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Review

Is resilience a unifying concept for the biological sciences?

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SUMMARY

There is increasing interest in applying resilience concepts at different scales of biological organization to address major interdisciplinary challenges from cancer to climate change. It is unclear, however, whether resilience can be a unifying concept consistently applied across the breadth of the biological sciences, or whether there is limited capacity for integration. In this review, we draw on literature from molecular biology to community ecology to ascertain commonalities and shortcomings in how resilience is measured and interpreted. Resilience is studied at all levels of biological organization, although the term is often not used. There is a suite of resilience mechanisms conserved across biological scales, and there are tradeoffs that affect resilience. Resilience is conceptually useful to help diverse researchers think about how biological systems respond to perturbations, but we need a richer lexicon to describe the diversity of perturbations, and we lack widely applicable metrics of resilience.

INTRODUCTION

One of the grand challenges in biology is how to integrate knowledge from different levels of biological organization.[1,2] Unifying the different subdisciplines of biology, consequently, would be a major step in solving this challenge. Resilience – the capacity of a system to recover from a perturbation – is pervasive in living systems and is viewed as so widely relevant in systems thinking that it has been proposed as a unifying concept that can integrate biology across all levels of organization, from the subcellular to the ecosystem scale.[3–6]

Resilience is important in a wide range of fields outside biology as well, such as economics,[7] engineering,[8] supply networks,[9] and physical and mental health,[10] although the terms used can differ by discipline. Interestingly, resilience research in its current form across many STEM fields arose conceptually from ecology.[11] Biological fields have often inspired research in other fields, such as the use of evolutionary algorithms for optimization used in engineering, datamining, and economics,[12–14] and in the fields of industrial ecology and the "biologicalization" of manufacturing.[15–17]

Nonetheless, resilience has not yet become a universally used concept across biology, and many important problems in biological resilience remain unresolved.[18–21] One major challenge is that many different models, definitions, and applications of resilience exist across biology subdisciplines. In each of these fields, the types of perturbations and spatial and temporal scales differ, making it difficult to see commonalities across models of resilience.[20] Additionally, the metrics used to quantify resilience in biological systems are not consistent across biological disciplines.[20,22]

We drew on selected articles from all levels of biological organization that were recommended by experts in the field, as well as lectures given as part of a graduate seminar in our department, from DNA to organisms to communities. Our goal was to look for notable commonalities across the organizational levels, if there were any. From this review, seven observations about resilience and its research in biological systems emerged. We acknowledge that there might be additional observations that one might include, and that our scope was constrained to biological fields. These observations synthesize problems and challenges for using resilience across biological scales and include propositions about where we see opportunities for research on biological resilience. We also discuss the degree to which resilience could be a unifying concept in biology for research.

OBSERVATION 1: ALL FIELDS OF BIOLOGY STUDY RESILIENCE, EVEN THOUGH THEY DO NOT ALL USE THE TERM

Extant biological systems are, by definition, resilient to some degree. That is, all biological systems vary over time within some range of what is considered "typical," they are subject to perturbations, and they recover from those perturbations – i.e., exhibit resilience – or they fail. As a general description, therefore, when an original state is perturbed, resilience refers to the return to the original state (top of Figure 1). Note that we limit our assessments here to recovery within the disturbed system, rather than cross-system resilience as might occur with human limb loss, where the limb cannot be regrown but there can be psychological resilience in the way the individual accommodates to the loss. As examples of within-system resilience, when a region of a genome is damaged, cellular machinery must repair the DNA segment for normal replication and transcription (resilience) to occur.[23] When tissue is cut from the tail of a planarian worm, resilience occurs when developmental

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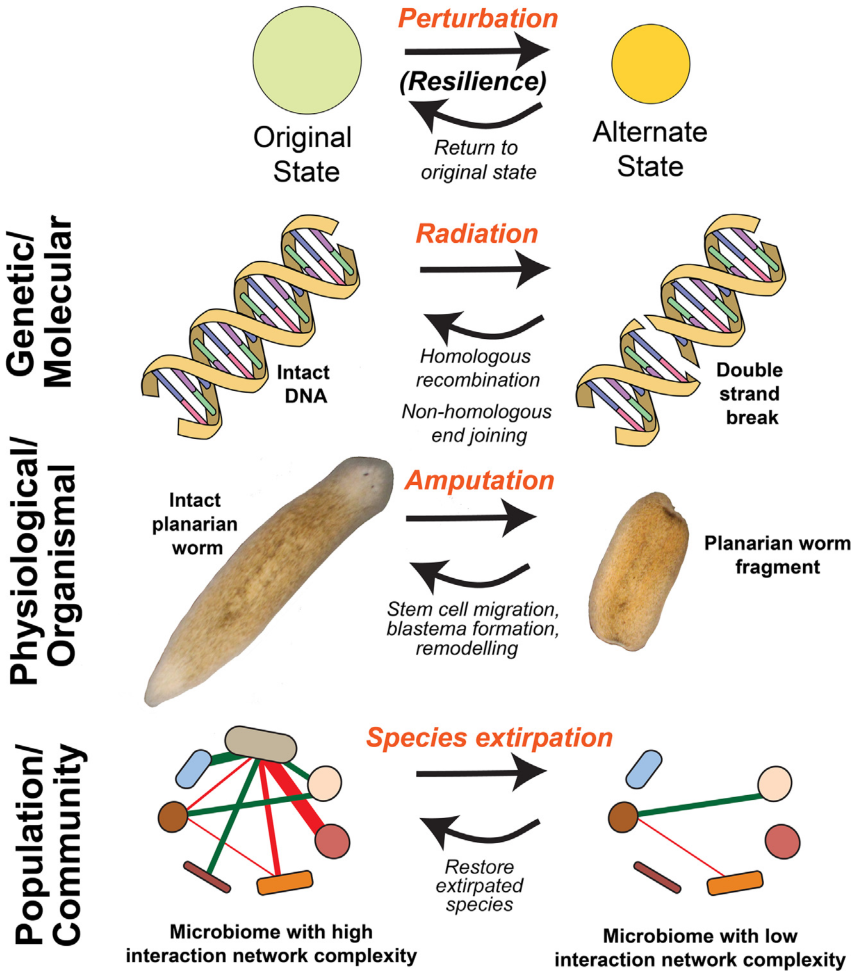


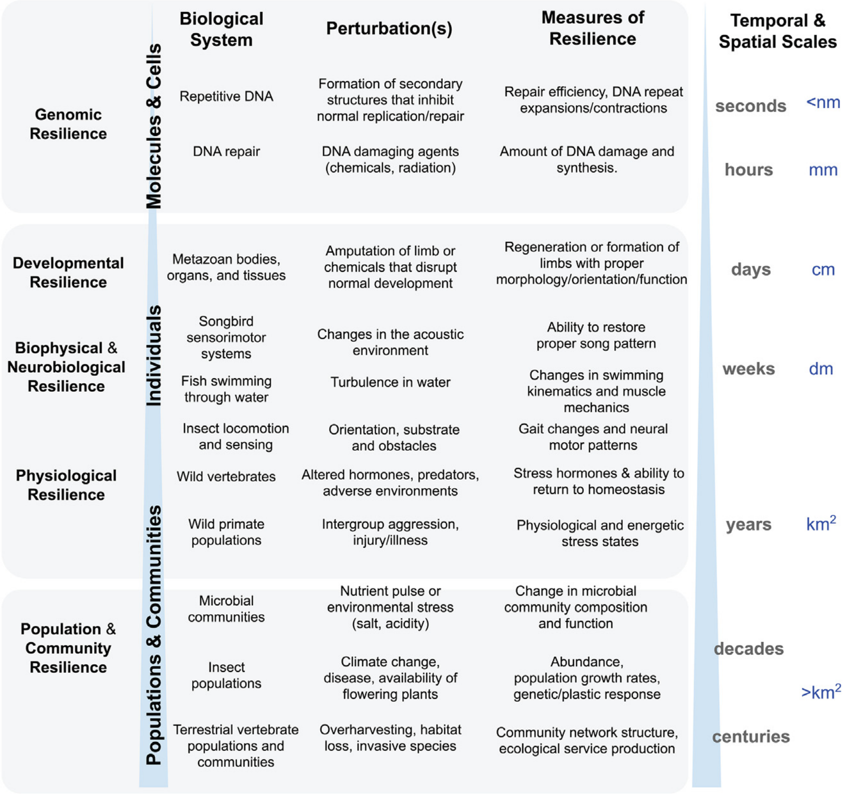
Figure 1. Examples of biological resilience

processes restore the organism to its original morphology.[24] When an individual or species is lost from an ecological community, function can be restored (resilience) through a variety of mechanisms, such as competitive release (altered community network structure, or increased abundance), behavioral or adaptive plasticity, functional redundancy, and immigration.[25] In each of these biological systems, *resilience* is the capacity of the system to return to an original state after a perturbation (Figure 1).

All biological fields and their associated study systems have some working concept of stability, or homeostasis, and how that system maintains that stability in the face of perturbations. However, confusion within and between fields sometimes occurs through inconsistent or field-specific nomenclature. For example, when discussing aspects of stability, fields within and outside biology also refer to resistance and robustness,[18] and definitions of these terms and resilience are often interchanged. We view resistance as the ability of a system to not change in the face of perturbations. Consistent use of terms across fields (even within them) is not something that can be resolved; every researcher wants their definitions and terms to be the standard. For the most part, let us ignore the extent to which the term "resilience" is or is not used in different fields of biology, and focus on the concept, which is universal. However, the importance of a particular term is relevant to the extent that it enhances – or is a barrier to – communication.[26–28] So, whether a genome is repaired following DNA damage, a body part regenerates following amputation, an individual maintains homeostasis of hormone levels despite stressors, a population persists in the face of catastrophic events, or a community recovers function following the loss of a species, all of these examples constitute system resilience as defined in this article: the capacity to return to an original state following perturbation,[29] regardless of field-specific jargon.[30–35] Another interesting aspect of resilience that is not widely investigated is understanding when there is a partial, but not full return, to the original state following a perturbation. For example, when double-strand breaks in DNA are made, the epigenetic information at the site of the break is often partially, but not fully, restored; this is one theory behind why we age.[36,37]

OBSERVATION 2: IT IS IMPORTANT TO BE SUFFICIENTLY SPECIFIC IN DEFINING THE STUDY SYSTEM

Assessment of resilience in biology depends on specifically defining the system. Specifying systems is key to selecting and interpreting resilience metrics. For example, defining your system as the individual is not sufficient because it could include downstream measures, such as



	Biological System	Perturbation(s)	Measures of Resilience
Genomic Resilience	Repetitive DNA	Formation of secondary structures that inhibit normal replication/repair	Repair efficiency, DNA repeat expansions/contractions
	DNA repair	DNA damaging agents (chemicals, radiation)	Amount of DNA damage and synthesis.
Developmental Resilience	Metazoan bodies, organs, and tissues	Amputation of limb or chemicals that disrupt normal development	Regeneration or formation of limbs with proper morphology/orientation/function
Biophysical & Neurobiological Resilience	Songbird sensorimotor systems	Changes in the acoustic environment	Ability to restore proper song pattern
	Fish swimming through water	Turbulence in water	Changes in swimming kinematics and muscle mechanics
	Insect locomotion and sensing	Orientation, substrate and obstacles	Gait changes and neural motor patterns
Physiological Resilience	Wild vertebrates	Altered hormones, predators, adverse environments	Stress hormones & ability to return to homeostasis
	Wild primate populations	Intergroup aggression, injury/illness	Physiological and energetic stress states
Population & Community Resilience	Microbial communities	Nutrient pulse or environmental stress (salt, acidity)	Change in microbial community composition and function
	Insect populations	Climate change, disease, availability of flowering plants	Abundance, population growth rates, genetic/plastic response
	Terrestrial vertebrate populations and communities	Overharvesting, habitat loss, invasive species	Community network structure, ecological service production

Figure 2. Example biological systems, perturbations, and measures of resilience, and associated scales of time and space

individual performance following genome or organ repair; metrics within the individual itself, such as the outcome of a physiological stress response; or upstream of the individual, such as focusing on mating success. Each of these is a system of the individual. In selecting/developing metrics, and making comparisons to other studies, it is also important to identify the focus of resilience assessment, such as specifying *identity* (*component*), *structure (trait)*, or *function* for the target system.[38] To provide a simple example, many crops are pollinated by native bees – if some of those species are lost from the community, but honeybees are imported to provide pollination, one function (crop production) is resilient, but a component metric (particular bee species) is not resilient.[39] In Figure 2, we provide examples of systems across levels of biological organization, along with related examples of perturbations, general metrics, and scales of time and space.

OBSERVATION 3: THERE ARE RESILIENCE TRADE-OFFS WITHIN AND BETWEEN SCALES OF BIOLOGICAL ORGANIZATION

It is a central theme in biology and evolution that compromises are common due to trade-offs, often in allocating limited resources.[40,41] With regards to resilience, trade-offs can occur proximately in resource allocation; (a) between levels of organization; (b) between systems within a single level of organization (such as between organs within an individual); or (c) within a system between resistance to a perturbation and resilience to it. If one's system is a limb of an amphibian, then resilience to loss of the limb requires regeneration, which diverts resources from other systems within an animal's body.[42] If a bird lays more eggs than it can successfully fledge based on food availability when the eggs hatch, brood reduction is beneficial (i.e., creates resilience) at the level of the parental genome or population, but it is certainly harmful to the individual chick that dies.[43] Trade-offs also can be the result of evolved responses to that under certain circumstance that conflict with each other, such as speed versus endurance in locomotory physiology. Examples of trade-offs between levels of organization can highlight the importance of defining the study system. Apoptosis is a resilience mechanism for individual survival or maintaining a particular tissue or organ, but represents failure of a system at the cellular level.[44]

The evolutionary trade-off between resistance and resilience is widely recognized in ecology and life-history studies. Taxa or ecosystems that are effective at resistance to perturbations, for example, tend to be less effective at resilience. To illustrate, forest composition is changing under climate change due to increasing droughts, and over the past half-century gymnosperms have become more resilient to drought (i.e., better able to bounce back when the drought ends) but less resistant (i.e., less able to maintain typical function as drought starts and persists). Consequently, gymnosperms are now exhibiting greater mortality and more severe reduction in growth.[45] Trade-offs related to resilience are also well-documented by the fast-slow lifestyle continuum across species, an empirical pattern of interspecific differences in either physiological responses, such as metabolic rate or stress reactivity, or demographically, via vital rates and offspring size.[46,47] For example, Capdevila et al.[48] found in a variety of animal species an apparent trade-off in vital rates associated with components of resilience, such as species that resisted change in age structure from perturbations tended to have a longer recovery time once impacted. In a more proximal, rather than evolutionary, trade-off, resources expended to regenerate the severed limb of a stick insect cannot be allocated to other purposes, such as reproduction.[49]

OBSERVATION 4: WE NEED A RICHER LEXICON TO DESCRIBE PERTURBATIONS AND RECOVERY FOR BIOLOGICAL SYSTEMS

A perturbation is an external event or driver that is defined by its effect on a system, causing it to leave its state – if it recovers, it is resilient. Perturbations should be defined and interpreted from the perspective and time frame of the species & system, not from human perspectives. Almost every discussion of perturbations within the context of resilience categorizes perturbations as "press" and "pulse" types (or chronic/acute, and so forth), where the former are long-term pressures from a perturbation and pulse is a short-term disturbance e.g.,[50]. For controlled laboratory experiments, this distinction might be sufficient because the perturbation is under the experimenter's control. Even in systems in natural or relatively natural settings, press and pulse perturbations can be meaningful. For example, an ice storm destroying a patch of forest, or rain washing nutrients into a lake, are typically treated as pulse perturbations. Press perturbations include occurrences such as harvest pressure on a population, aging of an individual (but not ontogenetic development, i.e., evolved developmental stages), or a chronic exposure to a pollutant. In natural settings, however, the distinctions can become less clear because perturbations occur as a continuum. Consequently, research on resilience might benefit from treating perturbations as a time continuum from a brief pulse to those that approach a permanent change in state (of the system). Even this, however, might be insufficient. To begin the conceptual expansion, we propose three additional broad types of perturbations: **non-stationary press**, **degrading pulse**, and **flow-kick**, and others have certainly been proposed.[51]

Examples of non-stationary press perturbations are climate change, which includes systematic changes in temperature and climate variability over time,[52] repeat expansion disease leading to worsening cellular disfunction,[53] and aging.[54] Stressors are non-stationary because the existence and intensity of stressors waxes and wanes over time.[55] For aging, we refer specifically to changes in resilience capacity such as cellular senescence, increased oxidative damage, accumulation of somatic mutations, ineffective clearance of cellular debris, and low-level chronic inflammation of the brain, and so forth.[56,57]

Our suggestion of a degrading pulse perturbation is also a degree-of-time issue in that once the pulsed perturbation occurs, it takes a long time to clear a system. This applies specifically to perturbations that linger, in the sense that the effect cannot be cleared rapidly from a system. This contrasts with a classic pulse perturbation, where there is an immediate and circumscribed disturbance from which the system either quickly or slowly recovers. As an example, it can take decades to recover from light influx in a tropical forest following the creation of a tree-fall gap.[58] This would be a degrading pulse because the light influx continues but diminishes over time, leading to different species taking advantage of the diminishing light levels as the tree-fall gap recovers. Other examples might include the clearance over years of human papillomavirus (HPV) infection, which can take 6–12 months,[59] and the long-term potentiation of synaptic strength in hippocampal neurons in response to brief excitation, which can take hours or days to return to pre-excitation levels.[60]

Flow-kick systems are characterized by repeated perturbations whose immediate effects dissipate rapidly compared to the rate of perturbation. These systems exhibit transient behavior when perturbed (kicked), and upon return to their original state (or original trajectory, as for non-stationary systems), they are in the flow state. One interesting assessment of flow-kick systems studied at the population and ecosystem levels is that resilience is overestimated by traditional approaches that consider the consequences of each disturbance separately.[51] This has been observed in ecological systems, such as fire-disturbance in savannahs,[61] and has been proposed for the physiological vulnerability of individuals facing repeated stressors that cause wear and tear.[62] These dynamics might even be generated through within-system feedback, as demonstrated by a recent model that predicts complex transient immune protection for a population due to flow-kick dynamics from the epidemiological behavior of disease spread.[63]

It is also important to define perturbation type by the potential type of outcome. For example, the introduction of an exotic species to an ecosystem could result in failure to establish, establishment but no proliferation, invasion but eventual push back, or permanent invasion causing permanent change to the system.[64] So, species introduction is a perturbation, and the type of perturbation depends on the outcome. In this example, a species introduction that does not disrupt the community demonstrates a the community's resistance (not resilience) to a pulse perturbation; the introduction is a pulse perturbation if it establishes and briefly disrupts local community dynamics; a press perturbation if/as it invades it puts sustained pressure on part of the community; a degrading press if it invades, then is pushed out over time; and a kick-flow perturbation if there are serial introduction/invasion events. If the community is not resilient, invasion could cause a change of system state if the species subsequently dominates the community.[65]

One final issue that touches on the problem of defining measures of recovery, is that natural systems are stochastic, so that the "baseline state," to which a system needs to return following perturbation, varies. So, natural systems have noise, leading to the question of whether "system noise" and "perturbations" are qualitatively different, or are they a continuum? And, if they are a continuum, what is the cut-off? This question also reveals a potential philosophical difference that could be a barrier to integrating across levels of the biological organization identified by Orzack and McLoone.[66] Research at finer levels of the biological organization often works with "model systems," where studies of a limited number of species or systems are thought to represent all species or systems, and that the difference between systems is "noise." That is, the presumption is that the basic principles will hold true across species, with variations between systems that add or remove complexity being the noise. In contrast, ecological and evolutionary research involves thousands of species, research questions and solutions might be situation-specific,[67] and there might be no universal models. Here, the differences between systems are the focus of interest, rather than being treated as noise. Consequently, how one views perturbations and system recovery might differ fundamentally by researchers of different levels of biological organization. We expand on the question of measuring resilience in Observation 5.

OBSERVATION 5: WE NEED TO SHARE AND IMPROVE METRICS OF RESILIENCE

At all levels of biological organization, researchers are creating and evaluating resilience metrics that are system specific. By "metric" we mean what specifically is being measured and compared before and after a perturbation. As examples, cellular viability can be used to measure genome resilience from DNA damage;[68] allostatic load drives the body's response to stressors.[62,69] vital rates determine a population's resilience to a reduction in population size.[70] With a few exceptions, such as rate of recovery, there is little apparent overlap in the use of metrics across levels of biological organization, though all assess some type of resilience. This could be because each field of biology at each level of organization has problems and solutions that are unique to the system, so that they are not transferable across systems. For example, DNA secondary structures in a chromosome (an undesirable stable state) caused by excessive trinucleotide repeats[71] has no apparent parallel to a fish correcting its swimming trajectory as it passes through turbulent water[72] (see Figure 2). And neither concept has an obvious role in explaining the restoration of energy flow across trophic levels in a food web after the invasion of an exotic species.[73] Alternatively, the proliferation of metrics with little interaction across fields could be a symptom of the siloed nature of biology. Developing and deploying universal metrics of resilience is a largely unresolved issue in resilience studies.

There is a wide-spread need for developing appropriate performance metrics to quantify deviations caused by perturbations as well as return to the baseline state – if you can't measure it, you can't understand it. Metrics of resilience need to account for inherent variation in the baseline of a system, such that the rate of return to pre-perturbation conditions should be to a range rather than a point. There are examples in some fields of biology. For example, Ives[74] presents a method to quantify population resilience in a stochastic system within the context of interactions with other species in the community. It is predictive, rather than mechanistic, so perhaps modifications to create a causal model[75] would resolve this, or using recent statistical tools for forecasting dynamics and species interactions.[76] It would be useful, then to determine whether such an approach could be made to fit other biological systems, addressing topics such as the amount of circulating hormone, biometrics of a regrown limb, initial population size, and community composition.

Advances are being made in developing metrics, but there is little or no attention paid to the possibility of having metrics, or families of metrics, that can be applied across multiple levels of biological organization. For example, from the microbiome world, Sorenson and Shade[77] use quantitative metrics of resistance and resilience to describe deviations from pre-perturbation communities following perturbation, but their baseline is a fixed suite of taxa even though the baseline state has variation. In another example, Field et al.[78] used a probabilistic framework for quantifying population resilience relative to a population's normal range of variation. Similar approaches are common in some fields of civil engineering, such as water resource systems. Interestingly, resilience in that field was inspired by Holling's[11] work on ecological resilience, and evaluating three features of a system is now common practice: reliability (the frequency of failures), resilience (the ability of a system to recover from a failure), and vulnerability (a measure of the magnitude of potential failures).[79,80] Approaches to resilience metrics have been developed in other fields, such as civil engineering, that might be adopted for our needs because they incorporate variation in baseline conditions, such as stream flow-duration curves,[81,82] or statistical bridge signatures.[83]

It could also be that there are approaches for evaluating resilience where the models used for assessment are field-specific, but the metric for evaluating recovery is generic. For example, some studies of metabolic resilience use receiver operator characteristics (ROC) curves and compare recovery using the area under the curve (AUC).[84,85] We note, however, that although ROC/AUC gives a measure of fit to a model and allows model comparisons (possible baseline vs. possibly recovered state), it (a) does not include variance in defining a baseline, and (b) there is no resolution to the question of "how close do the AUC values have to be to define a system as having 'returned' to baseline?" But this is a promising concept.

OBSERVATION 6: THERE ARE MECHANISMS OF RESILIENCE COMMON TO ALL LEVELS OF BIOLOGICAL ORGANIZATION

In our assessment, we found mechanisms driving resilience that appear to function at all levels of biological organization. Here we highlight five mechanisms that seem to be pervasive; we suspect that their ubiquity is a consequence of biological systems having to maintain some degree of homeostasis to persist.

Redundancy

Each level of biological organization that we investigated exhibits multiple ways to solve the same problem. There are multiple pathways to repair damaged DNA,[23] Bacterial pathogens can be resilient to the loss of particular effector genes (=perturbation) because of apparently duplicated genes, or to particular protein losses because of functional redundancy between two proteins, and there are examples of unrelated proteins compensating for loss through alternate host cellular processes, each of which restores function,[86] At another level of biological organization, ecosystems appear to be functionally redundant because multiple species can serve redundant functions (e.g., with the measure of energy flow through a community), making them resilient to rapid shifts in community composition associated with human-induced addition or loss of species to communities.[87] Note that we are treating redundancy in pathways to recovery (resilience) as distinct from redundancy that can make a system resistant to change caused by a perturbation).[88]

Plasticity

Plasticity refers to any variability in individual reaction with no change in genotype, including adaptive genetic variation (e.g., epigenetics), behaviors that allow flexible responses, evolutionary responses, and bet-hedging,[89–91] Examples of behavioral plasticity from studies of individual chimpanzees include exploration for new food types, particularly when moving to a new area,[92] and increased social selectivity as they age.[93] Exploring food types is a characteristic of diet generalists. In the latter example, individuals develop more-balanced friendships (reciprocal behaviors), socialize more with important partners, and exhibit more affiliative (less agonistic) behaviors. These changes are situation-specific, rather than being genetically programmed, and change with age. In developmental biology, plasticity can occur through up- or down-regulating transcription to respond to a perturbation, or through a temporary physiological response.[94] Phenotypic plasticity can occur through modulating gene expression, increasing individual resilience to changing environments,[95] and via different DNA polymerases used to bypass damage on a template during DNA replication.[96] Plasticity is also evident during physical and psychological development,[97] and interestingly, develops in part with two of our next mechanisms, negative feedback and system memory.

Negative feedback

Negative feedback is a pervasive regulatory mechanism in biological systems, making it a common resilience mechanism. For example, the physiological stress response is highly conserved in vertebrates through a hypothalamic-pituitary-adrenal (HPA) cascade. An external perturbation (such as a predator attack) causes first a catecholamine response (the fight-or-flight response), followed by a slower subsequent hormonal cascade ultimately causing the adrenal glands to release glucocorticoids. This increases blood pressure and decreases inflammation, among other responses, and prepares the body for subsequent perturbations.[98] Negative feedback is a mechanism that self-limits the physiological stress response and seems to be a major target of selection.[99,100] In some human pathologies, negative feedback increases metabolic resilience. For example, oxidative stress can cause neurodegenerative disease, such as endoplasmic reticulum stress caused by an accumulation of misfolded proteins.[101,102] Resilience occurs via the production of Nrf2-regulated vitagens that regulate cellular (redox) homeostasis.[103] A very different example at the level of the individual comes from the boxfish (*Ostracion meleagris*), whose body shape generates passive negative feedback to stabilize swimming when a fish is perturbed by turbulence - when the body tilts, the water flow causes vortices that push the body upright.[104] In gene expression, negative feedback can counter mutagenesis through a protein that induces the transcriptional repression of its own gene once its abundance reaches a certain level.[105]

Self-organization

Self-organization is pattern formation as a result of collective behavior governed by local (decentralized) rules, rather than being centrally controlled.[106] Self-organization is common in biological systems and is associated with greater resilience.[107,108] At the population level, examples of self-organization include changes in social affiliations (social networks) that affect vulnerability to disease spread,[109] and the distribution of individuals across space.[110] One type of self-organization is collective behavior, which manifests itself in some group dynamics, such as those exhibited by bird flocks, as well as emergent behavior in some human social systems.[111] Interesting advances are being made in understanding emergent behaviors in social systems in the field of graph theory, e.g.,[112,113]. In the development of multicellular organisms, initially identical cells differentiate through self-organization via cell-to-cell variability and feedback loops,[114] At the cellular and subcellular levels, self-organization increases resilience through mechanisms such as organizing keratin filaments into networks to protect epithelial cells.[115] The importance of self-organization appears to be an expanding field of resilience research.

System “memory”

Memory here refers to experience-based, or exposure-induced, changes in future responses or capacity of a system - specifically, the abilities to minimize or recover from the effects of future perturbations, or more rapidly recovering from them. This mechanism is apparent at multiple levels of biological organization, such as the immune response and its role in vaccine effectiveness,[116] vicariously gained knowledge transfer between individuals of the same or different species through public information,[117] horizontal gene transfer,[118] cellular memory in tissue regeneration,[119] and physiological habituation.[55] In ecological community systems, memory can be considered to affect recovery from disturbance through two major pathways, information (evolved life-history responses) and material (such as seed banks).[120] Memory plays a role in the resilience of plant systems at the genetic level, through physiological and metabolic responses to stressors (perturbations) that alter, for example, the production of secondary plant metabolites.[121]

OBSERVATION 7: RESILIENCE CAN BE NORMATIVE (BUT DOES NOT HAVE TO BE)

When evaluating resilience, a system’s recovery to baseline can also be to a desired state of a system.[122–125] This is what we mean here by “normative” – that there is a value judgment in selecting the baseline as a preferred state. Swimming fish that are perturbed by waves have a preferred state of righting themselves. For an individual as a system, even if it is not often stated explicitly, we consider “alive” as the typical and preferred state. For harvested and endangered species, resource managers prefer extant over extinct, both of which are stable states (we realize that, mathematically, 0 might not be a stable population size, but biologically it is). This concept is particularly central to synthetic biological systems, which are completely goal-oriented, and would be normative if enough people shared them as preferred states.[126] We are not sure how normative concerns might affect research and thinking about resilience in biological systems, but there is some precedence in the literature from fields such as the philosophy of science and the societal aspects of resilience.[127–129] Research into

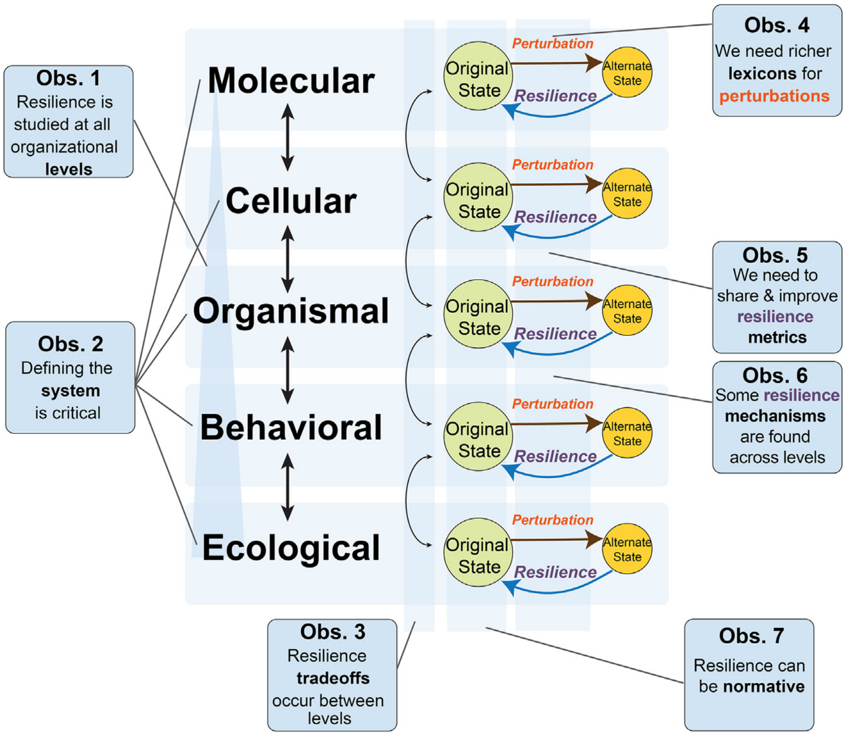


Figure 3. A depiction of the various levels of biological organization discussed here, and the associated observations about resilience

human psychology and development, in particular, also embraces the idea of developing resilience to achieve particular goals, such as improving well-being and developing interventions to traumas at both the individual and community levels.[130,131] Since a great deal of biological research and applications have a human-values interface, being aware of this aspect of resilience could be meaningful.

CONCLUSIONS

Resilience occurs at all levels of biological organization, and there are resilience mechanisms that appear to be common to all levels (Figure 3). The resilience concept is valuable as a research framework because it reinforces systems thinking, and it can be used to highlight interactions across levels of organization, including resource trade-offs. It is clear from our assessment of resilience that it (a) is a useful heuristic framework for understanding the dynamics of biological systems, (b) that there is work to do before it becomes a rigorous analytical tool within levels of biological organization, and (c) it has potential as an organizing framework for the vertical integration of biological systems. We think that our observations highlight both how challenging it can be to cross organization levels within a system, but they also identify potential for making those cross-level and cross-system comparisons. In fact, one challenge in our field is getting students to be able to make connections across systems and levels of biology. Resilience may be a terrific concept to unify these levels and systems to improve student learning. We encourage researchers to work collaboratively across multiple levels of biological organization, particularly on efforts to create a more nuanced view of perturbations, creating metrics of resilience that are strictly defined and incorporate the natural stochasticity of biological systems, and mechanistically linking systems across levels of biological organization.

LIMITATION

A comprehensive review of all the literature related to resilience at all levels of biological organization would be a book-sized endeavor, so we limited our review to specific examples at each organizational level. While we identified some mechanisms and tradeoffs of resilience in different biological systems, we are certain that there are more to be revealed. We also only touched on the concept of stable states of systems. Multiple stable states, metastability, and local vs. global minima are commonly referenced in community ecology and evolution,[132] but less so in other biological fields; this might be an opportunity for cross-organizational research. We also merely touched on some possibilities of statistical metrics of resilience – this needs to be explored deeply, across multiple biological systems. Future studies could expand usefully on any aspect of this review, filling gaps in our knowledge.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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