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Forum

Stressor-response functions as a generalizable model for context dependence

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Defining the context dependence of ecological states or processes is a fundamental goal of ecology. Stressor-response functions are the quantitative representation of context dependence, where the context (environmental contingency) is defined by location on the stressor (x) axis, and represents a unifying concept in biological science.

Context dependence in ecology and the role of stressor-response functions

Context dependence (see Glossary) in ecology generally references the environmental contingency of **ecological state** (e.g., individual fitness, population size) or **process** (production, nutrient cycling). However, in some subdisciplines such as community ecology, **environmental context dependence** is often defined as an interaction, that is, alteration of the sign or magnitude of an ecological relationship by another variable [1]. Here we articulate the value of an alternative definition of environmental context dependence in terms of **stressor-response functions** that is not limited to interactions, to lend more utility and precision to the concept and its application. Since ecology focuses on the interrelationships of organisms with one another and their environment, this broader interpretation of context dependence could be foundational to most ecological studies. Arguably, characterizing context dependence through quantitative stressor-response functions represents a unifying theme in ecology and environmental sciences.

We advocate using the term **stressor** in the broadest ecological sense as any biotic or abiotic variable that generates a positive or negative biological response (cf. [2]). In some disciplines the term stressor is exclusively interpreted as a negative relationship; however, stressors generally represent a gradient, and in this sense the term stressor is equivalent to **driver** or **factor** [2].

Stressor-based typology of context dependence

General typologies of ecological context can be defined by properties of both the response and the stressor-response function. Ecological context can influence **system state** (e.g., population size), or **ecological process** (e.g., nutrient cycling, trophic interactions), or both.

Single-stressor context

We frame the simplest ecological context as **single-stressor** (Figure 1A), where different values of the stressor (x axis) define different ecological contexts generating state differences along a shared environmental gradient. The stressor-response function may represent a simple linear gradient, or a more complex nonlinear transition between states such as dry savannah and forest, where rainfall is the stressor that mediates system state (Figure 1A). Biotic responses to predation and competition are also stressor-response functions that capture context dependence [3]. Divergence in state along single-stressor abiotic axes is a fundamental theme in applied ecology and environmental management, as when land-use stressors drive biological responses to anthropogenic change (Figure 1B). Stressor gradients are also a well-defined concept in species adaptation, distribution mapping, and multiple stable state transitions [3]. However, single-stressor ecological contexts neglect interactions and are most

Glossary

Context dependence: sensitivity of the slope or magnitude of an ecological process or state (e.g., production, biomass) to environmental conditions (temperature, salinity, etc.), which define the ecological context. Synonymous with contingency. In this article we primarily refer to environmental context dependence, as opposed to context dependence that also includes study design or statistical inference [1].

Driver: synonymous with stressor (q.v.).

Ecological process: causative mechanism (or chain of events) that leads to change in a biological response variable at an ecosystem scale.

Ecological state: current ecological properties of a biological system (e.g., individual, community, or ecosystem) at a discrete point or interval in time.

Environmental context dependence: context dependence related to environmental conditions and contingency, excluding context related to experimental design, methods, or statistical inference [1].

Factor: synonymous with stressor (q.v.).

Process: causative mechanism (or chain of events) that leads to change in a response variable.

Single-stressor context: an ecological context that is defined by one stressor (i.e., a univariate stressor-response function) as opposed to an ecological context defined by two or more stressors (e.g., as a multiple regression).

Stressor: any environmental variable (e.g., temperature, sediment, predation, competition) that can induce a biological response (positive or negative). Synonymous with 'driver' or 'factor'. Although 'stressor' is often associated with negative outcomes, we use it in a broader sense because (i) almost all environmental variables will have negative effects over some part of their range, and (ii) reduction in stress will result in positive outcomes. This is illustrated in Figure 1E depicting the Hutchinsonian niche, where blue broken line arrows indicate increasing stress, and unbroken green arrows indicate stress reduction.

Stressor-response function: a quantitative relationship between an environmental variable (biotic or abiotic) and a biological response in any linear or nonlinear form. Synonymous with 'dose-response relationship' in medicine, 'trait performance curve' in physiology, 'habitat suitability curve' in wildlife ecology, and 'reaction norm' in evolution.

System state: static property of a biological system (e.g., individual, community, or ecosystem) at a discrete point or interval in time.

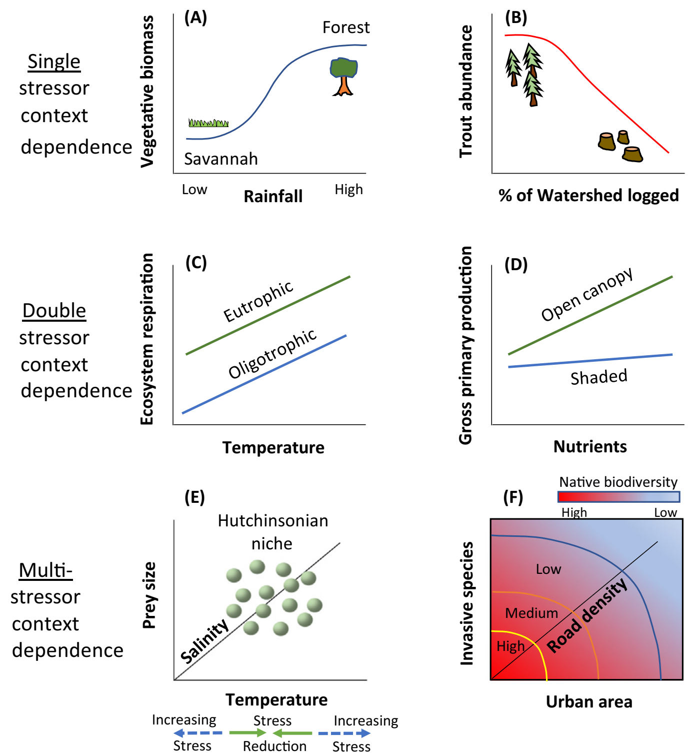

Figure 1. Stressor-based classification of context dependence. Context dependence can be defined in terms of a single dominant stressor (A,B) that drives differences in state along a common process axis (stressor-response function). Dual stressors may drive system state when stressors exert similar leverage, either along a shared process axis where one stressor elevates the intercept (C, no interaction), or where context dependence is driven by a process interaction between stressors (D, differences in slope). Multistressor context dependence is common, either in fundamental applications like the Hutchinsonian niche (E), or in applied problems like understanding the effects of cumulative multistressor impacts on native species diversity (F). Note: examples are hypothetical.

useful when a dominant stressor (e.g., temperature) plays a disproportionate role in determining system response [4]. Single-stressor response functions can also be viewed as the minimum quantile of ecological information required to generate a quantitative relationship for predictive purposes.

Double-stressor context

Paired environmental stressors can also drive ecological context; this can occur along a shared process axis with no mechanistic interaction but a difference in state (intercepts). For example, the slope of temperature effects on respiration (i.e., process) may be equivalent in oligotrophic and enriched streams, even though nutrient enrichment elevates the overall magnitude of respiration (system state) (Figure 1C). Alternatively, stressors may interact so that the sign or slope of the ecological process is strongly contingent on the state of the other stressor. For example, primary production in unshaded streams can respond much more strongly to nutrient addition than forested streams where light is limited (Figure 1D) [1,4].

Multistressor context

Ecological context is often conceptually or empirically defined by multiple stressors (Figure 1E) [5]. The Hutchinsonian niche is one example, where each axis is a single stressor-response function that interactively define the n-dimensional hypervolume in multivariate space where an individual or population can experience positive growth. Environmental and resource stressors define the fundamental niche, while the realized niche is generated by including stressor-response axes associated with predation, competition, and mutualisms. In this sense, stressor-response functions can be viewed as the fundamental building blocks (i.e., axes) of the Hutchinsonian niche, and therefore in a real sense are more foundational than the niche itself. Ecological contexts defined by multivariate stressors are pervasive in applied ecology; these include multistressor species distribution models and cumulative effects assessments to identify the extent of anthropogenic impacts under different land use or climate change scenarios. Double-stressor or higher order interactions represent context dependence as typically defined in community ecology [1]: for example, when species interactions shift from mutualistic to antagonistic along environmental or competitor density gradients [6].

Stressor-response functions as a unifying concept

Moving beyond qualitative description in biological science implicitly requires some form of stressor-response function. For example, medical sciences commonly develop dose–response relationships to quantify human response to drugs. Habitat and distribution models in applied ecology that define the presence, abundance, or survival of organisms are effectively stressor-response functions relating metrics of abundance to environmental context (temperature, flows, community structure) [7]. Similarly, animal physiology models relating individual performance (growth, survival, physiology) to environmental context are all contingency-based stressor-response functions. Stressor-response functions are therefore common across scales of biological organization [4], but data limitations might require the use of proxies or linked stressor chains to transition functions across scales.

Box 1. Integration of empirical and mechanistic stressor-response functions into process databases

Empirical stressor-response functions based on correlations between stream flow and fish production may be discordant (Figure I, panel A), with either positive or negative effects of increasing flow, indicating context dependence (i.e., opposite slopes). However, a mechanistic model of flow-related changes in available habitat for fish predicts a unimodal peak (panel B), so that functional nonlinearity provides a theoretical expectation for the observed context dependence in slope [1]. This demonstrates the complementarity of theoretical and empirical stressor-response functions [5]; theoretical models provide an understanding of underlying mechanisms that drive context dependence, while empirical models allow for model calibration and validation against real outcomes in nature [8,12].

Databases and repositories for organizing biological information generally focus on biological or environmental state (e.g., population size, species status, state of the environment) (Figure II, left double-framed boxes) and more rarely include ecological processes (libraries of stressor response functions such as growth responses to hypoxia or competition) (Figure II, right box). Running model projections of future state under climate change or other scenarios requires both types of database (Figure II, central oval). Integration of empirical and mechanistic functions into well-documented open-access stressor-response libraries is a key step in improving the efficiency and transparency of model development.

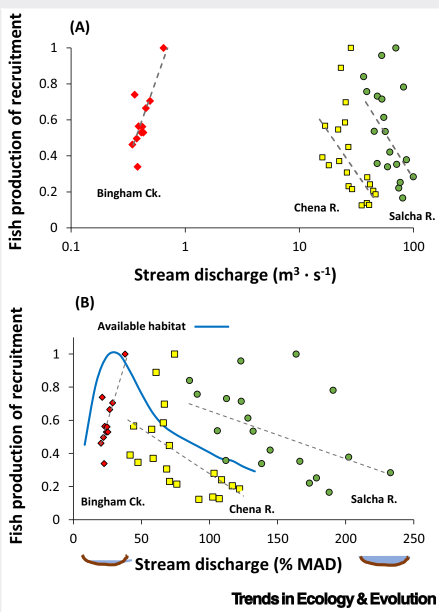

Figure I. Complementarity of empirical and mechanistic stressor-response functions. (A) Divergent stressor-response functions relating fish production to increasing discharge in Bingham creek (WA, USA) and the much larger Chena and Salcha rivers (AK, USA) based on empirical data [13]. (B) Theoretical predictions of changes in available habitat with flow (unbroken blue line) superimposed on empirical stressor-response functions rescaled to an axis of relative stream flow [percent of mean annual discharge (%MAD), an index of channel fullness]; context dependence of empirical stressor-response functions matches predictions from the theoretical model.

Stressor-response functions also conceptually unite disparate perspectives of ecology. Fundamental ecology often focuses on underlying process and mechanism, and proponents may value understanding mechanism over empirical prediction [8]. By contrast, predictive ecology values quantitative prediction over mechanistic process [9], which is viewed as an important but secondary goal. Stressor-response functions, as either empirical correlative models or mechanistic process models, are fundamental to both perspectives, and are key links bridging the transition between qualitative ecology and quantitative science (Box 1).

Developing public libraries of stressor-response functions

The two main forms of information pertinent to applied ecology and conservation relate to (i) biological/environmental state, or (ii) processes that transform state (i.e., stressor response functions). This information is generally dispersed in the primary scientific literature or government reports, although often concentrated in particular journals or meta-analyses. Centralized databases on ecological state are now fairly widespread, including databases on the historic and current status of populations, state of the environment, red lists of the International Union for Conservation of Nature (IUCN), and dedicated journals (e.g., *Scientific Data*). However, parallel process-focused repositories are scarce, partly because processes are diverse and difficult to categorize. Because stressor-response functions are the most basic and succinct information quantile summarizing ecological process, they are a logical unit for populating libraries or databases of biological process (Box 1).

Accounting for context dependence is fundamental to realistic modeling in natural resource management [10], and requires extracting or developing stressor-response functions from the primary literature or other sources for project-specific modeling. However, limited data and resources often constrain managers from generating quantitative stressor-response functions. This increases uncertainty in stressor impacts, creating a reliance on qualitative decision-making which undermines the credibility of conservation efforts under pressure from competing development values. Creating centralized public repositories (libraries) of stressor-response functions for different

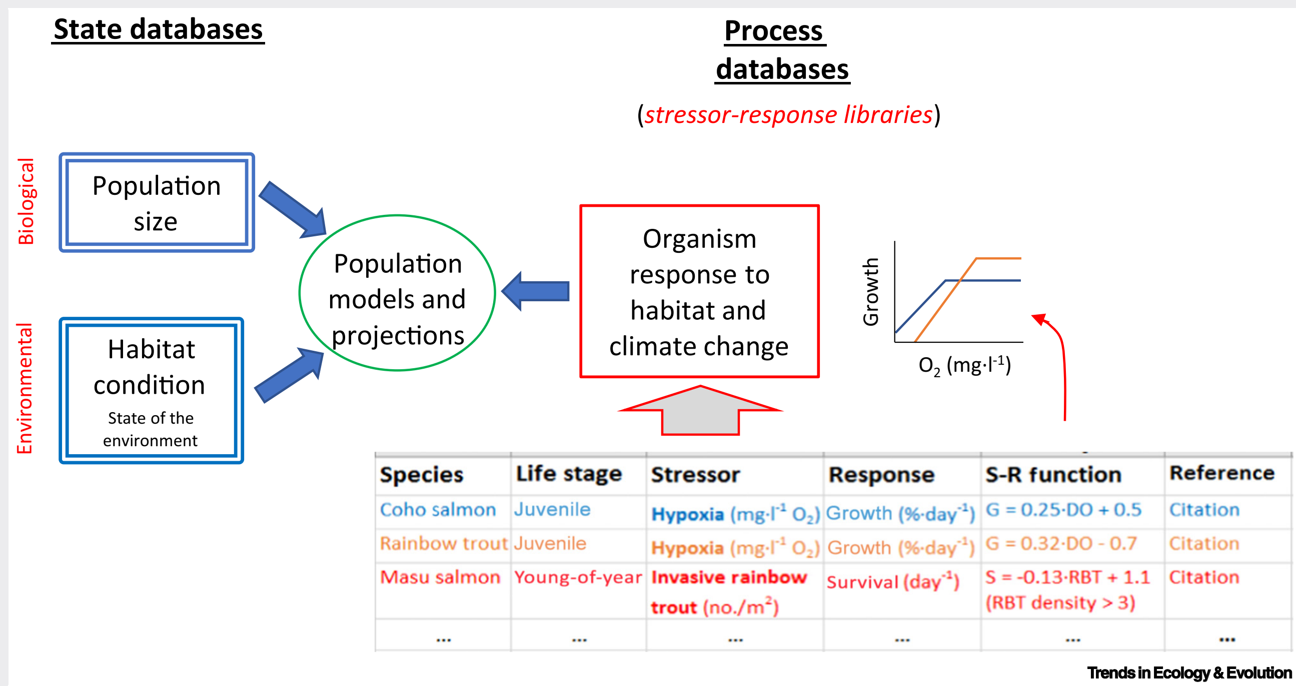

Figure II. Integration of biotic and abiotic stressor-response (S-R) functions with state and process databases. Abbreviations: DO, dissolved oxygen; G, growth; RBT, rainbow trout.

taxa or processes will greatly accelerate the efficiency and transparency of modeling and prediction [10], and is a natural extension of the drive towards open access science in conservation (e.g., [11]). Publicly accessible stressor-response libraries will also lower the barriers to developing regional cumulative effects models, and facilitate a transition to quantitative modeling for many taxa and ecosystems. Curating these libraries should ultimately be the responsibility of the natural resource management agencies who use them.

Prognosis for modeling context dependence

Context dependence is a consequence of adaptive peaks in organism performance along environmental gradients, and is therefore pervasive in ecological systems. Predictive ecology captures context dependence through quantitative stressor-response functions, the default framework for representing environmental contingency across multiple domains of biological science. More explicit recognition of stressor-response functions as integral building blocks of basic and applied ecology will streamline their organization into accessible databases and efficient application to pressing environmental issues.

Declaration of interests

No interests are declared.

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