activity level – derives from a simplified application of Dynamic Energy Budget (DEB) theory. DEB theory is a powerful, metabolically based framework widely used to account for environmental effects at the sub-individual, individual, population, and higher levels of organisation (Sousa *et al.*, 2010). Flows and pools of energy and nutrients are expressed as differential equations and state variables, based on empirically quantifiable parameters, resulting in predictions about components of metabolism and the structures and life-history components they generate. DEB models have been used extensively across levels of organisation (Nisbet *et al.*, 2000). At the individual level, a considerable amount of work has addressed stressors such as toxicological effects (Kooijman, 1993; Jager & Klok, 2010) and reactive oxygen species (van Leeuwen, Vera & Wolkenhauer, 2010). At the population level, the standard DEB model has been modified to capture taxon-specific effects like size dependence of required food quality (Kearney *et al.*, 2010), maturity-dependent survival (Nisbet, McCauley & Johnson, 2010), and moulting in crustaceans (Talbot *et al.*, 2019). That these models can be readily modified for particular taxa and allow for variation in time and space (Monaco & McQuaid, 2018), greatly extends their applicability. In particular, simplifications of model structure are often utilised to capture appropriate temporal and spatial scales (Sousa *et al.*, 2010), which largely accounts for our Fig. 1 as a simplified derivative of the DEB framework. Consistent with DEB but following our own trade-off-based approach, we incorporate the key energy flows, state variables, and causal links important for understanding how stressor effects influence life-history effects and fitness.

Although DEB models are useful in predicting responses to multiple stressors, it is not always feasible to use them as

they require extensive parameterization. Sokolova (2013) proposed a framework that integrates the logic of DEB models with oxygen- and capacity-limited thermal tolerance models (Pörtner, 2002) in order to assess the effects of multiple stressors rapidly on a range of species. The logic of these models is fundamental to our trade-off 3; in unstressed situations, the aerobic scope can supply enough ATP to meet the demands of maintenance, activity, growth, reproduction, and storage. Under moderate stress, or the 'pejus range', either the cost of maintenance increases or the aerobic scope decreases such that there is a reduction in energy allocated towards tasks beyond maintenance. With increasing stress, the animal enters the 'pessimum range' where no energy is allocated towards growth, reproduction, or storage and anaerobic respiration is required to supplement the needs of maintenance (Sokolova, 2013). While these models are an important bridge between physiology and whole-animal ecology and species distributions that acknowledge the importance of behaviour (Sokolova *et al.*, 2012), we argue that they do not go far enough to integrate behaviour into our understanding of an animal's responses to multiple stressors both in terms of small-scale changes in behaviour (trade-off 1) and foraging (trade-off 2) that influence the stressor exposure. After all, while these models have been used to predict species distributions based on environmental tolerances (Sokolova, 2013), behaviour has been shown to be an important response to environmental extremes (Sunday *et al.*, 2014).

(4) 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 discussed in Sections IV.1–3 on trade-offs 1–3), some organisms can escape environmental stressors in space or time through long-distance dispersal or migration 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 and undergoing the costs to do so. The option of EIS is largely limited to mobile species, and the potential for animals to evade stressors *via* EIS draws a clear dichotomy between animal and plant responses to stress (Bradshaw, 1972; Huey *et al.*, 2002). Sessile animals and plants may have the ability to make small-scale spatial adjustments in response to stress (e.g. plants growing towards light), but ultimately these organisms are likely to emphasise stress-resistant physiological responses (e.g. enhanced tolerance capacity) or escape in time (e.g. changes in phenology; see below) due to constraints on their mobility (Huey *et al.*, 2002; Ponge, 2020). 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 (Dingle, 2014; Merkle *et al.*, 2016). 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). EIS has also been observed in non-migratory butterfly species that 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 precluding the costs of tolerance, avoidance, or migration by, instead, entering into torpor (Humphries, Thomas & Kramer, 2003; Geiser, 2004), dormancy [including hibernation or aestivation (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 (Levins, 1969; Porter *et al.*, 1973; Thomas, Dorais & Bergeron, 1990; Danks, 2000; Goto *et al.*, 2001; Sarmaja-Korjonen, 2003; Hairston Jr. & Fox, 2009) but can leave inanimate individuals vulnerable to other dangers (Cowles, 1941). In the Sokolova (2021) framework, when an animal enters the pessimum range of extreme stress such that aerobic respiration cannot meet the needs of maintenance metabolic rates, it can begin anaerobic respiration or reduce its metabolic needs and enter a period of metabolic rate depression.

Theory on the evolution of adaptive dispersal and migration and/or dormancy provides insights regarding factors that influence when organisms should attempt to escape in space or time (Levin, Cohen & Hastings, 1984; Snyder, 2006; Bonte & de la Pena, 2009; Bonte & Dahirel, 2017). Whether large-scale dispersal or migration, 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, see below). Both large-scale movement and dormancy can involve substantial uncertainty about expected fitness. For long-distance movement, there is uncertainty about transit costs (which 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 behavioural 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 behavioural 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 Section III).

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 escape in space or time is not the spatiotemporal pattern of stressors *per se*; it is, instead, the spatiotemporal pattern of fitness adjusted for costs of large-scale movement 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, if range shifts introduce novel competitors (Sinervo *et al.*, 2010), 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 should scale with the potential for that escape to be possible. For instance, if stressors are highly localised in space or time, we would expect escape to be more likely, but when stressors are widespread over space or time (i.e. chronic), escape may not be an option. 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 eventually to shift from an optimal strategy of escape to one of remaining in the environment, where tolerance or local avoidance are the only options (Fig. 4A). In other words, when stressors occur at large enough scales in space and time, they become infeasible to escape and tolerance and, in some cases, local avoidance, become the only feasible strategies.

If we expand to consider animal behaviour in the context of multiple stressors, the horizon of possibilities quickly becomes 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 ten qualitatively distinct sets of possible behavioural responses (Fig. 4B). 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).

### (5) Interactions among trade-offs

Although we have discussed trade-offs one at a time, our approach (Fig. 1), emphasises that these behaviours and allocation decisions are together 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* (although in some instances responses may be developmentally fixed). 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. 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 highlights 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 behavioural responses? If stressor levels increase slowly, organisms have time both to build higher physiological capacity and to adjust behaviour, but if local stressor levels suddenly increase, this might exceed the speed of physiological plasticity (Seebacher, White & Franklin, 2015; Meng *et al.*, 2022). 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 responses 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).

V. BEHAVIOUR AND STRESSOR EFFECTS ON COMMUNITIES

The individual behavioural responses to stressors discussed herein can affect community-level outcomes *via* effects on species interactions (e.g. consumer–resource interactions, competition and mutualism). Conversely, species interactions can affect responses to stressors (Miller, Matassa & Trussell, 2014; Thompson, McLennan & Vinebrooke, 2018; Shantz *et al.*, 2022). Therefore, understanding how stressors impact behaviourally mediated species interactions is essential for predicting when synergistic interactions will
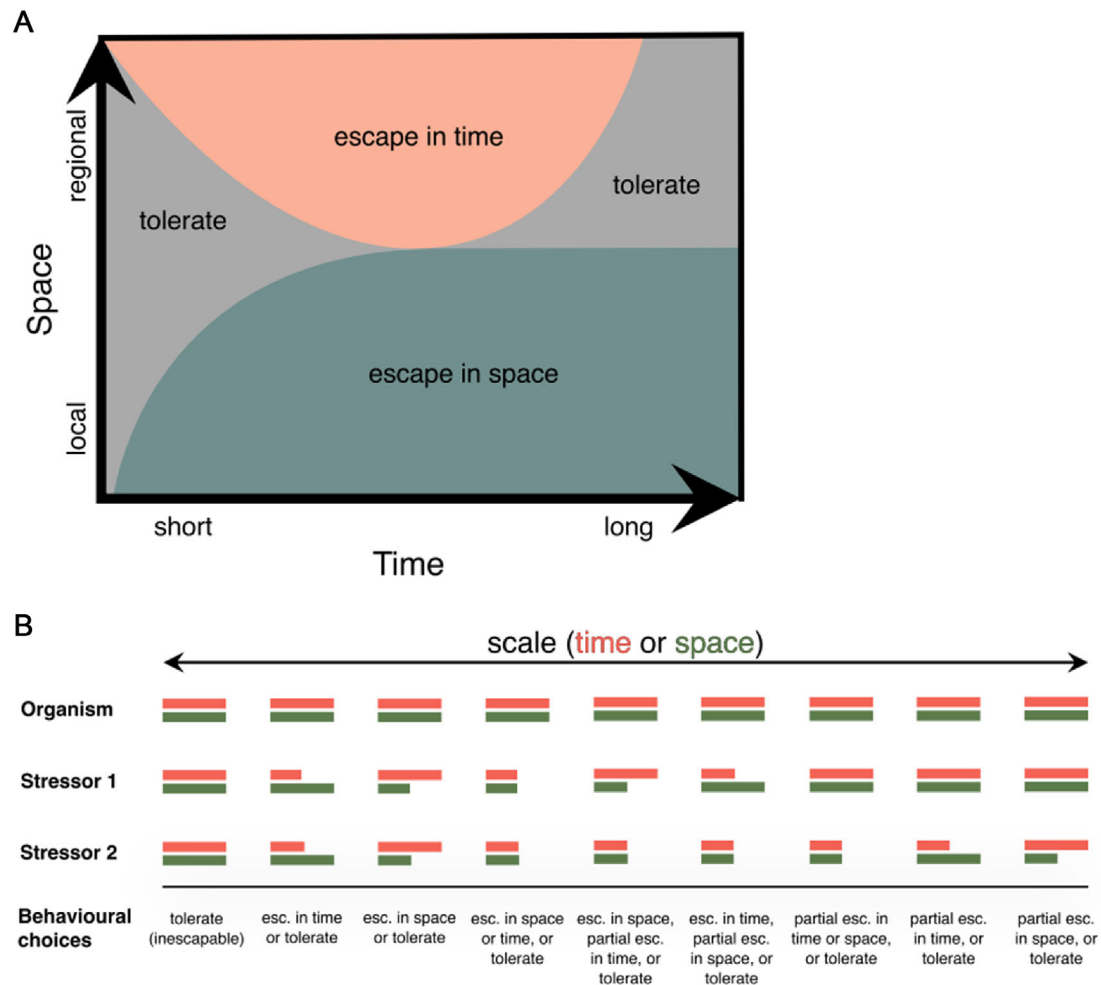
Fig. 4. Trade-offs and choices associated with stressors in time and space. (A) When a single stressor, or a combination of multiple stressors that co-occur in time and space, is highly constrained in space (e.g. it affects a small patch of habitat), costs of avoidance in space are low, and, thus, escape in space should be the optimal choice. If the stressor duration is very short and it is not highly isolated in space, it should generally be optimal to tolerate or locally avoid the stressor (grey area to the left), rather than invest in escape in time. However, as stressor duration increases, it can become optimal to escape in time, 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 or local avoidance is the optimal choice (grey area to the right). (B) The relative spatial (pink bars) and temporal (green bars) scales over which an organism and each of two stressors operate determine the set of behavioural 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 behavioural 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.

arise, but this fundamental aspect of ecology is often absent from multiple-stressor studies (Tylianakis *et al.*, 2008; Thompson *et al.*, 2018).

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). Single and multiple stressors can also directly and indirectly disrupt mutualisms or positive interspecific interactions (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; Fig. 5). 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 agrochemicals on honeybee foraging and survival reduces plant pollination which, in turn, will likely reduce food availability for herbivores [i.e. the indirect beneficiaries of the plant–pollinator mutualism (Botías *et al.*, 2021; Siviter *et al.*, 2021)] (Fig. 5). Alternatively, mutualisms or positive interspecific interactions can help buffer ecosystems against negative effects of environmental stress [e.g. the Stress Gradient Hypothesis (Thompson *et al.*, 2018, Shantz *et al.*, 2022)]. 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, Del Toro & Pelini, 2014).

Multiple-stressor effects on communities can be difficult to predict but are likely contingent upon the degree of relative 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. 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, Ortega & Cruz, 2009; White *et al.*, 2018). These effects can then spread to other members of the community. 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 behaviourally and density-mediated effects of their predators and increasing periphyton food abundance (Rumschlag *et al.*, 2020). By contrast, if stressors disproportionately change the behaviour 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).

If stressors specifically inhibit keystone predators, this can lead to the restructuring or collapse of entire ecosystems (Breitburg *et al.*, 1998; Rumschlag *et al.*, 2020). For example,
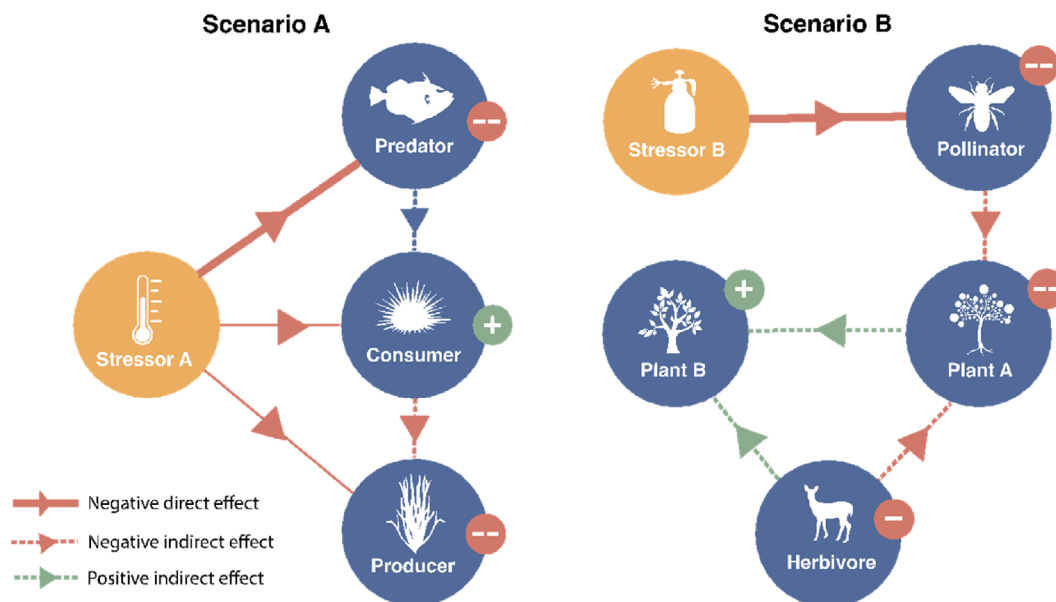
Fig. 5. Two hypothetical scenarios of how stressor effects can propagate across trophic levels leading to complex community outcomes and disruption of species interactions. In Scenario A, stressor A may disproportionately affect a single functional level (e.g. a keystone predator) which has positive 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. In 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.

higher temperatures reduce the top-down control of starfish predators on sea urchin populations, likely leading to increased overgrazing of kelp forests by sea urchins as ocean temperatures rise (Bonaviri *et al.*, 2017). 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 reduction, stressor effects tend to be weakened across trophic levels, leading to more resistant communities (Blake & Duffy, 2010; Jackson *et al.*, 2016). Indeed, the complexity inherent in ecological communities can often act as a buffer against multi-stressor effects across trophic levels. For instance, increased plant growth and quality in response to elevated CO_2 levels may compensate for the energetic and maintenance costs of ocean acidification and rising environmental temperatures on grazing consumers (Ghedini & Connell, 2016; Goldenberg *et al.*, 2018).

A less-studied mechanism potentially connecting multiple stressors and community dynamics revolves around information mutualisms; e.g. when co-occurring prey species share information about threats (e.g. predation risk; Gil *et al.*, 2018). Stress cues that are exchanged between species can provide recipients with an opportunity to prepare against impending periods of poor environmental conditions (e.g. xenohormesis; Howitz & Sinclair, 2008). If keystone information providers (e.g. species that are most vigilant about predation risk) are highly susceptible to stressors, this can have important negative effects on the ability of other species to cope with multiple stressors.

VI. FUTURE DIRECTIONS

Our framework, which emphasises the potentially fundamental and pervasive role that animal behaviour and life-history plasticity can play in shaping the effects of multiple stressors in the wild, calls for concerted empirical approaches to test and advance these ideas. Understanding direct effects (e.g. physiological damage) caused by different ecologically relevant combinations of stressors remains critical, but such physiology-centred approaches should be coupled, whenever possible, with *in-situ* work that estimates indirect effects of these same combinations of stressors, quantifying such metrics as diel movement (e.g. *via* telemetry data), foraging activity (e.g. *via* feeding assays that measure giving-up densities; Brown & Kotler, 2004), vigilance behaviour, and relative habitat and microhabitat use. In many cases, such field data and data on direct costs from laboratory experiments could be combined not only to assess the relative contributions of direct *versus* indirect stressor effects (and, thus, generalise findings better to other systems while accounting for contextual differences) but also to parameterise computational models to provide broader-scale quantitative predictions of stressor effects on natural populations.

With regard to understanding variation in how organisms respond to multiple stressors, for over two decades, 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, 2012; Reale *et al.*, 2007) 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.

A worthwhile future direction 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 (Donelan *et al.*, 2020; Orr *et al.*, 2022). The probability of a stressor still having deleterious effects for the next generation may affect the current choices of a would-be parent (e.g. nest position and timing), along with maternal effects on offspring traits. Examining ecological and social factors that, in the past or present, shape 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; Donelan *et al.*, 2020; Michelangeli *et al.*, 2022). In particular, understanding epigenetic or developmental effects can reveal otherwise hidden mechanisms of multiple-stressor effects discussed in Section III. With multi-generational transgenerational plasticity, behavioural responses to stressors in one generation can influence impacts of those stressors on other generations into the future (Bell & Hellmann, 2019).

While we focused primarily on individual responses to multiple stressors, we also expanded our scope to consider stressors, and their physiological and behavioural effects, in the context of natural communities (Fig. 5). Further theoretical and empirical investigations of how our comprehensive framework on stressor effects could help explain the structure and dynamics of natural communities should offer a timely and promising avenue for future study.

VII. CONCLUSIONS

(1) The effects of multiple stressors can be mediated by small-scale changes in animal behaviour, such as avoidance. While such changes may reduce exposure to one stressor, they may increase the impacts of others.
(2) Carry-over effects of multiple stressors may be observed where stressors do not overlap temporally, but where exposure to one stressor alters the impact of another later on. Animal movements can mediate exposure to spatially or temporally separated stressors.

(3) Exposure to multiple stressors can be energetically costly, giving rise to a suite of trade-offs including balancing the need for increased energy intake rates (*via* foraging, hunting) at the expense of greater exposure to predators and other dangers.

(4) Organisms may also need to trade off allocating energy to maintain behavioural *versus* physiological responses to survive multiple stressor exposure, alongside key life-history demands such as reproduction.

(5) Organisms can respond to stressors by escaping in space, *via* long-distance movement, or by escaping in time, *via* dormancy, but these strategies can incur energetic costs and/or lead to exposure to novel stressors.

(6) Stress responses, both behavioural and physiological, of organisms can alter the rate and/or nature of species interactions, thereby affecting community-level outcomes such as energy flow and nutrient cycling.

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IX. AUTHOR CONTRIBUTIONS

L. K. L., M. A. G., A. S., P. C. T. and P. H. C. developed the initial framework. All authors contributed to the writing of the first draft, revision and framework development.

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