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## A process framework for integrating stressor-response functions into cumulative effects

### models

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### Abstract

Stressor-response (SR) functions quantify ecological responses to natural environmental variation or anthropogenic stressors. They are also core drivers of cumulative effects (CE) models, which are increasingly recognized as essential management tools to grapple with the diffuse footprint of human impacts. Here, we provide a process framework for the identification, development, and integration of SR functions into CE models, and highlight their consequential properties, behaviour, criteria for selecting appropriate stressors and responses, and general approaches for deriving them. Management objectives (and causal effect pathways) will determine the ultimate stressor and target response variables of interest (i.e., individual growth/survival, population size, community structure, ecosystem processes), but data availability will constrain whether proxies need to be used for the target stressor or response variables. Available data and confidence in underlying mechanisms will determine

whether empirical or mechanistic (theoretical) SR functions are optimal. Uncertainty in underlying SR functions is often the primary source of error in CE modelling, and monitoring outcomes through adaptive management to iteratively refine parameterization of SR functions is a key element of model application. Dealing with stressor interactions is an additional challenge, and in the absence of known or suspected interaction mechanisms, controlling main effects should remain the primary focus. Indicators of suspected interaction presence (i.e., much larger or smaller responses to stressor reduction than expected during monitoring) should be confirmed through adaptive management cycles or targeted stressor manipulations. Where possible, management decisions should selectively take advantage of interactions to strategically mitigate stressor impacts (i.e., by using antagonisms to suppress stressor impacts, and by using synergisms to efficiently reduce them).

**Keywords:** stressor-response functions, adaptive management, multiple stressors, cumulative effects, process framework, decision-making

## 1. Introduction

As we continue to witness the Anthropocene unfold with its multiple and varied impacts on the Earth ecosystem, there is an urgency to better understand the short- and long-term implications of multiple stressors on ecosystem sustainability. Here, a stressor is defined as any physical, chemical, or biotic factor that has the capacity to affect another response variable in a linear or non-linear way, be it positive or negative in direction (Pirodda et al. 2022 and references therein). Assessing the combined effects of multiple stressors requires thoughtfully constructed cumulative effects (CE) models that are typically part of an adaptive management framework designed to reduce uncertainty in management interventions (Holling et al. 1978; Duinker et al. 2013; Rist et al. 2013; MacPherson et al. 2023). Simple CE assessments rank habitat impacts using spatial overlay and summation of multiple stressor scores (Halpern and Fujita, 2013), but this simple approach tends to be of limited value for exploring alternate management scenarios. More advanced CE modelling usually combine explicit relationships between stressors and a biological response variable, which we refer to as stressor-response (SR) functions (Larned and Schallenberg, 2019). This term is synonymous with stressor-effect functions, dose-response curves, physiological performance curves, and suitability curves; the abundance of similar terms demonstrates the ubiquity of SR functions across research disciplines in ecology, physiology, toxicology and environmental science. SR functions are a fundamental component of any predictive study, yet their central role in ecological modelling tends to be underappreciated (Rosenfeld et al. 2022). In a timely review, Pirodda et al. (2022) highlighted a data- vs. process-driven continuum as a key driver differentiating SR functions.

We built on their framework by identifying additional key attributes of SR functions including spatial and biological scale of application, theoretical considerations, and interaction types, followed by a pragmatic consideration of how to derive and apply them in data-rich and data-deficient contexts.

The intent of this review and synthesis is to guide the reader through the various stages of a CE process model centered around SR functions, from management objectives and causal effect pathways to SR function attributes and the continuous cycle of model testing and learning that defines adaptive management. We hope that this will enable readers to more thoughtfully derive and integrate SR functions into management questions, objectives, and decisions; all of which are integral to credible CE modelling and successful adaptive management plans (MacPherson et al. 2023). Understanding the role and impact of stressor interactions has also emerged as a priority concern in multi-stressor management (Birk et al., 2020; Lade et al., 2020); we turn a pragmatic eye towards interactions with the goal of providing guidance on how to deal with interactions under uncertainty, particularly in common data-deficient contexts.

## **2. Process model for the role of stressor-response functions in CE modelling**

The process model can be divided into three sequential steps (Fig. 1; see also MacPherson et al. 2023). The first focuses on the identification of target (priority) stressor and response variables, which will ultimately be driven by management objectives (i.e., the species, population, or ecosystem of concern and associated environmental stressors). The second step involves developing the optimal function for modelling the effects of the stressor(s) on the target

ecological response. The last step includes the adaptive loop of stressor simulation (e.g., CE) scenarios for management planning, implementation of management interventions, and monitoring of outcomes to generate data that can be used to either validate or better parameterize SR functions. We elaborate on these steps below.

## **2.1 STEP 1. Management objectives, priorities, and choosing response and stressor variable(s)**

The ultimate objective for natural resource managers is to ensure the sustainability of natural resources under environmental and societal changes (Dearing et al., 2014; Mangel et al., 1996; Rockström et al., 2009). More specifically, natural resource management agencies develop specific management targets and objectives for the priority ecosystem components under their jurisdiction. These become the focal response variables in both CE modelling and SR relationships. The choice of response variable is consequential for both management and the development of SR functions, and ultimately needs to be grounded in carefully considered management objectives (Schuwirth et al., 2019). Similarly, the corresponding stressors that drive change in the chosen response variables must also be based on clear management objectives and local knowledge, including the known dominant stressors and the subset that are actually subject to practical management intervention. These choices will then establish the basis for developing the SR functions that are foundational to all CE assessments.

### **2.1.1 Causal Effect Pathways and Stressor Chains**

While choice of the appropriate stressor may be obvious, in complex multi-stressor contexts the best driver to establish an SR function may be more cryptic, particularly if causation is ambiguous or key stressors are difficult to measure or manipulate (Geary et al., 2019). These

cases warrant identifying causal effect pathways (stressor chains; Fig. 2) that clearly describe the sequence of stressors that influence the response variable (Yuan et al. 2010; also referred to as “successive” interactions; Jackson et al. 2016). The pathway starts with the ultimate stressor—the overarching cause—and ends with the proximate stressor that is the direct driver of the terminal response (Fig. 2). Distinguishing between ultimate and proximate stressors is important for interpreting the results of a CE model and determining appropriate management interventions (Tyack et al., 2022). Developing an SR function linking the ultimate stressor and terminal response will necessarily integrate across the intervening stressor links (making it a composite SR function; Fig. 2), potentially obscuring intermediate causative mechanisms. These composite SR functions may represent very useful and empirically accurate links between ultimate causation and terminal responses in a stressor chain. However, treating the intervening stressor links as a black box can mask underlying mechanisms that may be informative for management decisions. For example—as illustrated in Fig. 2—landuse is an ultimate stressor that can cause a pathway of effects from nutrients to primary production to dissolved oxygen concentration (hypoxia). Hypoxia can then impact response variables like growth, survival, and fecundity (proximate responses) that are linked to population density (the ultimate response). Developing causal effect pathway diagrams is a useful practice at this initial stage because it will inform the suite of candidate variables available, and how they relate to one another (Plowright et al., 2008; Yuan et al., 2010). Once the causal effect pathways are established, the researcher can identify which response and stressor variables are easily measured or have available data, which can be effectively altered through management interventions, and which align best with management objectives.

## 2.2 STEP 2. Developing stressor response functions: Key attributes and considerations

### 2.2.1 *Empirical versus mechanistic stressor-response functions*

SR functions can be empirical relationships based on observational data collected across stressor gradients (e.g. Poff et al. 2010; Rosenfeld 2017; Larned and Schallenberg 2019), or mechanistic models based on established theory (ideally parameterized to local conditions), or some combination of both (Schuwirth et al. 2019; Connolly et al. 2017; see Pirotta et al. 2022 for deeper consideration of the empirical-theoretical continuum). Empirical SR functions are developed using empirical data from field studies (e.g., variation in animal abundance in habitats with different stressor levels; Rullens et al. 2022), or controlled factorial experiments that manipulate stressor levels (e.g., Piggott et al. 2022). Any type of linear or non-linear function can be fit to these data to generate the desired SR function (Larned and Schallenberg, 2019). The advantage of using data collected across stressor gradients in the field is that the relationship will be realistic and calibrated to the actual observed conditions in nature, increasing confidence in predictions; the disadvantage is that the data are correlative, and therefore stressor causation is inferred and may be confounded by other uncontrolled variables. Empirical SR functions derived from controlled experiments are more definitive in terms of stressor causation, but if performed in the lab their predictions may be less readily transferable to realistic field situations (Rullens et al., 2022).

Whether empirical or mechanistic approaches are optimal for any given stressor-response combination will depend on the availability of empirical data (or the difficulty obtaining it) vs. the maturity of appropriate theory to apply a mechanistic model in any particular sub-discipline



of ecology. Data-rich situations will allow for developing empirical SR functions (e.g., Yuan et al. 2010), while data poor circumstances will increase reliance on mechanistic functions, assuming that appropriate theory is available. In either case, researchers need to be explicit about how their SR function was derived. Some stressor impact pathways are empirically well described (e.g., effects of fine sediment on survival of salmonid eggs; Jensen et al. 2009) or may not lend themselves to mechanistic analysis. Other stressors (e.g., density-dependence) may have well-established theoretical models that can be reasonably applied with minimal data collection. Given the onerous nature of developing CE models that account for multiple stressors, some pragmatic combination of the two approaches will often be used (MacPherson et al. 2020).

Although there are proponents of both empirical and mechanistic approaches (e.g., Peters 1986; Railsback 2016), they are in fact highly complementary and can be used in combination to iteratively refine SR functions in a continuous cycle of data acquisition and model validation (Marquet et al., 2014; Pirotta et al., 2012; Schuwirth et al., 2019), as long as the sources of uncertainty in both classes of SR function are clearly recognized. Empirical data are essential for validating predictions from mechanistic models, or to calibrate (parameterize) them to regional conditions. However, confounding factors should be controlled using statistical methods (e.g., covariates in regression; Yuan et al. 2010; Feld et al. 2016) and inference of causation from empirical SR functions should be based on strong mechanistic underpinnings of existing ecological knowledge (Poff and Zimmerman, 2010). Further, extrapolating empirical relationships beyond their data range or to other regions with different stressor contexts may be problematic. In contrast, process-based mechanistic models are usually better at predicting

outcomes in unmeasured stressor ranges—particularly for non-linear relationships—but need to be parameterized using real data. Mechanistic models are often a simplification of a more complicated process, and often borrow parameters from different species or systems that can introduce considerable uncertainty in their predictions (Trudel et al. 2004). A clear understanding of model assumptions and limitations is essential to account for uncertainty (see the *Uncertainty* section below).

Developing SR functions is least challenging for data-rich species; the greatest challenge is the transition from narrative descriptions of stressor impacts to quantitative SR functions for severely data-deficient species or populations, a common scenario in fish and wildlife management, particularly for Species at Risk. However, tools are available to bridge the gap between narrative descriptions of stressor impacts and quantitative SR functions, and accelerate the transition from qualitative to quantitative modelling. For example, in a data-limited scenario, SR functions can be developed in workshops using expert opinion (MacMillan and Marshall, 2006). Here, experts must first determine the direction of the relationship (i.e., a positive vs. negative slope in the stressor-response space, informed by the endpoints of the relationship at the extremes of the stressor gradient), and then determine the functional shape of the relationship (e.g., linear, sigmoidal, asymptotic) by adding intermediate points to the curve (MacPherson et al. 2020; French et al. 2021). These semi-quantitative models can then serve as both starting points for quantitative modelling and management, and hypotheses that can be tested and refined through ongoing data collection and cycles of adaptive management (Fig. 1; Plowright et al. 2008; Downing, Van Meter, and Woolnough 2010; Pirotta et al. 2022).

### **2.2.2 Biological hierarchy/organization**

Biological hierarchy refers to the level of biological organisation of the response variable of interest, ranging from individual, to population, species, community, or whole ecosystems. Overall, it is a question of resolution and the answer depends on the researcher and their objectives: is it sufficient to use one SR function to describe a group of species (e.g. coldwater thermal guild, Hasnain et al. 2013; or size classes, Giacomini et al. 2016), or should multiple SR functions be used to describe the differences between species? A clear understanding of response variable location in the biological hierarchy is a pre-requisite for developing SR functions. CE models in ecology often focus on the population (i.e., local scale of a single species), but evaluating stressor impacts on community structure (multiple species within a taxonomic group) or ecosystem function (e.g. trophic level production) are also key goals of many CE assessments. SR functions can be developed with data explicit to any level within the biological hierarchy, and mechanistic theory can be used to scale functions up from one level to another (e.g., from the individual to the population; Schäfer and Piggott 2018; Pirotta et al. 2022). However, extrapolating responses across levels in a biological hierarchy should be done with care and transparency in underlying assumptions, as results may not scale as expected (Galic et al., 2018) and upscaling errors can propagate across levels.

SR functions at different levels of biological hierarchy are often qualitatively different (Simmons et al., 2021). At the individual level, multiple stressors affect individual performance (growth, fecundity, survival) in ways that can be directly measured using fairly standard ecophysiological or field ecology methods (Selong et al., 2001; Vander Vorste et al., 2020). Such methods allow

empirical SR functions to be developed to predict individual performance (e.g., effects of hypoxia on fish growth; Rosenfeld and Lee 2022); however, many biophysical models instead allow for the development of mechanistic SR functions of individual performance (e.g., drift-foraging bioenergetic models predicting temperature and velocity effects on salmonid growth; Naman et al. 2020). Similarly, many population-level SR functions are developed—either empirically or mechanistically (e.g., as individual-based models)—to link individual performance to population-level effects (Ayllón et al., 2019). At the community level, however, mechanistic SR functions are particularly challenging, as the response depends not only on the population performance of individual species along the stressor gradient, but also on interactions among multiple species (Turschwell et al., 2022). Similarly, mechanistic ecosystem-scale SR functions may be subject to complex interactions between species or functional groups (Turschwell et al., 2022). In contrast to mechanistic SR functions, developing empirical SR functions across all levels of the biological hierarchy is likely to be relatively straightforward, but will vary in difficulty depending on the linear or non-linear complexity of model fit to empirical data.

### ***2.2.3 Standardizing data for stressor-response functions***

Quantitative synthesis of multiple studies is a powerful way of building generic SR functions (Poorter et al. 2010; Rosenfeld and Lee 2022). Unlike conventional meta-analysis, the objective is not merely to document effect sizes and significance of a treatment, but rather to generate an empirical function that can be directly applied to prediction and management. Standardizing (normalizing) data from disparate studies may be an essential step in this process, particularly if the range of response and stressor values vary across studies. Various methods are available for

standardizing data, including dividing observations by the standard deviation (i.e., converting all response variables to units of SD; Smith 2000; Schielzeth 2010), or standardizing by the maximum value in each study, which re-scales all data between a range of 0-1 regardless of the original response variable or its units (Rosenfeld and Lee 2022; Wilding and Poff 2008). Poorter et al. (2010) provide a detailed overview of a third standardizing approach where the extracted data is normalized by dividing each observation by a shared reference value within the range of all datasets. It should also be noted that standardized data may not follow a normal distribution and transformation may be necessary for unbiased statistical inference.

#### **2.2.4 Spatial scale (dimension)**

Spatial scale refers to the geographical area of interest. Crudely defined, local scale refers to a relatively small area like a single lake or river site, where the subject is one or two populations or species, or a single community or ecosystem; regional scale might include multiple localities, usually with similar climatic or biogeographic characteristics (e.g., all lakes or rivers within the Great Lakes region or temperate lakes of North America); and global scale refers to multiple regions across the world. The appropriate scale for developing an SR function is study- and question-dependent, and classifying “domains” of spatial scale has challenged researchers for decades (Wiens, 1989). The challenge lies in understanding when ecological mechanisms do not hold across multiple scales, and thus choosing the correct spatial scale for modelling stressors and implementing management plans (Wiens, 1989).

Scale discontinuities or limitations in SR functions may arise due to local adaptation or other interacting stressors (see Interactions section below). For example, Meier et al. (2014) found

that the expression of genes related to immune and stress response differed among three Brown Trout (*Salmo trutta*) populations that experienced different temperature regimes in the wild; this local adaptation would limit the transferability of their SR relationships across sites and scales, particularly if similar local adaptation has taken place elsewhere. Whether or not a SR function spans multiple scales (i.e., can be generalized across a species' range) will likely depend on the specific stressor and the scope for local adaptation. Correctly identifying the appropriate domain of the stressor and response variables is a crucial step in CE modelling. Extrapolation of SR functions beyond the scale at which they were created requires transparency in assumptions and careful consideration of the potential for bias (MacPherson et al. 2020).

While spatial discontinuities in underlying mechanism may constrain SR function application to particular scales, scale mismatches between stressor and response may have far-reaching management implications. For example, management interventions to mitigate local effects of climate change on at-risk populations may require addressing proximate factors (e.g., riparian planting to cool and shade streams) rather than ultimate causation, because global warming is a global governance issue beyond the jurisdiction of regional wildlife management agencies.

### **2.2.5 Temporal scale**

Thinking about temporal scale in the context of SR functions and CE modelling can be a daunting task; the physiological and stage-specific processes of all organisms (e.g., growth, reproduction, metabolism) operate on different temporal scales, as do the stressors acting on them (Jackson et al. 2021). To simplify the overwhelming complexities associated with temporal

effects, recent stressor reviews categorize SR functions in terms of their trajectory type (e.g., pulse, constant, ramp, step; uni- or multivariable; stationary or non-stationary), modifying characteristics (e.g., duration, frequency), and pattern (e.g., presence of thresholds or time lags); all of which can vary across a single event, multiple events, or trajectories (Ryo et al., 2019). Such organisation can be helpful when thinking about the temporal scale of individual stressor relationships and the optimal frequency, duration, and lag time of observation to detect an effect. Understanding the characteristic generation or turnover time of a response (defined here as the time it takes to return to equilibrium following a perturbation) is essential. Failure to do so may result in temporal mismatches between stressor and response measurements with the potential to distort SR functions, or in extreme cases, a failure to detect them entirely. For example, a stressor like temperature can be defined in terms of maximum observed temperature, duration above a fixed threshold, maximum weekly average temperature, or cumulative degree days (Parkinson et al. 2016; Chezik et al. 2014), all of which differ in their duration of measurement and their suitability for characterizing different responses (Clusella-Trullas et al. 2021). To avoid getting lost in the overwhelming complexities of temporal considerations, it is important to have clearly defined stressor and response metrics that i) are grounded in clearly defined management objectives (Fig. 1, steps 2-3), and ii) integrate across the appropriate time scale based on a clear understanding of biology and underlying causation, as described below.

First, system (organism to ecosystem) response time must be understood. A system may have an immediate or delayed response to a stressor, and a short or prolonged response duration,

and thus the timing and duration of the measurement period is consequential. A misunderstanding of when and for how long a variable responds to a stressor, or the relevant duration of the stressor, will impact the shape of the SR function. For example, Hewitt and Norkko (2007) studied the effect of suspended sediment exposure (the stressor) on marine bivalve feeding rate (response). They found that increasing the duration of exposure to suspended sediment changed the shape of the feeding rate response from unimodal to a negative linear relationship. Although sample timing and duration may not always impact the validity of SR functions (and thus the CE model; Bell et al. 2013), it remains important to re-evaluate the shape of each stressor response function as new information becomes available (Pirotta et al., 2022). It is also important to evaluate the independence of consecutive stressor events; SR functions will need to account for an interaction between stressor order (timing) and impact if response times shorten with consecutive events, or if thresholds for response decline with consecutive perturbations (Fig. S1, Jackson et al. 2021; Ryo et al. 2019). For example, sensitivity of salmonids to high temperature events may increase over the summer low-flow period, lowering the temperature threshold where they seek thermal refuges by as much as 3°C (O'Sullivan et al., 2023).

Second, temporal mismatches between the data used to create SR functions and the duration of a simulation trajectory may inflate model error. It has been shown that estimates of minimum viable population size to avoid extinction increase with the length of the time series used to derive them, suggesting that empirical SR functions based on shorter data sets may underestimate true potential outcomes (Ludwig, 1999; Reed et al., 2003). Such temporal



mismatches could lead to systematic biases in CE model projections, which generally predict across temporal scales that greatly exceed the length of the data used to generate their constituent SR functions. Ultimately, if SR functions are calibrated using short-term studies—due to feasibility— model predictions and associated management interventions may have unexpected long-term outcomes. The potential for biases in SR functions due to short duration data sets needs to be carefully considered, particularly for processes that are sensitive to rare stochastic events (Ludwig, 1999).

Third, temporal complexities intensify at higher levels of biological organization. With multiple taxa to consider at community and ecosystem scales, some stressors (e.g., drought) will impact an entire generation of short-lived species but only a fraction of the lifespan of longer-lived species (Jackson et al. 2021; Fig. S1). Jackson et al. (2021) suggest—in the case of size-structured aquatic ecosystems—estimating the distribution of generation times within a community to decide on an appropriate timescale for measuring a community's response to multiple stressor events. Alternatively, an analysis of empirical data may help identify the intrinsic scale that best maximizes the explained variation in response.

### **2.2.6 Stressor Interactions**

Multi-stressor interactions have received considerable attention in the recent ecological literature (Duncan and Kefford, 2021; Schäfer and Piggott, 2018). The issues most relevant to practical stressor management are i) whether interactions are present for the stressors under

consideration; ii) whether they are consequential from a management perspective; and iii) how to accurately represent them in SR functions. Interactions are ultimately defined by a lack of independence between two or more stressors, but there is a confusing diversity of interaction types and impacts that are often difficult to discriminate among. Interactions are often classified based on the magnitude of their effect on the response (i.e., slope) relative to an additive model with no interactions. Synergy occurs when combined stressor effects are greater than expected relative to their independent effects, and antagonism represents muted combined stressor impacts relative to their additive independent effects (lower slope; Fig. 3a). Antagonisms that are sufficiently strong can lead to reversals, for instance, where the magnitude of impact or slope switches from negative to positive. However, this pattern is further complicated when the intercept (not just the slope) of the SR function is also altered under interactions because it can result in the interaction transitioning from antagonisms to synergies or vice versa over different ranges of stressor magnitude (Fig. 3b).

Although this simple classification of interactions based on the magnitude of biological outcomes is useful, it does not resolve the broad diversity of underlying *mechanisms* which can lead to synergy, additivity or antagonism (De Laender, 2018; Turschwell et al., 2022). This diversity of mechanism is best understood by first considering differences in underlying causation typology among interactions (i.e., the processes driving the interaction), their associated diagnostics, and differences in their biological consequences. The typology of interaction causation described below is intended to complement the well-established typology of magnitude and direction described above (i.e., synergies, antagonisms, and additivity).

### 2.2.6.1 Underlying causation types.

Causation type can be identified based on four broad categories of underlying process (mechanism) that generates the interaction. These include:

i) *Altered biophysical process.* In this case the biophysical mechanism underlying one stressor is altered by a second stressor, changing the biological response to a given magnitude (dose) of the first stressor. This is the most common understanding of an interaction, but not necessarily the most common causation in practice. One example is the joint effect of nutrient enrichment (eutrophication) and canopy cover (shading) on dissolved oxygen in stream ecosystems. Increased nutrients cause increased algal and microbial respiration, which depletes night-time dissolved oxygen, but only in unshaded streams, because light limitation under a closed canopy inhibits algal biomass accrual and associated respiration (Fig. 4a). This results in classic non-additivity of canopy and nutrient effects on dissolved oxygen (i.e., differences in slopes between low and high nutrient treatments; Fig. 4a). Note that in this classic case of a statistical interaction, the stressors involved may be completely uncorrelated (i.e., independent in magnitude; Fig. 4c).

ii) *Correlation of stressor magnitudes.* With this underlying mechanism, a second stressor does not alter the biological response to a given level of a first stressor, rather the second stressor directly alters the *magnitude* of the first stressor, resulting in an altered biological response along a single SR function (Fig. 4b). Often two stressors will co-vary because of a shared association with an underlying driver of both stressors (e.g., Lade et al. 2020); for

example, saturation levels of dissolved oxygen decrease with water temperature, purely as a consequence of thermally mediated physical gas exchange processes. Extending the riparian canopy example, a lack of canopy cover would be associated with disproportionately lower dissolved oxygen than a forested (shaded) treatment, but this is caused by higher temperatures in unshaded streams (i.e., a negative correlation between shading and temperature; Fig. 4d) rather than any functional effect of shading on the dissolved oxygen-temperature relationship (Fig. 4c), which remains unchanged.

**iii) Correlation of individual vulnerability to multiple stressors.** The “null model” for stressor interactions represents the expected pattern of stressor outcome when interactions are absent (i.e., a null hypothesis of no interaction). Schäfer and Piggott (2018) and earlier researchers (e.g., Folt et al. 1999) identified how the distribution of individual vulnerabilities to multiple stressors may affect the shape of the null model, which represents the inferred baseline additive condition without interaction. The three most basic null models are simple addition, multiplicative, and dominance, each associated with different individual responses to stressors (Fig. 5; see Schäfer and Piggott 2018 for additional null models).

Simple addition represents the classic ANOVA situation with no interaction, where the combined outcome is the additive effect of independent stressors (Fig. 5a). Computationally, stressor impacts on individuals can be thought of as acting in sequence (Schäfer and Piggott 2018; Orr et al. 2020; see mortality equations in Fig. 5). And if the stressor impact is mortality, full additivity is only possible if individual vulnerabilities to the different stressors

are strongly negatively correlated (Fig. 5a; i.e., individuals killed by stressor A would not be killed by stressor B). The multiplicative model occurs if individual stressor sensitivities are uncorrelated (Fig. 5b) because some individuals will in principle be killed by both stressors simultaneously, lowering the combined mortality rate relative to the simple additive model (Fig. 5b). Lastly, the dominance model occurs when vulnerability of individuals to both stressors is positively correlated; this implies that all individuals that would have died from the more moderate stressor would have also died from the most virulent stressor, so that the maximum stressor impact will be set by the stronger of the two stressors (Schäfer and Piggott 2018; Fig. 5c). According to Schäfer and Piggott (2018) each of these models, as described above and as illustrated in Fig. 5, represent null models with no interactions included, and differ only in the correlation of individual stressor vulnerabilities among individuals. However, the multiplicative and dominance null models can be considered antagonistic relative to the simple addition model because in both cases the effects of combined stressors are less than the simple addition model (Fig. 5, right hand panels), even without interactions (Dev and Koops, 2021). (Note that the ecological stressor pair chosen for illustration of dominance in Fig. 5—starvation and disease risk—may not be entirely independent).

It is important to note that the inferences above and illustrated in Fig. 5 apply best to mortality impacts (Schäfer and Piggott, 2018). For example, if stressor impacts are sub-lethal (e.g., reduced growth) then combined stressor effects on individuals will not be redundant in the dominant model as they are for mortality, i.e., growth of vulnerable individuals could be

simultaneously reduced by both stressors, resulting in a multiplicative stressor impact rather than a dominance one.

Understanding the mechanism underlying different null models may be useful for predicting the type of interaction outcome (e.g., additive, synergistic, antagonistic) from any unique pair of stressors under consideration, particularly when empirical data for interactions are lacking. For instance, individuals that are weak, starving, or have depressed immune systems will share vulnerability to mortality from multiple stressors like disease, parasites, and stress, leading to an expectation of dominance as the null stressor model. In contrast, stressors that generate mortality that is random, stochastic, or unrelated to organism performance would be expected to cooperate independently and follow a multiplicative null model. In both cases, combined stressor impacts could reasonably be expected to be less than the additive null model (Fig. 5).

Note that none of the null models in Fig. 5 generate synergistic effects relative to the simple additive null model (Dey and Koops, 2021). Synergies generally arise when one stressor alters the actual mechanistic pathway of a second stressor to make it more severe, and are therefore more idiosyncratic and do not necessarily fit well into the general pathways identified in Fig. 5. While antagonisms can also arise from stressor-specific pathway alterations, the nature of correlations of individual vulnerability in generating antagonisms may be generalizable in ecology and favour antagonisms over synergisms. This inference is supported by recent meta-analyses (see Tekin et al. 2020 and refs therein; Lopez et al. 2022) that identify antagonisms and additivity as the most common interactions.

However, this interpretation is sensitive to the choice of simple addition as the reference null model, since simple addition may generate higher mortality rates than other null models even in the absence of interaction (Dey and Koops 2021; Fig. 5).

**iv) *Statistical or analytic artefacts.*** This category of causation includes statistical design and power issues (Catford et al., 2022). For instance, data collection over a narrow range of low and high stressor values may cause a continuous bell-shaped non-linear performance curve to appear linear with opposite slopes (i.e., implying a hidden interaction) when sampled over truncated or non-overlapping stressor ranges (Catford et al. 2022; Rosenfeld et al. 2022).

Disjunct segments of sigmoidal functions can also be mistaken for spurious interactions.

#### **2.2.6.2 *Diagnostics of interaction presence.***

Often it is unknown whether interactions are present or likely to be severe. Carefully screening the results of monitoring or stressor management interventions can be used to qualitatively or statistically identify whether interactions are present. Non-independence of stressors in the form of correlations among stressor magnitudes, or correlations in the vulnerability of individuals, provide a strong reason for managers to anticipate correlative interactions. For linear relationships, a classic statistical interaction (i.e., non-additivity represented by a change in slope; Fig. 6 is the most robust evidence of a mechanistic stressor interaction. However, this picture becomes complicated for interactions among non-linear stressors. Additivity between non-linear stressors may generate patterns that look similar to interactions between linear stressors, and the ability to discriminate between these patterns may be limited if variance is

high (i.e., true non-linear functions with real slope changes may appear linear over their full range if error variation is high).

It is important to note that the diagnostics for interaction are not universal and may be in conflict (Duncan and Kefford, 2021). For instance, independence of stressor impacts is implied by classic additivity models where factorial designs result in parallel slopes (Figs. 4 and 5).

However, for models that consider the role of individual variation in stressor vulnerability, the simple additivity model assumes a negative correlation between sensitivity of individuals to the paired stressors (Fig. 5a), indicating a lack of independence in stressor sensitivities at the individual level. Similarly, while the null models illustrated in Fig. 5 do not include interactions, the multiplicative and dominance models are antagonistic in outcome relative to the simple addition model, and stressors outcomes on individuals in the simple addition and dominance models lack independence even though the models are null models without interaction.

### ***2.2.6.3 Putting interactions into perspective for applied management***

While the nuances of multi-stressor interactions are fascinating, they may be irrelevant for many practical ecological applications, particularly in many data deficient contexts that often confront natural resource managers. Unlike toxicological stressors which lend themselves to multi-factorial laboratory experiments, generating meaningful data to estimate population- or ecosystem-level impacts of multiple ecological stressors is very challenging (Rullens et al., 2022). In practical terms, understanding interactions is only worthwhile when it allows better prediction of stressor impacts and the safe operating space for stressor magnitudes (Fig. 7), or if



it meaningfully improves regulatory decisions to control stressor levels (e.g., harvest rates, effluent releases, habitat restoration, mitigation procedures).

Stressors that are harmful (e.g., sediment inputs to streams, eutrophication and associated hypoxia) are generally regulated out of concern for their main effects irrespective of any interactions. If interactions are present and substantive, then modifying stressor management to account for interactions may be warranted. On the other hand, if interactions are relatively small or within the range of detection error, then they will not meaningfully affect management decisions, which can therefore default to managing main effects (Fig. 7). Synergies are exceptional in that they may require control of stressors at low levels that might not otherwise warrant management for their main effects alone; these are the potential ecological surprises of greatest concern (Jackson et al., 2016; Wade et al., 2020), and have therefore received the greatest attention, leading to a publication bias in terms of their frequency relative to antagonisms (Côté et al., 2016; Tekin et al., 2020). In data deficient situations where interactions are uncertain, stressor mechanisms can be used to anticipate the null model and potential interaction types (e.g., Fig. 5); cycles of monitoring and adaptive management can then be used to identify greater- (synergism) or lesser-than-expected (antagonism) effects of stressor reduction to refine understanding of both interaction effects and management responses (Fig. 7). Thoughtful stressor management should ideally focus on exploiting interactions to mitigate stressor impacts and avoid tipping points (Gladstone-Gallagher et al., 2019; Larned and Schallenberg, 2019; Scholes and Kruger, 2011). Just as the goal of understanding non-linear main effects is to identify thresholds so that they can be avoided,

correctly identifying interactions should also allow identification of stressor ranges with rapid slope change.

Generally, managing interactions can be treated as an extension of managing main effects. Unless interactions are overwhelmingly strong, managing them usually requires a change in degree rather than a change in approach. The suite of available management activities to mitigate stressors should be similar irrespective of interactions, although the identity of the priority stressor may change. For instance, capitalizing on antagonism between riparian shading and eutrophication means that a short-term focus on streamside reforestation to reduce light may be the priority for reducing eutrophication and hypoxia, especially where nutrient inputs are difficult to control. While at face value the generalization to exploit interactions in management is insightful, most natural resource managers have been aware of and using antagonistic effects like riparian restoration for decades, even if they have not labelled them as such.

Inevitably, the appropriate investment of time and resources for assessing presence or strength of interactions will depend on their likely consequences. Arguably, the most pervasive ecological interaction globally is between species identity and stressor effects (e.g., how species identity affects temperature or salinity tolerance); this interaction is at the core of comparative physiology and community ecology (Thompson et al. 2018) as well as most climate change modelling. Differences in stressor tolerances among taxa may be hugely consequential for CE modelling, since it drives differences in safe operating spaces and the appropriateness of sharing SR functions among data-deficient species, a pervasive practice in ecological modelling

(Trudel et al. 2004). Beyond species identity interactions, the diversity of potential interactions is unlimited; without a priori reason to expect specific interaction combinations, natural resource managers and biologists are best served by managing main effects, while being alert to anomalies that could signal cryptic interactions.

### **2.2.7 Uncertainty**

The terms variability, stochasticity, and uncertainty are often used interchangeably but their meanings differ (Tumeo, 1994). Variability represents deviation of some quantity around the mean while stochasticity is variability caused by random fluctuations, with both contributing to uncertainty. Put simply, uncertainty is the notion of doubt about a quantity (Tumeo, 1994). Since there is always some doubt about the relationship between a stressor and response, there is uncertainty in all SR functions. SR functions are models created to simplify complex relationships for the purpose of predicting hypothetical outcomes and the lack of complete knowledge—due to data deficiency or the simplification process—begets uncertainty.

There are many frameworks for conceptualizing uncertainty, each with their own descriptions and classifications (Regan et al. 2002; Shea et al. 2002; Walker et al. 2003; Gissi et al. 2017; Stelzenmüller et al. 2020; Rullens et al. 2022). Among these, a well-cited study by Walker et al. (2003) presents a categorical matrix to visualise uncertainty in three key dimensions. We modified their original axis labels (location, level, and nature of uncertainty; Walker et al. 2003) to i) component of uncertainty; ii) magnitude of uncertainty; and iii) source of uncertainty, to make them more explicitly intuitive. The five components of uncertainty include context (e.g., issues, questions, outcomes of interest), model structure (e.g., density dependent vs. density

independent, discrete versus continuous), input data, and parameters (which to include?), all of which independently contribute to emergent uncertainty. Magnitude of uncertainty represents a spectrum ranging from determinism (complete knowledge) to total ignorance (the unknown unknown, i.e., completely data deficient species). Source of uncertainty represents a reducibility spectrum, and refers to whether uncertainty is epistemic or inherent; epistemic uncertainty is reducible by increasing knowledge, whereas inherent uncertainty is irreducible, because improving our understanding of the variability of the system or natural phenomena is unattainable (i.e., further knowledge acquisition will not reduce uncertainty). Other studies may categorise uncertainty differently (Tumeo 1994; Regan et al. 2002; Shea et al. 2002; Lande et al. 2003; McGowan et al. 2011) but Walker et al.'s (2003) breakdown is comprehensive, and the uncertainty matrix provides a useful tool to help prioritise uncertainty reduction based on data acquisition and reducibility (Gissi et al., 2017; Rullens et al., 2022; Stelzenmüller et al., 2020).

Understanding and minimizing uncertainty when creating SR functions requires i) identifying the components of uncertainty; ii) categorizing them by source and magnitude; and iii) minimizing epistemic (reducible) uncertainty while accounting for inherent (irreducible) uncertainty (Fig. 8). Adaptive management allows this to be an iterative process. Uncertainty is particularly problematic when there is little information about a species, and expert opinion becomes a good starting point during the early stages of SR function development. The following recommendations may aid the reader in moving beyond the early stages of data deficiency.

i) Regan et al. (2002) recommended using conventional statistical techniques (e.g., confidence intervals, upper and lower bounds) and probability distributions to represent uncertainty, or in the case of systematic errors, recognizing and removing potential biases. For empirical SR functions, this can be as simple as including 95% confidence intervals around predictions; for expert-based SR functions, upper and lower bounds can be established based on the most extreme of plausible functions. More advanced non-linear modelling approaches (e.g., Generalized Additive Mixed Models, Hastie and Tibshirani 1986) also generate confidence intervals around model predictions, and methods are available for creating confidence intervals around optima and range limits of non-linear functions (e.g., Ashcroft et al. 2016). Transparency is key in dealing with uncertainty (Schuwirth et al., 2019), and confidence in the SR function and underlying assumptions needs to be carefully documented, ideally in an open-access data base (Rosenfeld et al. 2022; MacPherson et al. 2020).

ii) Milner-Gulland and Shea (2017) suggest power analyses to understand the benefits of increasing sampling effort to reduce uncertainty and to assess the cost of error, which are often asymmetric. For example, in the context of recovery planning for Species at Risk, the cost (in terms of extinction) of incorrectly identifying a population decline (type I error) is much lower than failing to identify a population decline (type 2 error; Milner-Gulland and Shea 2017), which can be catastrophic. Strategic consideration of uncertainty for individual SR functions may identify particular ranges that will disproportionately benefit from reducing uncertainty (e.g., by collecting data). For instance, there is often high confidence in stressor

impacts at very high and very low stressor levels (i.e., negligible vs. catastrophic); in this case, resolving uncertainty at intermediate stressor levels becomes the priority (i.e., determine the shape of the SR function), particularly when thresholds are suspected. In contrast, the opposite may be true for linear functions if data at high and low stressor levels is sparse.

iii) McGowan et al. (2011) recommended sensitivity analyses, which allow researchers to assess sensitivity of model outcomes to uncertainty in different parameters. This is most relevant to mechanistic SR functions with multiple parameters, or in CE models with SR functions of different uncertainty.

One recurring problem for data deficient applications of complex models is that multiplicative error rapidly inflates uncertainty so that confidence intervals on predictions overlap with zero. This does not mean that quantitative prediction should be abandoned; rather it provides a graphic reminder of the scale of systematic uncertainty, and the need to reduce it by increasing confidence in underlying SR functions or other sources of error.

### 3. Adaptive management

The CE modelling approach presented here fits into an adaptive management framework, a paradigm created to navigate an uncertain future through a constant cycle of evolving goals, models, predictions, interventions, and outcomes (Lindenmayer and Likens, 2009). Plowright et al. (2008) cleverly argue that this approach uses triangulation—analogueous to land surveying—where multiple methodologies (e.g., theoretical, lab, and field studies) are used to refine the most effective strategies for maintaining complex systems. In this way, the manager can make

adjustments based on learned information from previous iterations of the cycle or complimentary methodologies supported by multiple lines of evidence (Plowright et al., 2008; Shea et al., 2002). Therefore, rather than reacting only when issues arise (i.e., “putting out fires”), adaptive management attempts to predict and prevent unwanted or unexpected outcomes (Boyd et al., 2015; Fuerth, 2011; Shea et al., 2002). An unexpected outcome tells us that we might have misinterpreted the underlying mechanism(s), while an expected outcome tells us that our assumptions were likely valid, and a switch from expected to unexpected outcomes (or vice versa) may be a warning that the environment is changing and/or that the system’s components (i.e., stressors and responses) might be interacting in novel, unexplored ways (Côté et al. 2016). All of this information is critical for assessing the long-term success of management interventions.

#### **4. Concluding remarks**

In this review, we provide pragmatic guidance on developing SR functions. The outcome of management decisions and trade-offs in complex socio-ecological systems are neither intuitive nor obvious, and unstructured decisions based on qualitative impressions can be severely biased (Kahneman, 2011). Scientists and managers need to accelerate the transition from qualitative decision-making to a process that is more explicitly informed by quantitative relationships with transparent uncertainty (Hodgson et al. 2019). SR functions are central to this transition; as discrete components embedded in higher order models (e.g., cumulative effects or PVA), they provide a durable foundation for structured decision-making in natural resource management.

As a final recommendation, we ask the researcher to keep the big picture in mind and not get lost in the weeds. It is important to remember that with limited data availability, developing and implementing SR functions for use in a CE modelling framework is a continuous cycle of manipulation and validation (Castañeda et al., 2021). This process takes time. Therefore, if available data and expert opinion suggests that particular stressors or interactions are not important to a specific question or system, this inference should be documented, and energy and resources directed to more pressing concerns.

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### **References**

Ashcroft, M.B., Casanova-Katny, A., Mengersen, K., Rosenstiel, T.N., Turnbull, J.D., Wasley, J.,

Waterman, M.J., Zúñiga, G.E., Robinson, S.A., 2016. Bayesian methods for comparing species physiological and ecological response curves. *Ecol. Inform.* 34, 35–43.

<https://doi.org/10.1016/j.ecoinf.2016.03.001>

Ayllón, D., Railsback, S.F., Harvey, B.C., García Quirós, I., Nicola, G.G., Elvira, B., Almodóvar, A.,

2019. Mechanistic simulations predict that thermal and hydrological effects of climate



change on Mediterranean trout cannot be offset by adaptive behaviour, evolution, and increased food production. *Sci. Total Environ.* 693.

<https://doi.org/10.1016/j.scitotenv.2019.133648>

Bell, T., Neill, W.E., Schluter, D., 2003. The effect of temporal scale on the outcome of trophic cascade experiments. *Oecologia* 134, 578–586. [https://doi.org/10.1007/s00442-002-1135-](https://doi.org/10.1007/s00442-002-1135-x)

x

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.F., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioglu, M., Bondar-Kunze, E., Borja, A., Branco, P., Bucak, T., Buijse, A.D., Cardoso, A.C., Couture, R.M., Cremona, M., de Zwart, D., Feld, C.K., Ferreira, M.T., Feuchtmayr, H., Gessner, M.O., Gieswein, A., Globevnik, L., Graeber, D., Graf, W., Gutiérrez-Cánovas, C., Hanganu, J., Işkan, U., Järvinen, M., Jeppesen, E., Kotamäki, N., Kuijper, M., Lemm, J.U., Lu, S., Schiemann, A.L., Mischke, U., Moe, S.J., Nöges, P., Nöges, T., Ormerod, S.J., Panagopoulos, Y., Phillips, G., Posthuma, L., Pouso, S., Prudhomme, C., Rankinen, K., Rasmussen, J.L., Richardson, J., Sagouis, A., Santos, J.M., Schäfer, R.B., Schinegger, R., Schnitzler, S., Schneider, S.C., Schülting, L., Segurado, P., Stefanidis, K., Sures, B., Thackeray, S.J., Torunen, J., Uyarra, M.C., Venohr, M., von der Ohe, P.C., Willby, N., Hering, D., 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nat. Ecol. Evol.* 4, 1060–1068. [https://doi.org/10.1038/s41559-020-1216-](https://doi.org/10.1038/s41559-020-1216-4)

4

Boyd, E., Nykvist, B., Borgström, S., Stacewicz, I.A., 2015. Anticipatory governance for social-ecological resilience. *Ambio* 44, 149–161. <https://doi.org/10.1007/s13280-014-0604-x>

- Castañeda, R.A., Ackerman, J.D., Chapman, L.J., Cooke, S.J., Cuddington, K., Dextrase, A.J., Jackson, D.A., Koops, M.A., Krkošek, M., Loftus, K.K., Mandrak, N.E., Martel, A.L., Molnár, P.K., Morris, T.J., Pitcher, T.E., Poesch, M.S., Power, M., Pratt, T.C., Reid, S.M., Rodríguez, M.A., Rosenfeld, J., Wilson, C.C., Zanatta, D.T., Drake, D.A.R., 2021. Approaches and research needs for advancing the protection and recovery of imperilled freshwater fishes and mussels in Canada. *Can. J. Fish. Aquat. Sci.* 78, 1356–1370.  
<https://doi.org/10.1139/cjfas-2020-0374>
- Catford, J.A., Wilson, J.R.U., Pyšek, P., Hulme, P.E., Duncan, R.P., 2022. Addressing context dependence in ecology. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2021.09.007>
- Chezik, K.A., Lester, N.P., Venturelli, P.A., 2014. Fitting growth and degree-days II: selecting a base temperature for an among-population study. *Can. J. Fish. Aquat. Sci.* 71, 1303–1311.  
<https://doi.org/10.1139/cjfas-2013-0015>
- Clusella-Trullas, S., Garcia, R.A., Terriblanche, J.S., Hoffmann, A.A., 2021. How useful are thermal vulnerability indices? *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2021.07.001>
- Connolly, S.R., Keith, S.A., Colwell, R.K., Rahbek, C., 2017. Process, Mechanism, and Modeling in Macroecology. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2017.08.011>
- Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B Biol. Sci.*  
<https://doi.org/10.1098/rspb.2015.2592>
- De Laender, F., 2018. Community- and ecosystem-level effects of multiple environmental

change drivers: Beyond null model testing. *Glob. Chang. Biol.*

<https://doi.org/10.1111/gcb.14382>

Dearing, J.A., Wang, R., Zhang, K., Dyke, J.G., Haberl, H., Hossain, M.S., Langdon, P.G., Lenton, T.M., Raworth, K., Brown, S., Carstensen, J., Cole, M.J., Cornell, S.E., Dawson, T.P., Doncaster, C.P., Eigenbrod, F., Flörke, M., Jeffers, E., Mackay, A.W., Nykvist, B., Poppy, G.M., 2014. Safe and just operating spaces for regional socio-ecological systems. *Glob. Environ. Chang.* 28, 227–238. <https://doi.org/10.1016/j.gloenvcha.2014.06.012>

Dey, C.J., Koops, M.A., 2021. The consequences of null model selection for predicting mortality from multiple stressors. *Proc. R. Soc. B Biol. Sci.* 288. <https://doi.org/10.1098/rspb.2020.3126>

Downing, J.A., Van Meter, P., Woolnough, D., 2010. Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels, *Animal Biodiversity and Conservation*.

Duinker, P.N., Burbidge, E.L., Boardley, S.R., Greig, L.A., 2013. Scientific dimensions of cumulative effects assessment: Toward improvements in guidance for practice. *Environ. Rev.* <https://doi.org/10.1139/er-2012-0035>

Duncan, R.P., Kefford, B.J., 2021. Interactions in statistical models: Three things to know. *Methods Ecol. Evol.* <https://doi.org/10.1111/2041-210X.13714>

Feld, C.K., Segurado, P., Gutiérrez-Cánovas, C., 2016. Analysing the impact of multiple stressors in aquatic biomonitoring data: A ‘cookbook’ with applications in R. *Sci. Total Environ.* 573,

1320–1339. <https://doi.org/10.1016/j.scitotenv.2016.06.243>

Folt, C.L., Chen, C.Y., Moore, M. V., Burnaford, J., 1999. Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* 44, 864–877.

[https://doi.org/10.4319/lo.1999.44.3\\_part\\_2.0864](https://doi.org/10.4319/lo.1999.44.3_part_2.0864)

French, S., Hanea, A.M., Bedford, T., Nane, G.F., 2021. Introduction and overview of structured, in: French, S., Hanea, A.M., Nane, G.F., Bedford, T. (Eds.), *Expert Judgement and Risk Analysis*. 2021 Springer Nature Switzerland AG, pp. 1–16. [https://doi.org/DOI:10.1007/978-3-030-46474-5\\_1](https://doi.org/DOI:10.1007/978-3-030-46474-5_1)

Fuerth, L., 2011. Operationalizing Anticipatory Governance. *Prism* 2, 31–46.

<https://doi.org/10.2307/26469147>

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. *Ecol. Lett.* <https://doi.org/10.1111/ele.12923>

Geary, W.L., Nimmo, D.G., Decherty, T.S., Ritchie, E.G., Tulloch, A.I.T., 2019. Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.13427>

Giacomini, H.C., Shuter, B.J., Baum, J.K., 2016. Size-based approaches to aquatic ecosystems and fisheries science: a symposium in honour of Rob Peters. *Can. J. Fish. Aquat. Sci.* 73, 471–476. <https://doi.org/10.1139/cjfas-2016-0100>

Gissi, E., Menegon, S., Sarretta, A., Appiotti, F., Maragno, D., Vianello, A., Depellegrin, D.,

- Venier, C., Barbanti, A., 2017. Addressing uncertainty in modelling cumulative impacts within maritime spatial planning in the Adriatic and Ionian region. *PLoS One* 12. <https://doi.org/10.1371/journal.pone.0180501>
- Gladstone-Gallagher, R. V., Hope, J.A., Bulmer, R.H., Clark, D.E., Stephenson, F., Mangan, S., Rullens, V., Siwicka, E., Thomas, S.F., Pilditch, C.A., Savage, C., Thrush, S.F., 2019. Old Tools, New Ways of Using Them: Harnessing Expert Opinions to Plan for Surprise in Marine Socio-Ecological Systems. *Front. Mar. Sci.* 6. <https://doi.org/10.3389/fmars.2019.00696>
- Halpern, B.S., Fujita, R., 2013. Assumptions, challenges, and future directions in cumulative impact analysis. *Ecosphere* 4. <https://doi.org/10.1890/ES13-00181.1>
- Hasnain, S.S., Shuter, B.J., Minns, C.K., 2013. Phylogeny influences the relationships linking key ecological thermal metrics for North American freshwater fish species. *Can. J. Fish. Aquat. Sci.* 70, 964–972. <https://doi.org/10.1139/cjfas-2012-0217>
- Hastie, T., Tibshirani, R., 1986. Generalized additive models. *Stat. Sci.* 1, 297–310.
- Hewitt, J.E., Norkko, J., 2007. Incorporating temporal variability of stressors into studies: An example using suspension-feeding bivalves and elevated suspended sediment concentrations. *J. Exp. Mar. Bio. Ecol.* 341, 131–141. <https://doi.org/10.1016/j.jembe.2006.09.021>
- Hodgson, E.E., Halpern, B.S., Essington, T.E., 2019. Moving beyond silos in cumulative effects assessment. *Front. Ecol. Evol.* 7. <https://doi.org/10.3389/fevo.2019.00211>
- Holling, C.S., Bazykin, A., Bunnell, P., Clark, W.C., Gallop, G.C., Gross, J., Hilborn, R., Jones, D.D.,

- Peterman, R.M., Rabinovich, J.E., Steele, J.H., Waters, C.J., 1978. Adaptive environmental assessment and management, First. ed. John Wiley & Sons, London.
- Jackson, M.C., Loewen, C.J.G.G., Vinebrooke, R.D., Chimimba, C.T., 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Glob. Chang. Biol.* 22, 180–189.  
<https://doi.org/10.1111/gcb.13028>
- Jackson, M.C., Pawar, S., Woodward, G., 2021. The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems. *Trends Ecol. Evol.*  
<https://doi.org/10.1016/j.tree.2021.01.005>
- Jensen, D.W., Steel, E.A., Fullerton, A.H., Pess, G.R., 2009. Impact of fine sediment on egg-to-fry survival of pacific salmon: A meta-analysis of published studies. *Rev. Fish. Sci.* 17, 348–359.  
<https://doi.org/10.1080/106412609027116954>
- Kahneman, D., 2011. *Thinking fast and slow*, 1st ed. Farrar, Straus and Giroux, New York.
- Lade, S.J., Steffen, W., de Vries, W., Carpenter, S.R., Donges, J.F., Gerten, D., Hoff, H., Newbold, T., Richardson, K., Rockström, J., 2020. Human impacts on planetary boundaries amplified by Earth system interactions. *Nat. Sustain.* 3, 119–128. <https://doi.org/10.1038/s41893-019-0454-4>
- Lande, R., Engen, S., Saether, B.-E., 2003. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press.
- Larned, S.T., Schallenberg, M., 2019. Stressor-response relationships and the prospective management of aquatic ecosystems. *New Zeal. J. Mar. Freshw. Res.*

<https://doi.org/10.1080/00288330.2018.1524388>

Lindenmayer, D.B., Likens, G.E., 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends Ecol. Evol.* 24, 482–486.

<https://doi.org/10.1016/j.tree.2009.03.005>

Lopez, B.E., Allen, J.M., Dukes, J.S., Lenoir, J., Vil, M., Blumenthal, D.M., Beaury, E.M., Fusco, E.J., Laginhas, B.B., Lyn Morelli, T., O, M.W., B Sorte, C.J., Maceda-Veiga, A., Whitlock, R., Bradley, B.A., by James Clark, E., designed research, B., performed research, B., analyzed data, R., 2022. Global environmental changes more frequently offset than intensify detrimental effects of biological invasions. <https://doi.org/10.1073/pnas>

Ludwig, D., 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80, 298–310.

<https://doi.org/https://doi.org/10.2307/176998>

MacMillan, D.C., Marshall, K., 2006. The Delphi process - An expert-based approach to ecological modelling in data-poor environments. *Anim. Conserv.* 9, 11–19.

<https://doi.org/10.1111/j.1469-1795.2005.00001.x>

MacPherson, L., Sullivan, M., Reilly, J., Paul, A., Canada, O., 2020. Canadian Science Advisory Secretariat (CSAS) Alberta's Fisheries Sustainability Assessment: A Guide to Assessing Population Status, and Quantifying Cumulative Effects using the Joe Modelling Technique.

MacPherson, L.M., Reilly, J.R., Neufeld, K.R., Sullivan, M.G., Paul, A.J., Johnston, F.D., 2023.

Every little bit doesn't help: a cumulative effects modelling process to prioritize recovery actions for bull trout and species at risk. *Fish. Manag. Ecol.* In Revision.

Mangel, M., Talbot, L.M., Meffe, G.K., Agardy, M.T., Alverson, D.L., Barlow, J., Botkin, D.B., Budowski, G., Clark, T., Cooke, J., Crozier, R.H., Dayton, P.K., Elder, D.L., Fowler, C.W., Funtowicz, S., Giske, J., Hofman, R.J., Holt, S.J., Kellert, S.R., Kimball, L.A., Ludwig, D., Magnusson, K., Malayang III, B.S., Mann, C., Norse, E.A., Northridge, S.P., Perrin, W.F., Perrings, C., Norse, E.A., Northridge, S.P., Perrin, W.F., Perrings, C., Peterman, R.M., Rabb, G.B., Regier, H.A., Reynolds III, J.E., Sherman, K., Sissenwine, M.P., Smith, T.D., Starfield, A., Taylor, R.J., Tillman, M.F., Toft, C., Twiss Jr., J.R., Wilen, J., Young, T.P., 1996. Principles for the conservation of wild living resources. *Ecol. Appl.* 6, 338–362.

Marquet, P.A., Allen, A.P., Brown, J.H., Dunne, J.A., Enquist, B.J., Gillooly, J.F., Gowaty, P.A., Green, J.L., Harte, J., Hubbell, S.P., O'Dwyer, J., Ollie, J.G., Ostling, A., Ritchie, M., Storch, D., West, G.B., 2014. On theory in ecology. *Bioscience*.  
<https://doi.org/10.1093/biosci/biuc098>

McGowan, C.P., Runge, M.C., Larson, M.A., 2011. Incorporating parametric uncertainty into population viability analysis models. *Biol. Conserv.* 144, 1400–1408.  
<https://doi.org/10.1016/j.biocon.2011.01.005>

Meier, K., Hansen, M.M., Normandeau, E., Mensberg, K.L.D., Frydenberg, J., Larsen, P.F., Bekkevold, D., Bernatchez, L., 2014. Local adaptation at the transcriptome level in brown trout: Evidence from early life history temperature genomic reaction norms. *PLoS One* 9.  
<https://doi.org/10.1371/journal.pone.0085171>

Milner-Gulland, E.J., Shea, K., 2017. Embracing uncertainty in applied ecology. *J. Appl. Ecol.*  
<https://doi.org/10.1111/1365-2664.12887>



Naman, S.M., Rosenfeld, J.S., Neuswanger, J.R., Enders, E.C., Hayes, J.W., Goodwin, E.O.,

Jowett, I.G., Eaton, B.C., 2020. Bioenergetic Habitat Suitability Curves for Instream Flow Modeling: Introducing User-Friendly Software and its Potential Applications. *Fisheries* 45, 605–613. <https://doi.org/10.1002/fsh.10489>

O’Sullivan, A.M., Corey, E.M., Collet, E.N., Helminen, J., Curry, R.A., MacIntyre, C., Linnansaari, T., 2023. Timing and frequency of high temperature events trend the onset of behavioural thermoregulation in Atlantic salmon ( *Salmo salar* ). *Conserv. Physiol.* 11. <https://doi.org/10.1093/conphys/coac079>

Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C., van den Brink, P.J., de Laender, F., Stoks, R., Holmestrup, M., Matthaei, C.D., Monk, W.A., Penk, M.R., Leuzinger, S., Schäfer, R.B., Piggott, J.J., 2020. Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. *Proc. R. Soc. B Biol. Sci.* <https://doi.org/10.1098/rspb.2020.0421>

Parkinson, E.A., Lea, E. V., Nolitz, M.A., Knudson, J.M., Moore, R.D., 2016. Identifying Temperature Thresholds Associated with Fish Community Changes in British Columbia, Canada, to Support Identification of Temperature Sensitive Streams. *River Res. Appl.* 32, 330–347. <https://doi.org/10.1002/rra.2867>

Peters, R.H., 1986. The role of prediction in Limnology. *Limnol. Ocean.* 31, 1143–1159.

Piggott, J.J., Lange, K., Townsend, C.R., Matthaei, C.D., 2012. Multiple Stressors in Agricultural Streams: A Mesocosm Study of Interactions among Raised Water Temperature, Sediment

Addition and Nutrient Enrichment. PLoS One 7.

<https://doi.org/10.1371/journal.pone.0049873>

Pirotta, E., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., Kraus, S.D., Miller, P.J.O., Moore, M.J., Photopoulou, T., Rolland, R.M., Schwacke, L., Simmons, S.E., Southall, B.L., Tyack, P.L., 2022. Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. *Sci. Total Environ.*

<https://doi.org/10.1016/j.scitotenv.2022.153322>

Plowright, R.K., Sokolow, S.H., Gorman, M.E., Daszak, P., Foley, J.E., 2008. Causal inference in disease ecology: Investigating ecological drivers of disease emergence. *Front. Ecol. Environ.* <https://doi.org/10.1890/070086>

Poff, N.L., Richter, B.D., Arthington, A.H., Burn, S.E., Naiman, R.J., Kendy, E., Acreman, M., Apse, C., Bledsoe, B.P., Freeman, M.C., Henriksen, J., Jacobson, R.B., Kennen, J.G., Merritt, D.M., O’Keeffe, J.H., Olden, J.D., Rogers, K., Tharme, R.E., Warner, A., 2010. The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. *Freshw. Biol.* 55, 147–170. <https://doi.org/10.1111/j.1365-2427.2009.02204.x>

Poff, N.L., Zimmerman, J.K.H., 2010. Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshw. Biol.*

<https://doi.org/10.1111/j.1365-2427.2009.02272.x>

Poorter, H., Niinemets, Ü., Walter, A., Fiorani, F., Schurr, U., 2010. A method to construct dose-

response curves for a wide range of environmental factors and plant traits by means of a meta-analysis of phenotypic data. *J. Exp. Bot.* 61, 2043–2055.

<https://doi.org/10.1093/jxb/erp358>

Railsback, S.F., 2016. Why it is time to put PHABSIM out to pasture. *Fisheries* 41, 720–725.

<https://doi.org/10.1080/03632415.2016.1245991>

Reed, D.H., O'grady, J.J., Brook, B.W., Ballou, J.D., Frankham, R., 2013. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biol. Conserv.* 113, 23–34.

Regan, H.M., Colyvan, M., Burgman, M.A., 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology, *Ecological Applications*.

Rist, L., Felton, A., Samuelsson, L., Sandström, C., Rosvall, O., 2013. A new paradigm for adaptive management. *Ecol. Soc.* 18 <https://doi.org/10.5751/ES-06183-180463>

Rockström, J., Steffen, W., Noone, K.N., Persson, Å., Chapin, S.F., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J.A., 2009. A safe operating space for humanity. *Nature* 461, 472–475.

Rosenfeld, J., Gonzalez-Espinosa, P., Jarvis, L., Enders, E., Bayly, M., Paul, A., Macpherson, L., Moore, J., Sullivan, M., Ulaski, M., Wilson, K., 2022. Stressor-response functions as a generalizable model for context dependence. *Trends Ecol. Evol.* 37, 1032–1035.

- Rosenfeld, J., Lee, R., 2022. Thresholds for Reduction in Fish Growth and Consumption Due to Hypoxia: Implications for Water Quality Guidelines to Protect Aquatic Life. *Environ. Manage.* 70, 431–447. <https://doi.org/10.1007/s00267-022-01678-9>
- Rosenfeld, J.S., 2017. Developing flow–ecology relationships: Implications of nonlinear biological responses for water management. *Freshw. Biol.* <https://doi.org/10.1111/fwb.12948>
- Rullens, V., Stephenson, F., Hewitt, J.E., Clark, D.E., Pilditch, C.A., Thrush, S.F., Ellis, J.I., 2022. The impact of cumulative stressor effects on uncertainty and ecological risk. *Sci. Total Environ.* 842. <https://doi.org/10.1016/j.scitotenv.2022.156877>
- Ryo, M., Aguilar-Trigueros, C.A., Pinek, L., Miller, L.A.H., Rillig, M.C., 2019. Basic Principles of Temporal Dynamics. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2019.03.007>
- Schäfer, R.B., Piggott, J.J., 2018. Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. *Glob. Chang. Biol.* 24, 1817–1826. <https://doi.org/10.1111/gcb.14073>
- Schielezeth, H., 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* 1, 103–113. <https://doi.org/10.1111/j.2041-210x.2010.00012.x>
- Scholes, R.J., Kruger, J.M., 2011. A framework for deriving and triggering thresholds for management intervention in uncertain, varying and time-lagged systems. *Koedoe* 53. <https://doi.org/10.4102/koedoe.v53i2.987>
- Schuwirth, N., Borgwardt, F., Domisch, S., Friedrichs, M., Kattwinkel, M., Kneis, D., Kuemmerlen,

- M., Langhans, S.D., Martínez-López, J., Vermeiren, P., 2019. How to make ecological models useful for environmental management. *Ecol. Modell.*  
<https://doi.org/10.1016/j.ecolmodel.2019.108784>
- Selong, J.H., McMahon, T.E., Zale, A. V., Barrows, F.T., 2001. Effect of Temperature on Growth and Survival of Bull Trout, with Application of an Improved Method for Determining Thermal Tolerance in Fishes. *Trans. Am. Fish. Soc.* 130, 1026 -1037.  
[https://doi.org/10.1577/1548-8659\(2001\)130<1026:eotog>2.0.co;2](https://doi.org/10.1577/1548-8659(2001)130<1026:eotog>2.0.co;2)
- Shea, K., Possingham, H.P., Murdoch, W.W., Roush, R., 2002. Active adaptive management in insect pest and weed control: intervention with a plan for learning, *Ecological Applications*.
- Simmons, B.I., Blyth, P.S.A., Blanchard, J.L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C.A., Jacob, U., Pennekamp, F., Petchev, O.L., Poisot, T., Webb, T.J., Beckerman, A.P., 2021. Refocusing multiple stressor research around the targets and scales of ecological impacts. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-021-01547-4>
- Smith, B.D., 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for snowmelt-driven watersheds of British Columbia in relation to freshwater discharge.
- Stelzenmüller, V., Coll, M., Cormier, R., Mazaris, A.D., Pascual, M., Loiseau, C., Claudet, J., Katsanevakis, S., Gissi, E., Evagelopoulos, A., Rumes, B., Degraer, S., Ojaveer, H., Moller, T., Giménez, J., Piroddi, C., Markantonatou, V., Dimitriadis, C., 2020. Operationalizing risk-based cumulative effect assessments in the marine environment. *Sci. Total Environ.*  
<https://doi.org/10.1016/j.scitotenv.2020.138118>

- Tekin, E., Diamant, E.S., Cruz-Loya, M., Enriquez, V., Singh, N., Savage, V.M., Yeh, P.J., 2020. Using a newly introduced framework to measure ecological stressor interactions. *Ecol. Lett.* <https://doi.org/10.1111/ele.13533>
- Thompson, P.L., MacLennan, M.M., Vinebrooke, R.D., 2018. An improved null model for assessing the net effects of multiple stressors on communities. *Glob. Chang. Biol.* 24, 517–525. <https://doi.org/10.1111/gcb.13852>
- Trudel, M., Geist, D.R., Welch, D.W., 2004. Modeling the Oxygen Consumption Rates in Pacific Salmon and Steelhead: An Assessment of Current Models and Practices, *Transactions of the American Fisheries Society*.
- Tumeo, M.A., 1994. The Meaning of Stochasticity: Randomness and Uncertainty in Environmental Modeling. pp. 33–38. [https://doi.org/10.1007/978-94-011-1072-3\\_3](https://doi.org/10.1007/978-94-011-1072-3_3)
- Turschwell, M.P., Connolly, S.R., Schärer, R.B., De Laender, F., Campbell, M.D., Mantyka-Pringle, C., Jackson, M.C., Kattwinkel, M., Sievers, M., Ashauer, R., Côté, I.M., Connolly, R.M., van den Brink, P.J., Brown, C.S., 2022. Interactive effects of multiple stressors vary with consumer interactions, stressor dynamics and magnitude. *Ecol. Lett.* <https://doi.org/10.1111/ele.14013>
- Tyack, P.L., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., Kraus, S.D., Miller, P.J.O., Moore, M., Photopoulou, T., Pirodda, E., Rolland, R.M., Schwacke, L.H., Simmons, S.E., Southall, B.L., 2022. Managing the effects of multiple stressors on wildlife populations in their ecosystems: Developing a cumulative risk approach. *Proc. R. Soc. B Biol. Sci.* 289.

<https://doi.org/10.1098/rspb.2022.2058>

Vander Vorste, R., Obedzinski, M., Nossaman Pierce, S., Carlson, S.M., Grantham, T.E., 2020.

Refuges and ecological traps: Extreme drought threatens persistence of an endangered fish in intermittent streams. *Glob. Chang. Biol.* 26, 3834–3845.

<https://doi.org/10.1111/gcb.15116>

Walker, W.E., Harremoës, P., Rotmans, J., van der Sluijs, J.P., van Asselt, M.B.A., Janssen, P.,

Krayer von Krauss, M.P., 2003. Defining Uncertainty: A Conceptual Basis for Uncertainty Management in Model-Based Decision Support. *Integ. Assess.* 4, 5–17.

<https://doi.org/10.1076/iaij.4.1.5.16466>

Wiens, J.A., 1989. Spatial Scaling in Ecology. *Funct. Ecol.* 3, 385–397.

<https://doi.org/10.2307/2389612>

Wilding, T., Poff, L., 2008. Flow ecology relationships for the watershed flow evaluation tool 1–49.

Yuan, L.L., Thomas, D.A., Paul, J.F., Paul, M.J., Kenney, M.A., 2010. Using stressor-response relationships to derive numeric nutrient criteria. Washington, DC.

## Figures

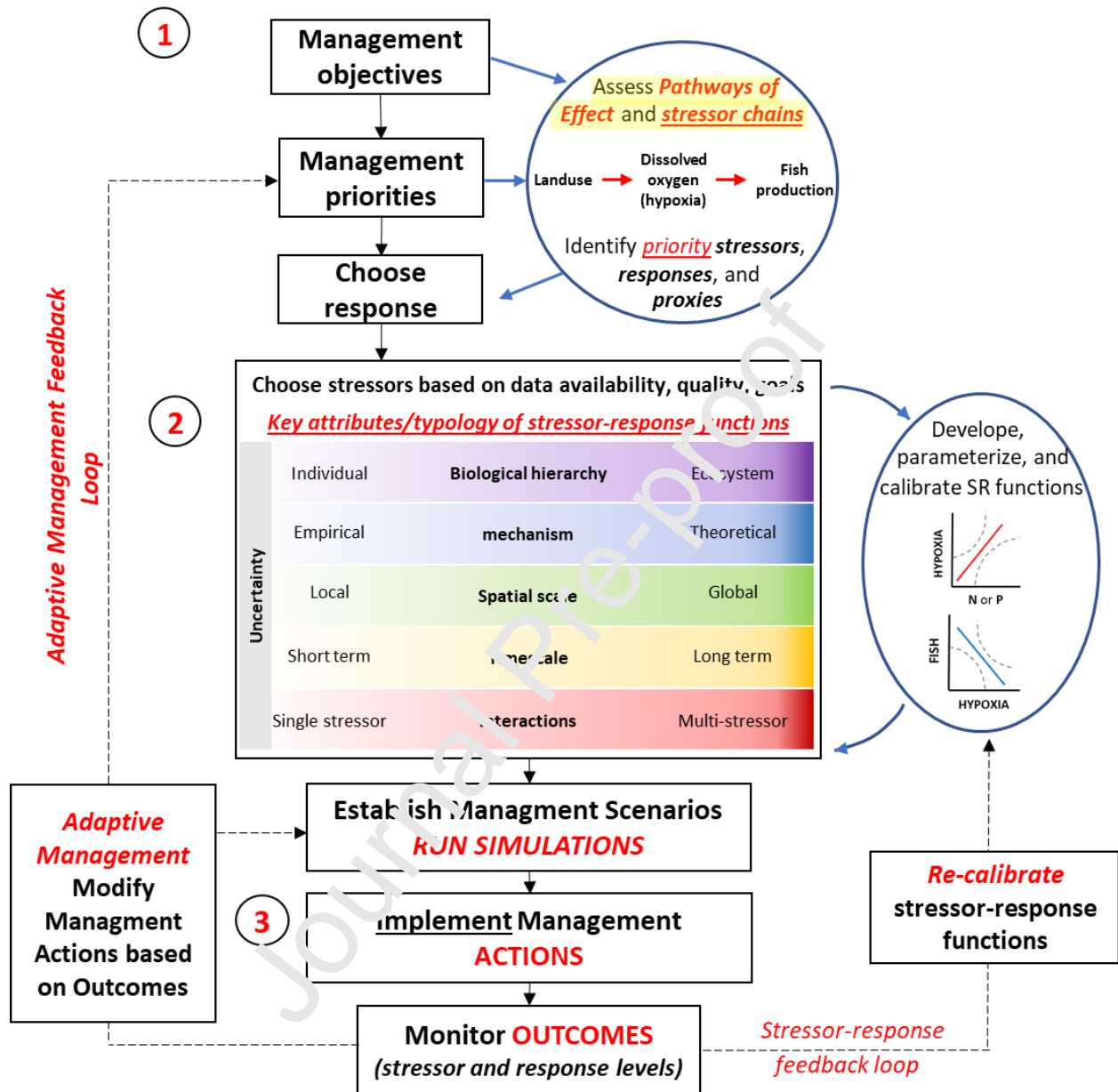


Figure 1. Process model for stressor-response functions embedded within the Cumulative Effects (CE) modelling framework. Step 1 is identifying priority management objectives, stressors, and responses, and the appropriate stressors, responses, and their surrogates to model. Step 2 is developing the appropriate stressor-response (SR) functions based on a suite of



considerations, including data and mechanistic theory availability, understanding of causation, and the suite of stressor attributes under consideration. The third step is the simulation process for the chosen management intervention scenarios, associated monitoring of outcomes, and the adaptive management feedback loop where monitoring data is used to adaptively modify management priorities, as well as to re-assess, refine, and re-calibrate the stressor-response functions (after Pirotta et al. 2022).

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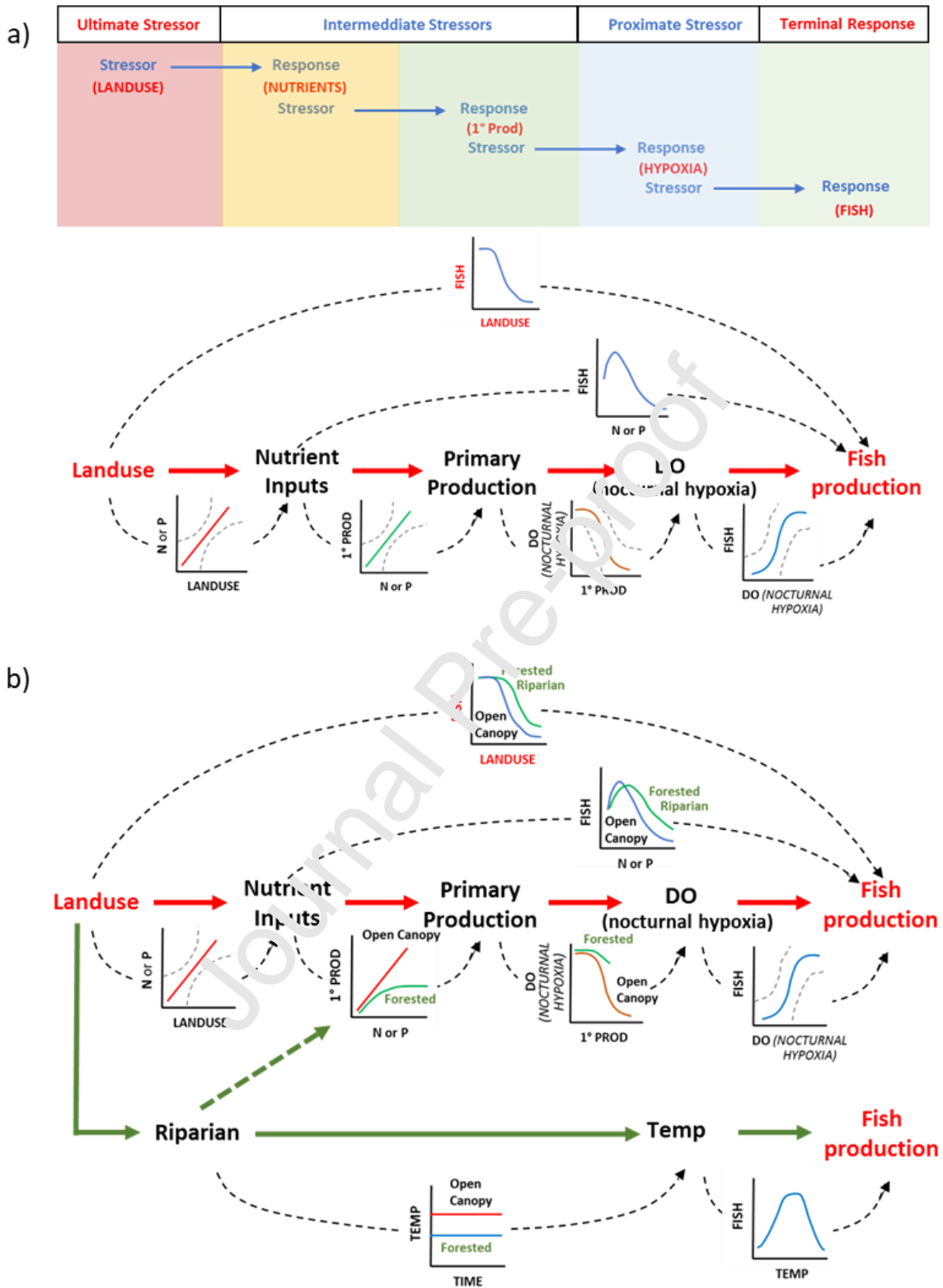


Figure 2. Pathways of effect (stressor chain) leading to eutrophication effects on fish

production. a) Stressor-response (SR) chain linking landuse (the ultimate stressor) and fish production (the terminal response) through a chain of discrete SR functions with hypoxia as the proximate stressor. Note that nutrients, primary production, and hypoxia act as both response and stressor variables linking the chain of functions. Higher-level composite SR functions will integrate (and may obscure) the causative links in the chain but may be empirically accurate. Also note that while photosynthesis generates daytime dissolved oxygen (DO), excessive primary production is often associated with low DO at night when respiration predominates, as illustrated here. b) Addition of a second SR chain where land-use alters riparian forest cover and ultimately temperature as a second proximate stressor. Note that riparian cover type (open canopy with no shade vs. forested riparian with full shade) generates an interaction with the first stressor chain (broken green arrow), where full riparian shading reduces light and primary production, partially mitigating hypoxia associated with eutrophication. Note that this manifests as an interaction (different SR functions) for the intermediate and composite stressor-response functions, but not for the proximate ones (temperature and dissolved oxygen (DO)/hypoxia) because riparian shading constrains the range of the proximate stressor value but does not alter the slope of the proximate SR function.

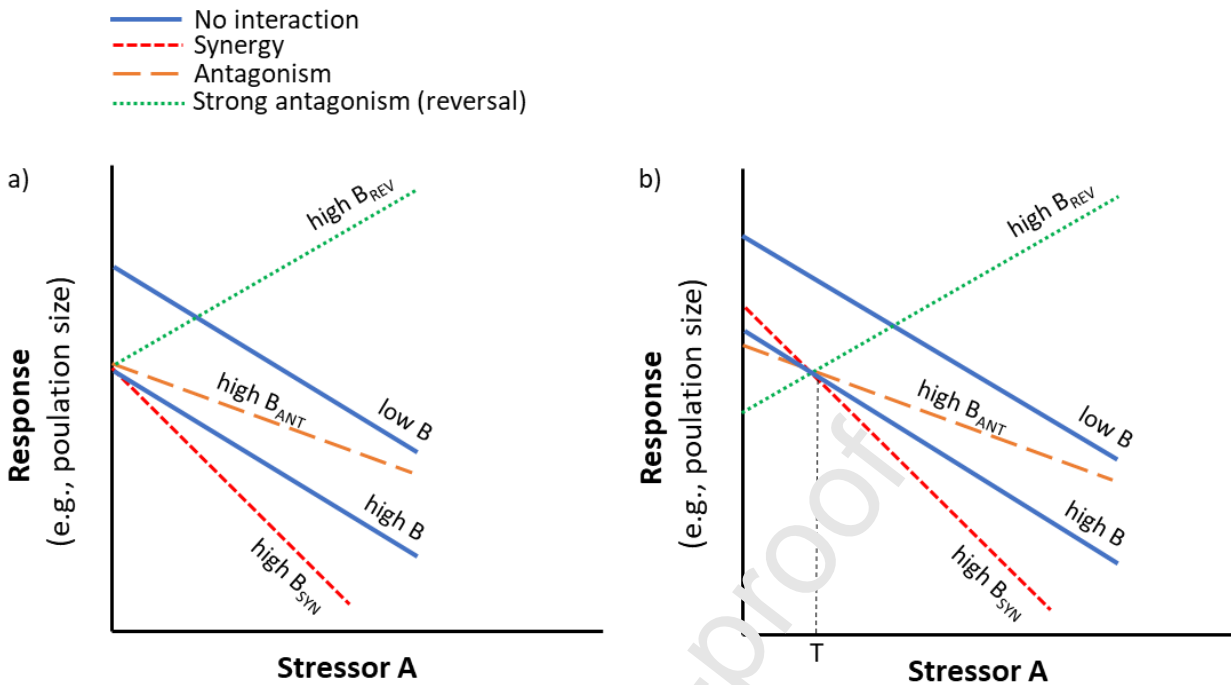


Figure 3. Illustration of additive, synergistic, and antagonistic interactions between two stressors A (a continuous variable represented by the X axis) and B (represented by two stressor levels, low B and high B). Solid blue lines represent the classic additive model with no interaction, characterized by parallel lines, indicating that stressor A and B operate independently of one another. The short-dashed red line indicates a synergy, where the effects of stressor A and the high level of stressor B result in stronger effects (in this case a steeper slope) than expected based on the individual effects of A or high B. The long-dashed orange line indicates an antagonism, where the effects of stressor A and high B are less than expected under additivity (lower slope). The green dotted line represents a very strong antagonism known as a reversal, because the direction of the effect (slope) is reversed relative to the expectation under additivity with no interaction. Note that (a) illustrates a change in slope under interaction with no change in intercept and (b) illustrates an interaction scenario with a change

in intercept as well as slope. This complicates the pattern of interaction, with interaction type becoming dependent on the range of stressor A. For example, the synergy illustrated by the short-dashed red line transitions to an antagonism to the left of the threshold indicated by T.

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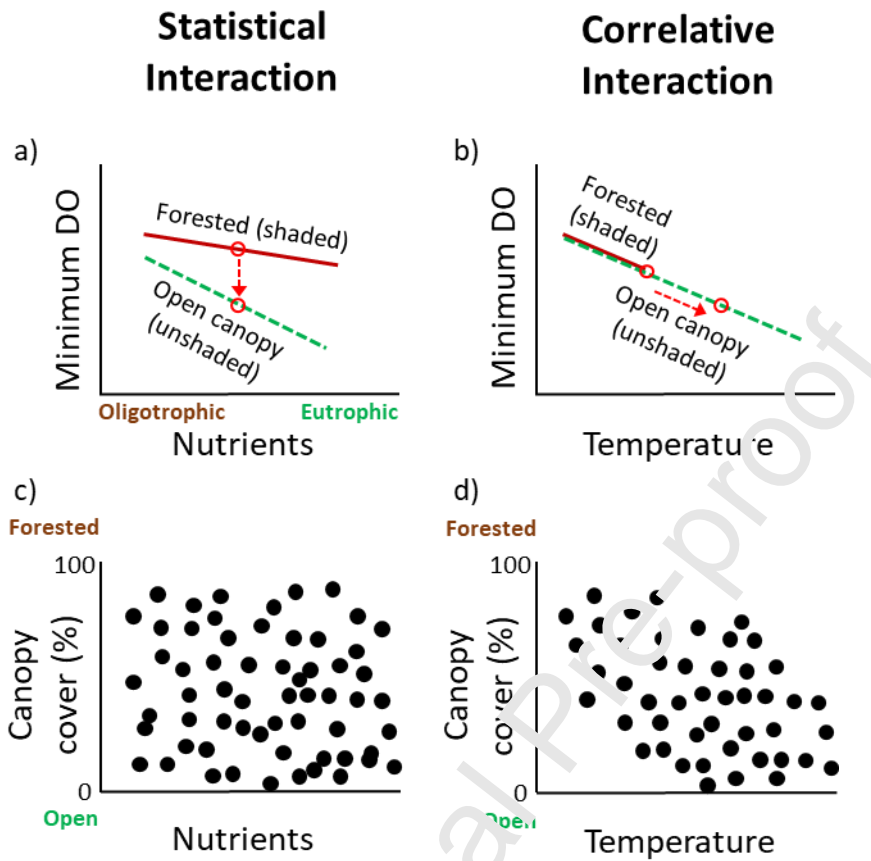


Figure 4. Statistical vs. correlative interaction. Statistical interactions (a) result from change in one stressor (e.g., canopy cover or shading) altering the stressor-response function (slope) of a second stressor without a change in the magnitude of the second stressor (red circles and broken arrow in panel [a]). In this example increased nutrients results in increased primary production and respiration that drives down nocturnal dissolved oxygen (DO), but not in shaded streams where light limits primary production. Note that the stressors canopy cover and nutrients in panel (a) may be uncorrelated (independent; [c]; black filled circles are individual streams). In contrast, correlative interactions result from covariance between stressors, rather than one stressor altering the stressor-response function of a second stressor. For example, increased temperature acts on gas saturation levels to reduce DO in lakes

and streams; the negative correlation between shading and temperature causes lower DO in open canopy streams (b). However, unlike in panel (a), the decline in DO in (b) is driven by a change in stressor magnitude (red circles and broken arrow in panel [d]) associated with lack of shading at open sites, rather than a change in the stressor-response function (i.e., a second line with a different slope). Note that the different mechanistic pathways illustrated in panels (a) and (b) are not mutually exclusive and both may operate simultaneously, complicating their discrimination.

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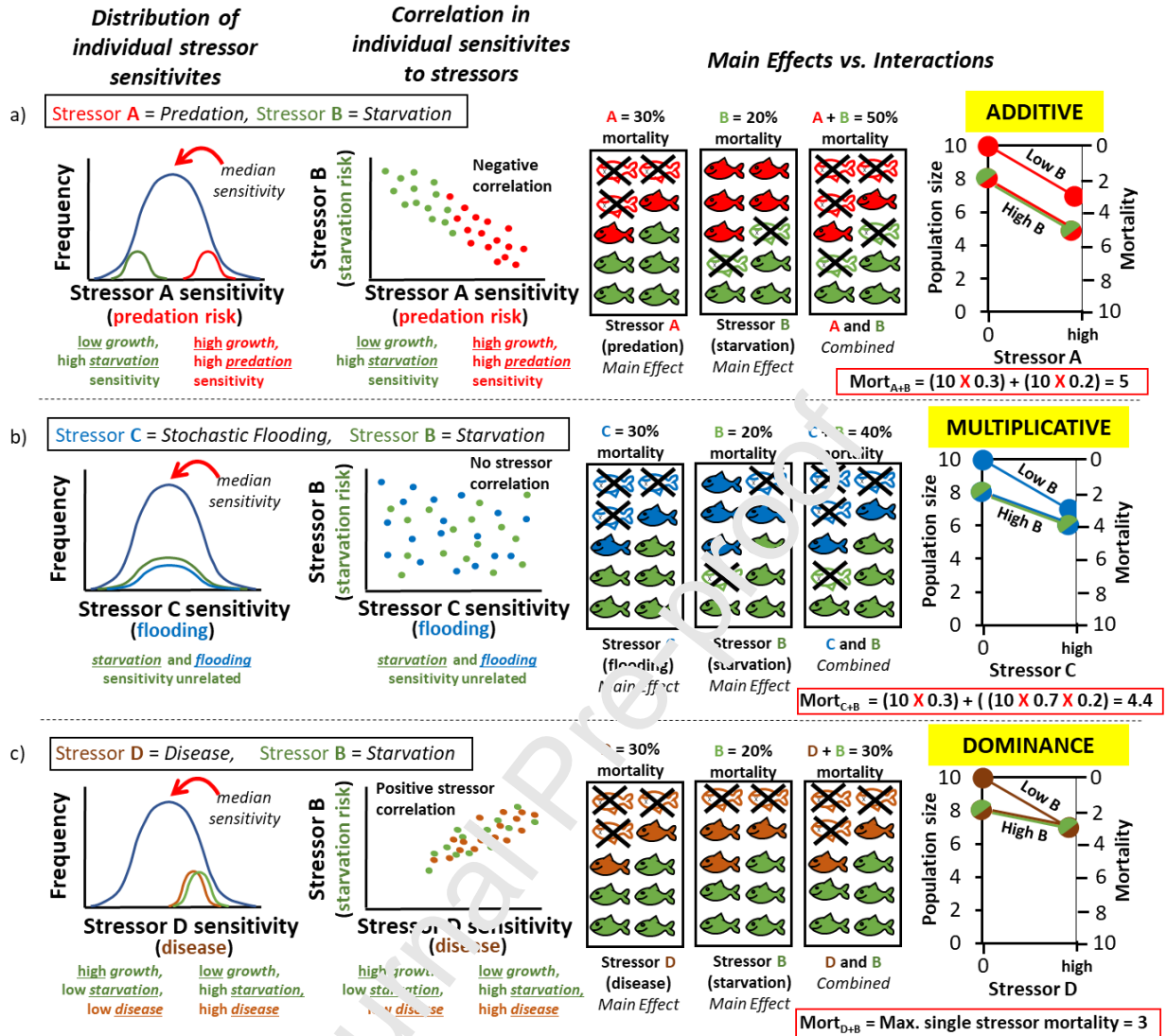


Figure 5. Effects of correlation between individual vulnerability to different stressors on combined stressor outcomes (i.e., null model predictions for different stressor vulnerability correlations). Left panels show hypothetical frequency distributions of sensitivity to the first stressor for the entire population (blue line) and for individuals with high sensitivity to the first or second stressors (subsidiary distributions). The second row of panels illustrates the correlation between each stressor pair, followed by panels illustrating the main and combined effects of the two stressors on a hypothetical population of 10 individuals. (a) Simple additivity,



which requires that individuals that are vulnerable to one stressor have low vulnerability to the second stressor, as illustrated by the non-overlapping sensitivities of individuals with a high risk of starvation vs. a high risk of predation (i.e., a negative correlation in vulnerabilities), generating the classic additive interaction. This example assumes that greater time spent foraging reduces risk of starvation, but increases vulnerability to predation. (b) Multiplicative null model, which assumes that sensitivity of individuals to stressor mortality is independent (uncorrelated; for example, individual vulnerability to starvation vs. stochastic mortality from floods). Because stressor covariance is zero stressors can act on the same individuals, resulting in lower combined mortality than in A where stressors are unlikely to affect the same individuals (far right panel). (c) Dominance null model where vulnerability of individuals to both stressors (e.g., disease and starvation) is assumed to be positively correlated. In this case the maximum mortality rate is set by the most severe stressor, and the combined effect of both stressors is much less than in (a) (simple addition). Note that the combined effects of stressors under the multiplicative and dominance models are antagonistic relative to the simple addition model, even though as null models interactions are not included (see text for details; figure details after Schafer and Piggott (2018)).

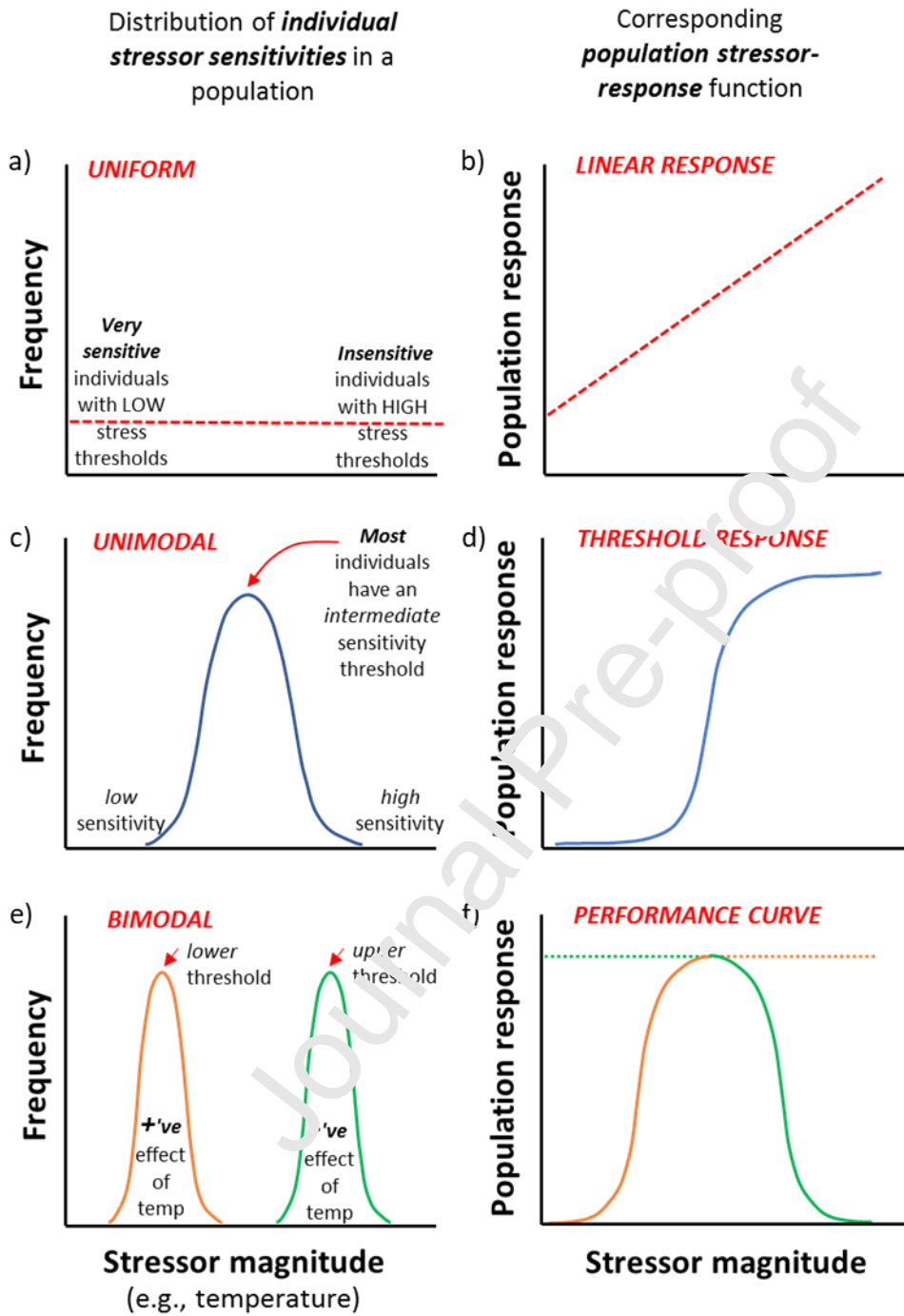


Figure 6. Effects of the frequency distribution of individual stressor sensitivities within a population on shape of the stressor-response (SR) function, assuming that the population

stressor-response function is an aggregate of individual responses. A linear SR function (b) implies that the distribution of individual sensitivities to the stressor is uniform (a), i.e., that for every incremental increase in stressor a constant number of individuals die, or pass growth threshold etc. A more typical normal or hump-shaped distribution of sensitivities will result in a sigmoidal population-level stressor-response function (c, d). The classic normal-shaped performance curve can be thought of as representing two opposite sigmoidal curves for lower and upper stressor performance thresholds (e, f), e.g., the positive effects of temperature on growth at low temperatures, and negative effects at high temperatures.

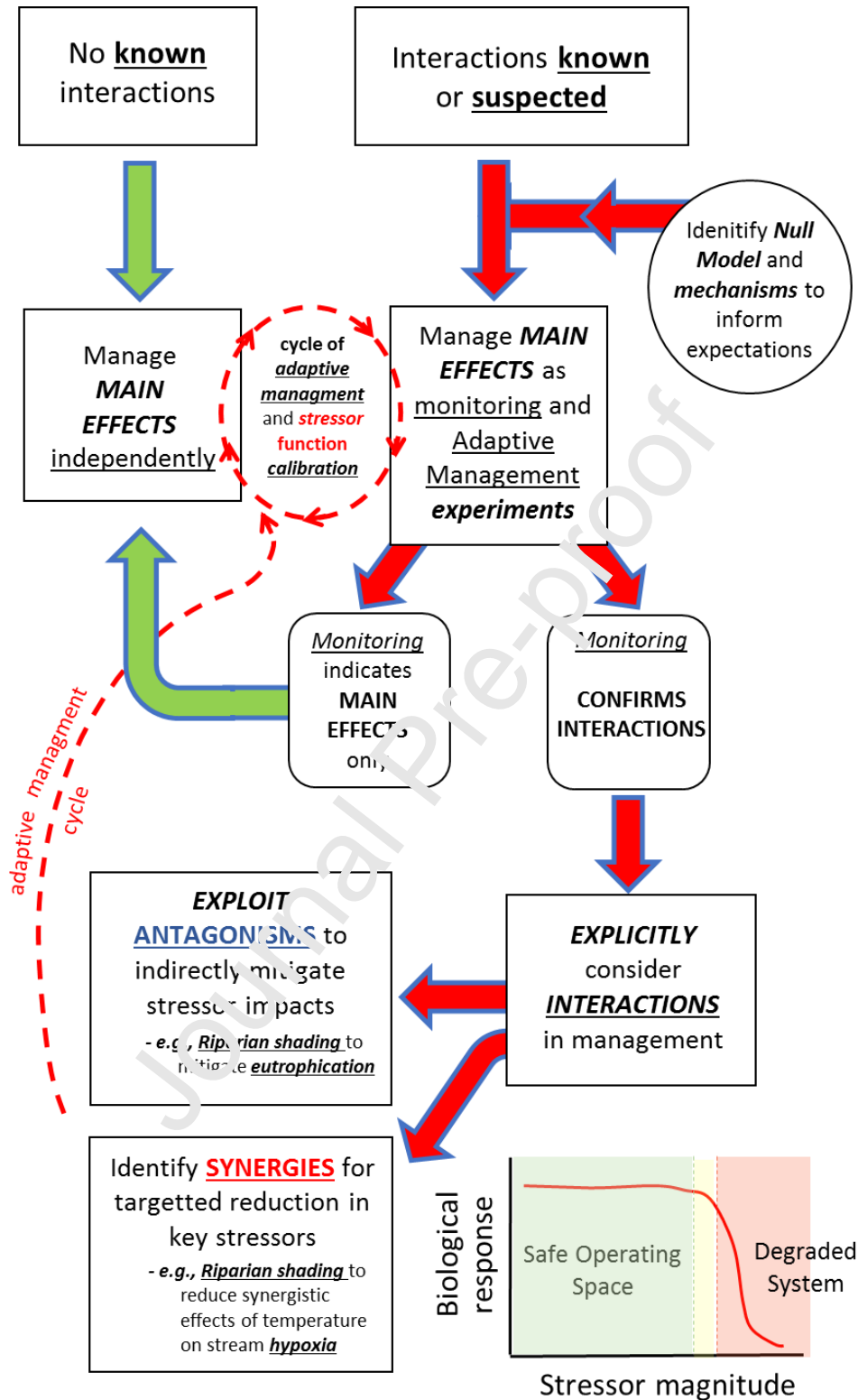


Figure 7. Practical guidance for managing stressor interactions under uncertainty. If there are

no known interactions, then management should focus on main effects (i.e., assuming independence) while monitoring responses to assess the potential for synergies (larger than expected responses to stressor reduction) or antagonisms (unexpectedly small responses to stressor reduction). If interactions between candidate stressors are known or anticipated based on prior knowledge of underlying mechanisms, then the null model and potential for synergies and antagonisms should be identified and assessed through monitoring and adaptive management. If interactions are confirmed, then synergies and antagonisms should be strategically exploited to differentially reduce stressor impacts with minimal stressor reduction. If interactions are well understood, then management can directly skip to the last stage, i.e., the effectiveness of riparian shading in mitigating eutrophication impacts is well established, and a monitoring cycle is not required to initiate riparian restoration under eutrophic conditions.

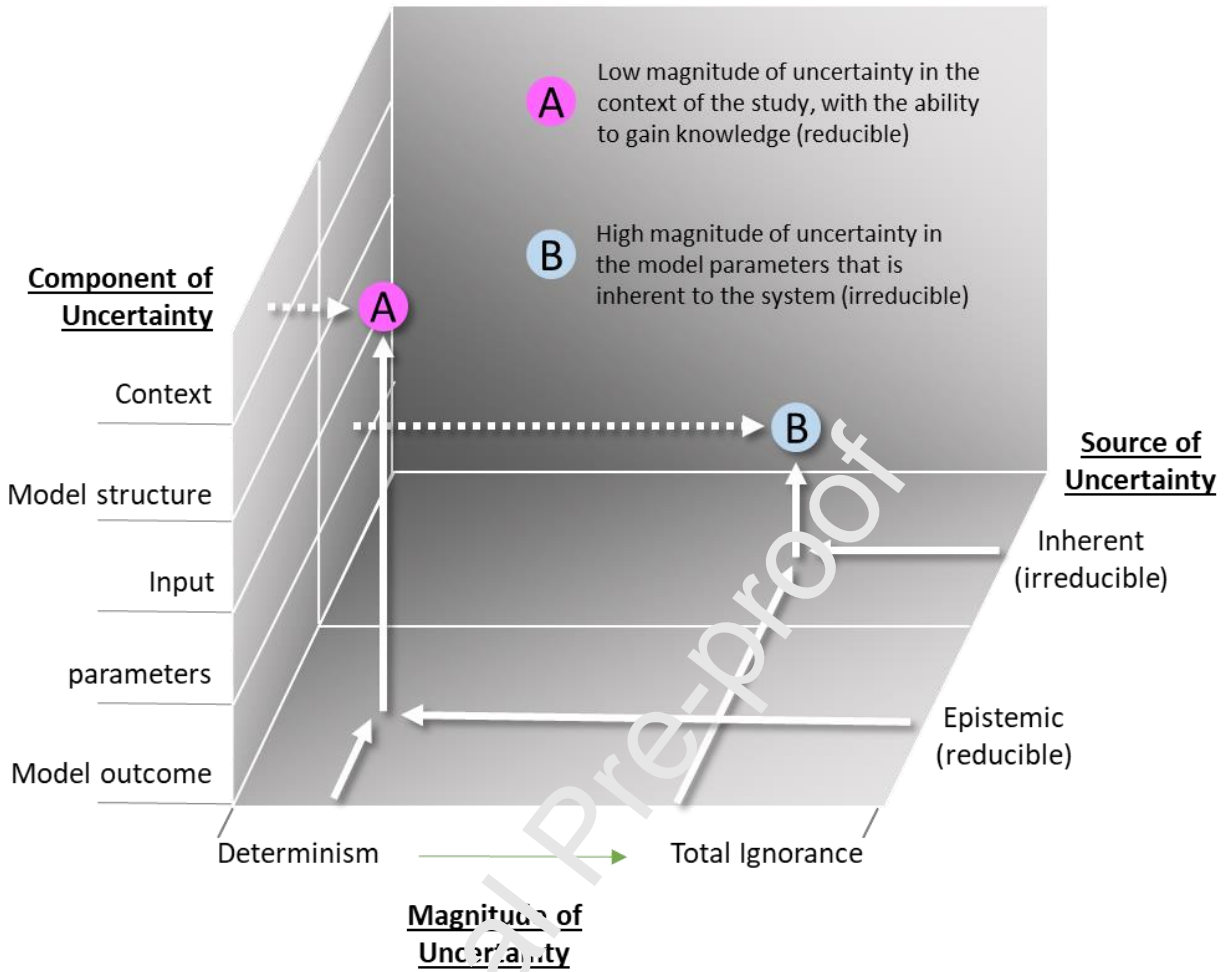


Figure 8. Uncertainty matrix adapted from Walker et al. 2003. The three axes of uncertainty are component, magnitude, and source. This matrix can help categorize and thus prioritize uncertainty to be dealt with (or ignored) in subsequent analyses (i.e., how the uncertainty is accounted for in the model).

**Author contributions**

Lauren Jarvis: conceptualization, writing – original draft, review & editing, visualization, funding acquisition

Jordan Rosenfeld: conceptualization, writing – original draft, review & editing, visualization, supervision

Eva Enders: conceptualization, writing – review & editing, supervision, funding acquisition

Pedro Gonzales – conceptualization, writing – review & editing

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**Declaration of interests**

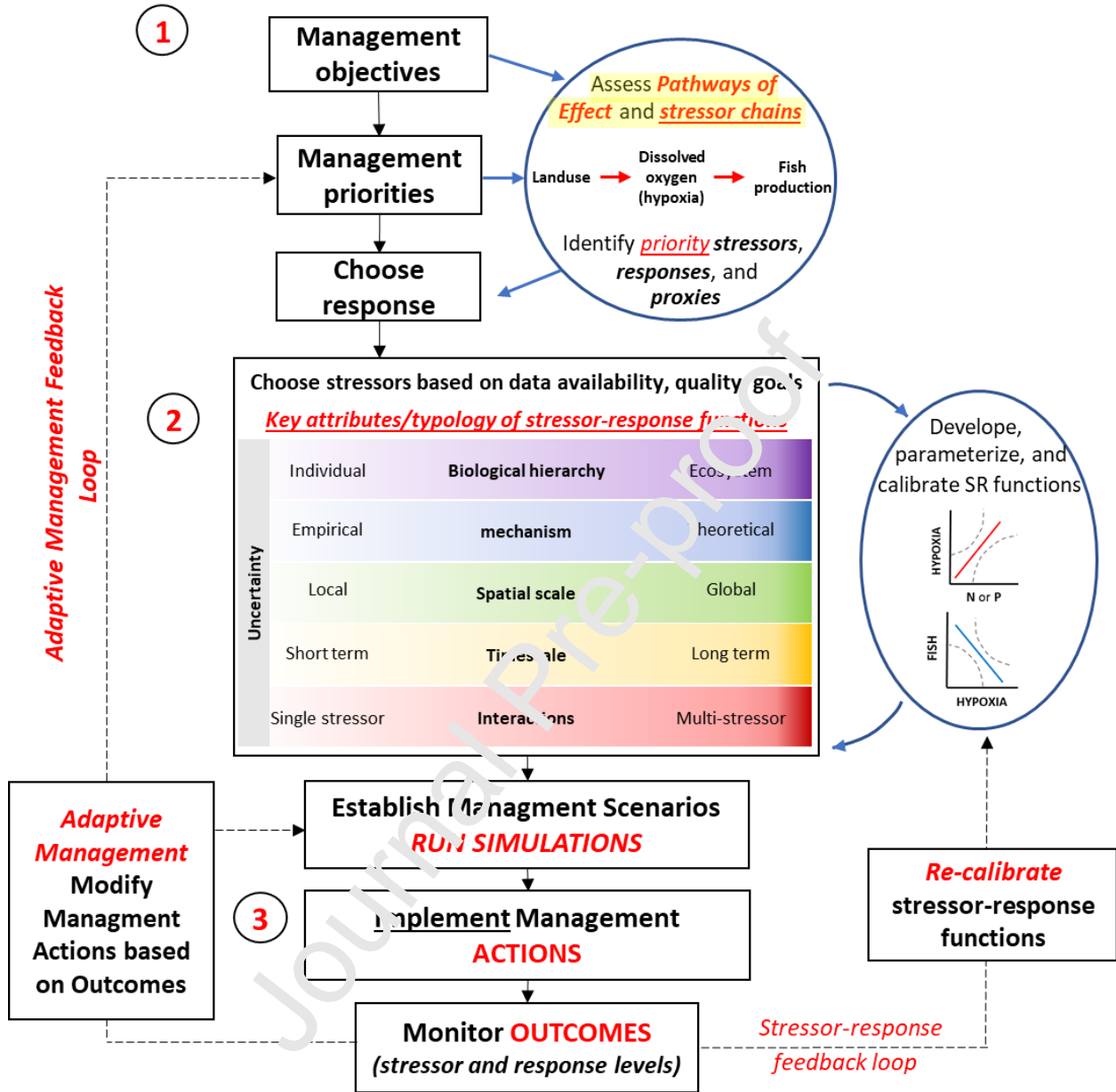
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Graphical abstract



### Highlights

- i. Cumulative effects (CE) modelling is a priority for conservation and management
- ii. Stressor-response (SR) functions are core drivers that modulate the severity of CE
- iii. We review how to derive and integrate SR functions into CE models
- iv. We expand an existing CE process framework to include SR function attributes
- v. This framework is intended to accelerate the adaptive management process

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