Title: How do we predictively model how resilience/robustness at one level affects other levels?

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Summary: What's the big question?
The robustness or resilience (R&R) of a function transcends levels of biological organization, though R&R does not scale directly across levels. We live in an era of novel stressors and unprecedented change. We envision a common framework for developing models to predict R&R of functions associated with complex systems. Such a model must consider cross-scale interactions of potentially infinite complexity. However, modeling everything is not feasible. Are there systematic ways to evaluate complexity at adjacent levels to determine how to simplify while still producing an accurate model with regards to a specific function or collection of functions? The vision is that a common structure exists that can be utilized to identify the minimal system components and interactions that predict R&R.

What's the exciting science?
All systems respond to perturbations, but the degree and mechanism of response varies and there can be feedbacks across levels of organization. Robustness and resilience (R&R) have been used as metrics to describe the adaptability of systems to perturbations. Robustness is the ability to tolerate environmental changes without adapting or moving to another state. Resilience refers to the ability to survive the change following the impact and potentially returning to its original state. Robustness and resilience are essential for responding to stress and change across hierarchical levels. Our hypothesis is that a common framework exists that can be utilized to identify the minimal system components and interactions that predict R&R with regards to a specific function or collection of functions. Functional robustness and resilience are widespread in biology across organizational levels including, for example, protein folding, gene expression, physiology, organism survival, population persistence, and community assembly. The question is how to create a general model that captures key interactions and dynamics across organizational levels. Moreover, what features and scale (i.e., spatial and temporal) should be the focus of resilience and robustness strategies for biological systems? This sort of model can enable a multi-level view of systems rather than the typical discipline-specific approach.

The fundamental structure of a model commonly consists of the system state variable and a quantitative description of the desired state. Of all possible interactions, at hierarchical levels above and below the focal system state function, which interactions are most important to the R&R of the function (Figure 1)? Many subdisciplines of biology and disciplines with connections to biology have developed definitions of R&R and methods for assessing and predicting R&R that fit the unique needs of the level of biological organization that they work at (Levin and Lubchenco 2008, Scholz et al. 2012, Mumby et al. 2014). In most cases, there are dependencies and feedbacks with other organizational levels. While there may not be a universal model of R&R that applies across spatial and temporal scales, the development of a

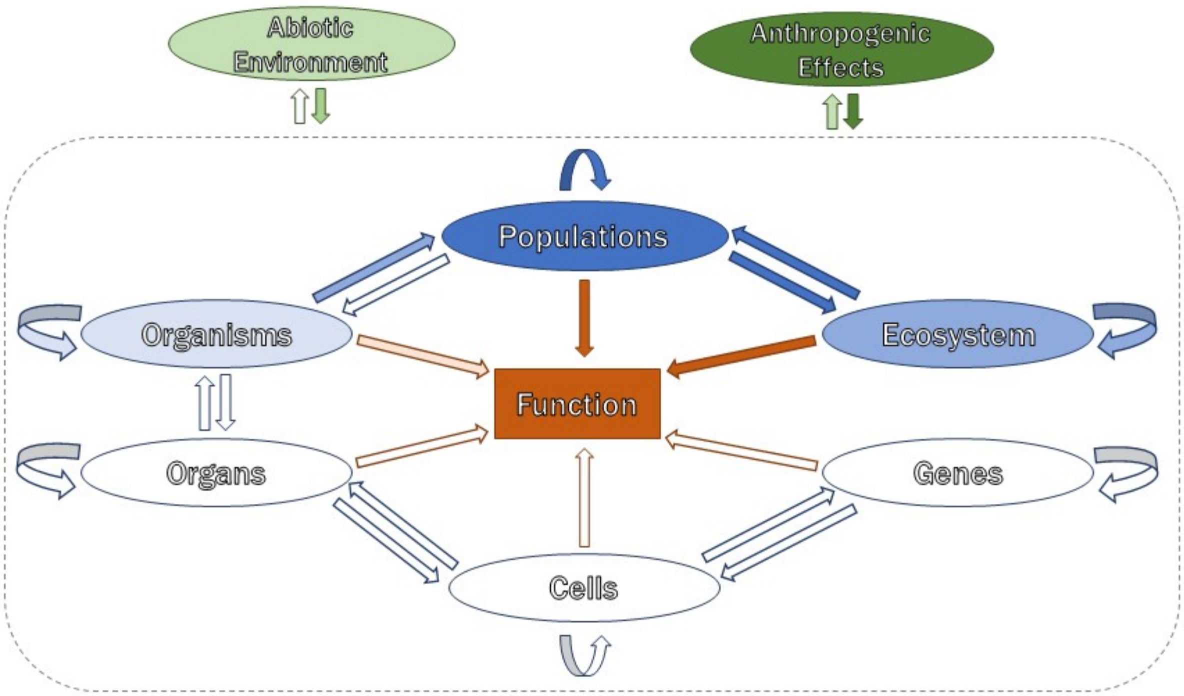

Figure 1. Example of a function of a biological system that is primarily mediated at the population level (such as pollination). Arrows indicate interactions within and between levels with darker shading indicating the strength of the levels of organization and interactions in determining the resilience and robustness of the function.

framework to identify the key interactions between levels and the degree of complexity needed to model these interactions may be possible. Such a framework would be used to determine:

- The minimum level of granularity needed to model each level while still producing an accurate model of the R&R of the function.
- What new data describing adjacent levels would be useful for improving the model rather than using the data that is available.
- When coupled models across levels are genuinely necessary.
- The temporal and spatial scales over which interactions between levels occur.

What's the potential impact?

In the face of growing challenges and changes to coupled physiochemical and biological systems there is a growing need to quantify functions that are influenced by feedbacks and interactions across hierarchical scales. Perturbations are not equal within and across scales. Perturbations are generally described by the magnitude, duration, frequency, and predictability within a system across scales. Diversity and heterogeneity capture the adaptive capacity of a system in a changing environment; without variation or phenotypic plasticity, there can be no adaptive response. Adaptation takes place in complex systems and can be deconstructed at levels below that of the entire system. For example, it is generally understood that ecosystems with low species richness are more vulnerable to catastrophic change than systems containing higher biodiversity (e.g., Tillman et al. 1996) and that low genetic diversity can make populations less able to persist in the face of environmental challenges (Amos and Balmford 2001, Sgro et al. 2011).

However, as originally demonstrated by Robert May (1973), the behavior of complex systems is inherently nonlinear and chaotic and increased complexity of ecosystems does not lead to population stability. As a result, nonlinear mathematical modelling approaches are now at the center of ecological thinking and approaches (Carpenter et al. 1999). System response is anticipated to vary as a response to the stochasticity vs predictability of a change or perturbation. Recent developments in global change research show the need to address how the dynamics generated by feedbacks within one level play out across spatial and temporal scales across levels of organization (Anderies et al. 2013, Page and Baird 2016). Unfortunately, it is not clear how much complexity is needed to translate a fundamental understanding of all components and interactions of complex systems to its emergent properties. A robust approach to address this question in the context of specific functional properties across diverse biological and other fields will enable predictive capabilities of complex biological systems needed to address many of today's Grand Challenges including protecting human health and understanding the food, energy, water nexus.

Why now?

There is a need to facilitate understanding the feedbacks across levels of organization as systems are undergoing rapid anthropogenic impacts and change, pushing towards tipping points. While individual disciplines and subdisciplines have developed detailed definitions and analyses of R&R within their contained systems there has been little effort to coordinate efforts and find patterns across levels. Cross-pollination of these ideas will produce better predictive ability. A number of software tools have been developed within R, Matlab, and Stella, for example, to analyze R&R issues, accelerating the development of R&R case studies. Further, machine learning and AI techniques offer new approaches for recognizing patterns and reducing complexity.

Potential Approaches and Key Barriers (What we need to get there):

There is a large body of literature concerning R&R and a growing body of literature of case studies that model R&R supported by the development of new software tools. However, there has yet to be a coordinated effort to understand adaptability across systems. This will allow us to determine whether, and if so, how these processes parallel one another across scales of biological organization and what the common problems are. Clearly defining this function and the hierarchical level it operates at is the fundamental starting point in the process. This is followed by identifying and analyzing the levels immediately above and below it. If needed, the levels above and below these first levels may be considered. The major challenges that need to be addressed include identification of the temporal and spatial boundaries, model development to determine the function and its variability, and development of methods to describe the impact of relevant interactions and interaction strength among each hierarchical scale. Meta-analyses of complex systems across diverse biological and other disciplines to identify commonalities will lead to deep understanding, novel insights, recognition of knowledge gaps, and new practical approaches for system management. This will allow for a definition of the relevant minimum granularity needed to capture complex emergent behaviors that are simple enough to translate across organizational levels.

Broader Impacts - reintegrating biology, applied, workforce development and diversity
A framework to support efficient interdisciplinary collaboration to accurately model R&R would enable rapid, context-specific assessment of the R&R of biological systems. There are many R&R functions of biological systems that are important to people such as disease transmission, conservation of endangered species, pollination, food provisioning, primary productivity, and soil stability (Levin and Lubchenco 2008, Oliver et al. 2015).

The availability of generic modeling tools that can be applied broadly to a range of problems would benefit diverse applications in community management, engineering, manufacturing, agriculture, and medicine. The availability of a general but adaptable modeling framework that is open and transparent (e.g., agent based modeling, mechanistic effect models) to explore the interconnectedness of the resilience and robustness of biological function will facilitate broad training in multiple biological and engineering disciplines by helping students to see their intellectual niche in the context of understanding complex systems. Interactive tools developed to improve understanding of biological systems in K-12, university, and professional development contexts, such as SimBIO Collections, can be enhanced by the new framework to connect topics and people across traditional divisions.

How does it reintegrate biology?
Responses to perturbations occur at all levels of organization and time scales. Determining how R&R operates at one level and is coupled to other levels and the feedbacks operating within and between levels is a fundamental rule governing biological and system organization and adaptability. Developing a framework to describe and predict processes spanning system scales will engage biologists from all sub-disciplines and disciplines related to biology allowing research and problem solving arising from multiple perspectives.

Processes, organisms, and ecosystems all respond to change. Our vision is that this framework would be applicable to functions across types of systems and hierarchical levels. It integrates subdisciplines with expertise that spans these systems and levels. For example:

Genetics: The rate of evolutionary change is controlled by several factors including selective forces, genetic variance, gene transfer and re-organization in the population. Without variance and capacity for change there can be no adaptation; and without this adaptive capacity, populations are at risk.

Physiology: The structure and function of organisms and their response to change forms the basis for many processes that would be considered robust or resilient.

Ecology & Ecosystem Science: The R&R of ecosystem functions and services is a primary concern of many scientists in this subdiscipline. The interactions of individuals within and between populations and with the abiotic environment contributes to R&R on multiple levels.

There are similar examples across many other subdisciplines and disciplines, allowing for the reintegration of biology. Additionally, the boundaries of many questions regarding R&R cross over to abiotic or human systems and will require the engagement of physical scientists, sociologists, or economists.

The framework would provide a conceptual model for collaboration across subdisciplines and disciplines. It would improve integration across these areas by allowing collaborators to focus on the concepts that are most important for accurately modeling the R&R of a function.

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