Feature Issue: Some Thoughts on Resilience

Resisting regime-shifts: the stabilising effect of compensatory processes

Sean D. Connell and Giulia Ghedini

Southern Seas Ecology Laboratories, School of Biological Sciences and The Environment Institute, The University of Adelaide, Adelaide, 5005 SA, Australia

Ecologists seem predisposed to studying change because we are intuitively interested in dynamic systems, including their vulnerability to human disturbance. We contrast this disposition with the value of studying processes that work against change. Although powerful, processes that counter disturbance often go unexplored because they yield no observable community change. This stability results from compensatory processes which are initiated by disturbance; these adjust in proportion to the strength of the disturbance to prevent community change. By recognising such buffering processes, we might also learn to recognise the early warning signals of community shifts which are notoriously difficult to predict because communities often show little to no change before their tipping point is reached.

Ecosystem collapse need not be surprising

Ecologists seem predisposed to studying change, particularly the response of communities to disturbance (see Glossary). This predisposition has resulted in a large amount of ecological research into the processes that shift a system from one state to another and back (i.e., resilience). We now recognise that community transitions are difficult to stop and reverse once they have started, often appearing as sudden shifts because of the difficulty of predicting tipping points [1]. Emerging research suggests that there are processes acting well in advance of processes of recovery; such early responses adjust the dynamics of a system to counter the otherwise unchecked effects of disturbance [2,3]. Such compensatory effects powerfully underpin the resistance of communities to change [3] and maintain overall stability by gaining in strength with increasing intensity of disturbance [4]. Whereas compensation appears to be an important mechanism through which communities resist change, the theory of compensation is nowhere near as developed as that of resilience theory.

When disturbance causes no change in community structure

Awareness of stabilising processes is governed by the definition of disturbance

We believe that the predisposition of ecologists to the study of change, hence resilience, comes from the way we think about disturbance. A disturbance is considered to have occurred when it causes visible changes in some structural property of interest; for example, biomass, species density, or community structure. Where these changes are observed, we then recognise community perturbation; in other words the disturbance (cause) triggered a response (effect). Conversely, if there is no observable change in community structure, we conclude that the disturbance had no effect (i.e., no perturbation). Hence, a perturbation only occurs when a disturbance is large enough to overcome the inertia of the system. This ecological definition of disturbance focuses attention on to structural change; hence the greater focus by ecologists on properties of resilience (change in response to disturbance) rather than resistance (no change).

However, it is difficult to deny that communities might be perturbed by a disturbance even when they show no observable change in structure [5]. Such stasis might result from the seemingly paradoxical situation where a potential disturbance to an ecological community is met by little to no change. Where ecologists are open to this possibility, they are also open to a deeper consideration of stabilising responses. Compensatory processes can maintain community stability by absorbing or countering the effects of disturbance. To date, the theory of compensatory dynamics has been approached from the perspective of biodiversity loss and ecosystem function ([3] for review). This focuses on how species diversity maintains ecosystem stability through processes of density compensation (e.g., adjustments in species densities maintain overall community biomass) [6,7] or functional compensation (e.g., the functional role of a species that is lost is taken up by another species; i.e., functional redundancy) [8,9].

Glossary

Compensation: a process that changes in strength in proportion to the effect of disturbance to prevent change.
Disturbance: a force potentially capable of changing population or community structure by altering the biotic or abiotic environment.
Inertia: similar in concept to 'resistance' (see below), but 'inertia' conveys the idea of non-response to disturbance, whereas 'resistance' conveys the possibility of a system withstanding a disturbance through processes that counter change.
Phase shift: the change of a system from one state to another.
Resilience: the capacity of a system to reorganise and return to a prior state after a disturbance.
Resistance: the capacity of a system to absorb the effects of disturbance without changing.
Stability: the persistence of a system within a specific state.

Corresponding author: Connell, S.D. (sean.connell@adelaide.edu.au).
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Invisible hand: powerful stabilisers result from individual actions

We propose broadening the ideas of compensatory dynamics to include adjustments in the strength of pre-existing processes to absorb the effects of disturbance [2,10]. If we move beyond the current focus on changes in biodiversity, then there is scope to understand how compensatory dynamics can maintain community stability without major loss or change in biodiversity, in other words without community restructure. Such stability, therefore, requires pre-existing processes to change in strength in proportion to the effect of disturbance [4]. Thereby, compensatory processes act as inconspicuous mechanisms that counter the effects of disturbance, and can explain why observed community shifts are smaller than expected after disturbance events.

We argue that compensatory processes act at the level of individual organisms, but affect entire communities. Changes in *per capita* consumption can absorb the expansion of opportunistic species favoured by human-driven increases in resource availability [4]. Such individual-level responses prevent community change by adjusting the interaction strength between trophic levels to negate the effect of disturbance. Individuals can also adjust their competitive strength such that a reduction of intraspecific competition compensates for the negative effects of global warming that cause a phenological mismatch between the breeding time of birds and availability of their prey [11]. Similarly, a reduction in antagonistic interactions between species can compensate for the loss of dominant plant species and stabilise communities after extreme events [2]. In each of these examples, stability is an emergent property of the aggregate of individual responses.

Although compensatory processes are measurable, there have been few attempts to establish their existence and strength across ecosystems. Since the introduction of compensation as an ecological concept more than 50 years ago [7,9], ecologists seem to have been held back from the study of such biotic feedback mechanisms that stabilise communities. We argue that ecology needs to be stimulated to face this challenge that is founded on a deeply ingrained view of what disturbance means (as above) and how we think about community organisation (see below).

Could studies of compensation advance our understanding of stability?

Homeostatic properties involve feedbacks

If we are to recognise consistent structures of a community (stability) through fluctuating environments (time) and heterogeneous landscapes (space) as being more than random chance, then we must also be open to the idea of more tightly interacting sets of species that work to maintain temporal stability. Although we recognise that the persistence of co-occurring species occurs for reasons greater than random processes of chance (Box 1), accounts of patterns of temporal stability have not progressed much further than traditional models; for example, competition and facilitation.

The stability of communities through changing environments might not only be a product of mechanisms that adjust to change (resilience) but also involve mechanisms that prevent change in the first place (resistance). To incorporate this aspect of resistance into resilience theory we must broaden our models to include feedback mechanisms that act against change to stabilise the system [12,13]. It seems to be time to reconsider the idea of communities as homeostatic systems as proposed by ecologists such as Odum and McNaughton. Compensation underpins this idea as a mechanism through which communities counter disturbance by absorbing its effects such that the overall stability of the system is maintained. If communities represent the result of processes of random chance, then compensatory mechanisms would not be a general characteristic of how communities respond to disturbance.

Changes in dominant feedbacks are common explanations for regime shifts in resilience theory [14]. Although changes in positive and negative feedbacks drive transition from and recovery of a state, they are often difficult to study because they create circular causality where cause and effect cannot be differentiated [15]. Importantly, whereas positive feedbacks can enhance and negative can negate disturbance, compensatory mechanisms do not exert any control over the disturbance. Compensation can only temporarily buffer the effects of disturbance such that this does not result in community change. When compensatory mechanisms cannot absorb the effects of disturbance, this failure triggers community shifts by altering dominant feedbacks. By studying compensation we not only identify the processes that resist disturbance but we also identify the point at which these processes fail (i.e., recognise thresholds of collapse) such that community shifts are less surprising.

Disturbance regimes affect relations between resistance and resilience

There is general support for the idea that the stability of a system (resistance and resilience) is proportionally related to the intensity of disturbance experienced over evolutionary timescales, such that systems evolved from highly variable environments are more stable to disturbance than those from less variable environments [10,16]. For systems

Box 1. Two opposing views of community organisation

Since the beginning of the 20th century, ecology has swung between two extreme views of ecological communities and their organisation. At its most extreme simplification, the Clementsian view suggested that community organisation is analogous to physiological homeostasis within individual organisms, such that communities were considered as 'super-organisms'. Consistency of community structure across time and multiple generations led to the view of plants and animals as being interdependent upon each other and integrated communities. Opposing this view, the Gleasonian model considered communities as simply convenient descriptions of sets of organisms that tend to be found at the same place and time because of similarities in physiology and resource requirements. Today, the general view of ecosystems or communities lies as being somewhere between completely random assemblages of co-occurring species and completely integrated super-organisms. Nevertheless, ecologists remain largely sceptical of the idea of communities as homeostatic systems, suggesting that the pendulum between these extreme views has swung too far from the encouragement needed for deeper research on processes of stability.

stable to disturbance, the relative contributions of resistance and resilience are likely to vary as a function of the intensity the disturbance. Indeed, stability might be more reliant on compensatory processes where disturbance is moderate, but more reliant on recovery processes where disturbance is extreme. Where the absorptive capacity of compensation is overwhelmed by disturbance, stability then relies on the regenerative capacity for recovery. Such differences suggest that resistance and resilience to disturbance are not necessarily directly proportional to one another [17].

In a noteworthy study, Hoover, Knapp, and Smith [18] assessed the stability of a grassland community to extreme disturbance. The community initially resisted disturbance via a physiological response (i.e., reduced growth) that occurred equally across species to result in no change in community structure. This compensatory effect was overwhelmed by the persistence of the disturbance to drive a shift in community composition. In this case we may characterise the community as having relatively low resistance, but high resilience, because it made rapid progress towards recovery via density compensation. Hence, community stability initially involves resistance by absorbing change, and then recovery when change cannot be countered.

Do we need to rebalance ideas about resilience with resistance?

The general public and natural resource managers have long been concerned with the impacts of human-driven environmental change on ecological communities. Ecological research has responded by focusing on the mechanisms that lead to community change, including processes that shift a system from one state to another and back (i.e., resilience). Nevertheless, this emphasis on resilience may also belie the instinctive tendency for ecologists to be drawn to the study of change, possibly because change is more interesting to study and report than no change.

A key difficulty in studying resistance is the detection of compensatory processes where the masking effects are immediate and result in no change; therefore, how would ecologists know how to embark on such a study? We suggest that monitoring or experimental programs should measure processes that oppose the crucial transition. The diversity of compensatory effects is likely to be wider than has been considered to date; such as, trophic compensation [4], and mortality or recruitment compensation [2,11], through physiological compensation [18]. Regime shifts have been notoriously difficult to predict because communities often show little to no sign of change before the tipping point is reached. We argue that, by recognising processes that buffer the effects of disturbance to prevent community change, we might also learn to recognise the early-warning signals of shifts. In practice, such awareness provides managers with the opportunity to bolster compensatory processes (e.g., harvest or recovery of herbivores) that counter unwanted change (e.g., runaway expansion of weedy species).

Concluding remarks

The persistence of communities across multiple generations suggests processes operate to maintain stability [2], and the recent identification of trophic compensation to compounding disturbances has revealed such stabilising mechanisms [4]. These mechanisms can underpin the resistance of communities to disturbance, and thus their stability, well before resilience processes are triggered. Identifying these mechanisms of resistance and the thresholds at which they are breached necessarily involves the study of compensatory dynamics. Such study may need a shift in thinking; ecologists may need to relax their scepticism of ecological communities as homeostatic systems. If compensatory dynamics are a common feature of communities, then understanding their contribution to resistance would be of value, not only by way of improved predictions of community change but also as a way to prevent undesirable change in the first place.

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