

paragraph actually discusses community change. Ecosystems are more than a community and community change ought not to be conflated with regime shifts, which are generally understood to occur at the level of ecosystems or higher levels of organization. Changes in community dynamics can drive an ecosystem-level regime shift, but they are not the same thing. For example, in Caribbean reefs the functional extirpation of an entire community (herbivorous fishes) did not immediately induce a regime shift because urchins were able to compensate until disease wiped them out [10]. Defining resilience as the study of change (Box 1) is both vague and inaccurate. Much resilience research has been precisely concerned with identifying system attributes that allow ecological and social-ecological systems to buffer disturbance without undergoing a regime shift [3,8,11]. Indeed, the literature is so large we cannot begin to do it justice.

Ironically, resistance and its accompanying mechanism, trophic compensation, fit quite neatly within the theoretical framework of (ecological) resilience theory. Classifying the mechanism under resistance is unnecessary, as the mechanism of trophic compensation likely belongs alongside the panoply of other mechanisms such as functional compensation, functional reinforcement, and response diversity that contribute to ecological resilience. We say likely, because the premise of Connell and Ghedini appears to rest on one mesocosm experiment confined to two species [12]. Although mesocosm experiments can provide powerful insights into community dynamics that may well scale up to more realistic and complex communities and ecosystems, at the present time the role of trophic compensation as a buffering mechanism against disturbance remains largely hypothetical. In failing to differentiate between engineering and ecological resilience and then also ascribing conflicting, flattened, and even inaccurate

definitions to resilience, they inadvertently diminish the strength of what they were intent on communicating, which is that 'quiet' mechanisms such as trophic compensation may play a role in buffering disturbance and understanding the limits of such mechanisms may allow us to better characterize the degree of resilience in any given system, or its vulnerability to a regime shift. Unfortunately, the merits of the mechanism in the context of ecological resilience are unlikely to receive due attention given their misuse of resilience in framing their argument.

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References

1. Connell, S.D. and Ghedini, G. (2015) Resisting regime shifts: the stabilising effect of compensatory processes. *Trends Ecol. Evol.* 30, 513–515
2. Hughes, T.P. *et al.* (2013) Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends Ecol. Evol.* 28, 149–155
3. Peterson, G.D. *et al.* (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1, 6–18
4. Desjardins, E. *et al.* (2015) Promoting resilience. *Q. Rev. Biol.* 90, 147–165
5. Pimm, S.L. (1984) The complexity and stability of ecosystems. *Nature* 307, 321–326
6. Holling, C.S. (1973) Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23
7. Scheffer, M. *et al.* (2001) Catastrophic shifts in ecosystems. *Nature* 413, 591–596
8. Allen, C.R. *et al.* (2005) The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8, 958–966
9. Hoover, D.L. *et al.* (2014) Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* 95, 2646–2656
10. Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551
11. Sundstrom, S.M. *et al.* (2012) Species, functional groups, and thresholds in ecological resilience. *Conserv. Biol.* 26, 305–314
12. Ghedini, G. *et al.* (2015) Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. *Ecol. Lett.* 18, 182–187

Letter

Ecological Resistance – Why Mechanisms Matter: A Reply to Sundstrom *et al.*

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How do ecological systems respond when faced with a disturbance? Connell and Ghedini [1] suggested that the ability to anticipate and to manage such responses could benefit from studies that explicitly investigate processes that limit change in ecological communities; that is, processes that enhance resistance to disturbance. They [1] highlighted compensatory effects as a suite of processes that not only buffer against change to species diversity (i.e., density and functional compensation; see review in [2]) but can also buffer against structural change. Sundstrom *et al.* [3] argued that Connell and Ghedini's ideas ought to have been nested more clearly within the theoretical framework of 'ecological resilience' and that if this were done it would be unnecessary to classify such processes under 'resistance'.

Consideration of the issues raised by Sundstrom *et al.* [3] is timely because discussion is growing on whether investigation into extensive transformation of ecological systems should be restricted by a concept (i.e., ecological resilience) that bounds the admission of solutions to understanding resistance [4,5]. Sundstrom *et al.* stated that resilience theory is a cohesive, and internally consistent, conceptual model of disturbance-induced

ecological change [3]. While it is perhaps a coherent theory, we are concerned that an expectation of conformity with this thinking can stymie broader conceptual development and limits such development to a subset of systems with specific features and at specific biological levels. For example, Sundstrom *et al.* [3] argued that abrupt community-level change cannot be considered to be a regime shift – only change at the ecosystem level satisfies their criteria. This signals a limitation of resilience thinking; namely, that the focal biological level is the ecosystem and above (socioecological systems). We believe that the concepts of resistance and resilience can lead to insights about disturbance-induced change over all ecological levels, from individuals to socioecological systems.

We consider there are substantial benefits to be gained by differentiating between processes that limit change (i.e., resistance) and processes that adjust and recover from disturbance (i.e., resilience) rather than conflating these processes within definitions of resilience (e.g., [3]). Recent theoretical advances have explicitly addressed the relative contributions of resistance and resilience to ecological stability in varying environments [6,7], suggesting that such an approach could rapidly progress our understanding of ecological responses to environmental change. If we fail to recognize resistance and resilience as distinct components, we are unlikely to be able to effectively manage for the consequences of disturbance. There may be different factors governing resistance and resilience, so that different approaches are needed to enhance each in the face of disturbance [4]. Indeed, one may assess the relative contributions of resistance and resilience to disturbance-induced change. Such knowledge has practical significance, potentially contributing to more effective management, which is a common reason for seeking such understanding [4].

A unified framework for stability based on combinations of processes that underpin

resistance and processes that underpin resilience remains to be developed. However, such a framework is crucial if we are to anticipate and to manage substantial changes in increasingly variable environments [4,8]. We see merit in broadening theories of stability to account for multiple levels of responses (i.e., individuals to ecosystems) by both resisting and restructuring to initial change. We consider the study of mechanisms of resistance at any ecological level of organization to be useful and thus are not able, or seek, to ‘fit quite neatly within the theoretical framework’ in which ‘classifying the mechanism under resistance is unnecessary’ [3].

Despite the current dominance of resilience thinking, there are alternative views on how ecologists view and study resilience (see discussions in [5,8]). Historically, resilience has been recognized as one of the ecological concepts related to stability [9,10]. Since then, research on resilience has generated many influential papers and deeply influenced theories of community stability. However, attention to other properties that underpin stability (i.e., resistance) has faded. Restoring a strong focus on resistance as a component of ecological response to disturbance, and the mechanisms that underpin it, will enhance our ability to predict and to deal with ecological change in the face of disturbance.

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References

1. Connell, S.D. and Ghedini, G. (2015) Resisting regime-shifts: the stabilising effect of compensatory processes. *Trends Ecol. Evol.* 30, 513–515

2. Loreau, M. and de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* 16, 106–115
3. Sundstrom, S.M. *et al.* (2016) Resisting resilience theory: a response to Connell and Ghedini. *Trends Ecol. Evol.* 31, 412–413
4. Nimmo, D.G. *et al.* (2015) *Vive la résistance: reviving resistance for 21st century conservation.* *Trends Ecol. Evol.* 30, 516–523
5. Hodgson, D. *et al.* (2015) What do you mean, ‘resilient’? *Trends Ecol. Evol.* 30, 503–506
6. Hoover, D.L. *et al.* (2014) Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* 95, 2646–2656
7. Isbell, F. *et al.* (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526, 574–577
8. Mori, A.S. (2015) Resilience in the studies of biodiversity–ecosystem functioning. *Trends Ecol. Evol.* 31, 87–89
9. Connell, J.H. and Sousa, W.P. (1983) On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121, 789–824
10. Grimm, V. and Wissel, C. (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109, 323–334

Spotlight

How Monkeys Sequester Carbon

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Unsustainable hunting does more than threaten wildlife populations and human livelihood – Carlos Peres and colleagues recently showed that it can also reduce how much carbon the forest stores. Maintaining primates and other important seed dispersing animals in tropical forests could be an important piece of the climate change mitigation puzzle.

Tropical forests store vast quantities of carbon, leading to international interest and investment in programs to Reduce Emissions from Deforestation and forest Degradation (REDD+). Such programs focus on protecting trees – but is that sufficient in a biome characterized by intricate webs of species interactions? Is it enough to leave forests uncut but still destroy the pollinating and seed