Feature Issue: Some Thoughts on Resilience

Vive la résistance: reviving resistance for 21st century conservation

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Confronted with increasing anthropogenic change, conservation in the 21st century requires a sound understanding of how ecological systems change during disturbance. We highlight the benefits of recognizing two distinct components of change in an ecological unit (i.e., ecosystem, community, population): 'resistance', the ability to withstand disturbance; and 'resilience', the capacity to recover following disturbance. By adopting a 'resistance–resilience' framework, important insights for conservation can be gained into: (i) the key role of resistance in response to persistent disturbance, (ii) the intrinsic attributes of an ecological unit associated with resistance and resilience, (iii) the extrinsic environmental factors that influence resistance and resilience, (iv) mechanisms that confer resistance and resilience, (v) the post-disturbance status of an ecological unit, (vi) the nature of long-term ecological changes, and (vii) policy-relevant ways of communicating the ecological impacts of disturbance processes.

Resistance and resilience: key concepts for 21st century conservation

A fundamental goal of conservation biology is to prevent the loss of species despite the diverse pressures in human-dominated environments [1,2]. This is an immense task because many ecosystems have experienced extensive transformation for agriculture, resource production, or urbanization [3], and now face a changing global climate with associated alteration to disturbance regimes (e.g., climatic extremes [4]). Global and regional disturbance processes, often beyond the immediate control of regional policy makers and practitioners, have led to an emphasis on local actions aimed at enhancing the capacity of ecosystems to withstand such pressures [5,6]. Terms such as 'resilience' have become synonymous with a growing raft of policies aimed at buffering ecological systems from the tide of large-scale disturbances [7–9].

For ecological knowledge to guide such policies, a sound understanding of how ecological systems change due to disturbance is required [6]. This will be influenced by how ecologists conceive and measure disturbance-induced ecological change. The concept of resilience has been central to ideas about human-induced ecological change for over four decades [10,11]. Holling [10,12] introduced the now-dominant concept of 'ecological resilience'. A resilient ecosystem is one that can 'absorb' disturbances and maintain a qualitatively similar state [12–14]. A second view of resilience recognizes two distinct and measurable components of the way ecological units (e.g., ecosystems, communities, populations) respond to disturbance: (i) 'resistance' is the ability to persist during the disturbance, and (ii) 'resilience' is the capacity to recover or 'bounce back' following alleviation of the disturbance [15–17].

Resistance and resilience largely are merged within 'ecological resilience' [14,18], whereas the latter view recognizes them as sibling concepts: closely related but independently measurable variables. While ecological resilience is concerned largely with responses to the disturbance at the ecosystem level and above (i.e., socio-ecological systems [19]), the resistance–resilience framework is a general concept of ecological change not linked to a biological level: ecosystems, communities, populations, even individuals, can be measured in terms of their resistance and resilience to disturbance. Conceptually similar to Holling's (1996) 'engineering resilience' [12], we refer to this as the 'resistance–resilience' framework.

Ecological resilience has generated many influential articles [20,21], books (e.g., [22]), and a dedicated journal (*Ecology and Society*). Meanwhile, the resistance–resilience framework seems to have languished. Our view is that this latter approach has much to offer scientists and conservation practitioners. Our aim here is to reinvigorate interest in the resistance–resilience framework by bringing into focus the benefits and insights it offers in understanding disturbance-induced ecological change.

Characteristics of the resistance–resilience framework

Studies using a resistance–resilience framework share two characteristics. First, they use empirical data that reflect two distinct components: (i) resistance, measured as change in an ecological unit (e.g., community, population) arising from a disturbance; and (ii) resilience, change in an

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ecological unit following the relaxation of the disturbance. Second, such research directly quantifies resistance and resilience by measuring change through time in relation to the disturbance (cf. surrogates of resilience, such as functional redundancy [23,24]). Sampling is ideally conducted over the entire disturbance cycle, namely, before (at least immediately before but ideally long enough to establish a pre-disturbance baseline), during (or immediately after for pulse disturbances), and following the relaxation of the disturbance (continued for a period sufficient to measure a potential return to the initial state) (Box 1).

The focus on change relative to a pre-disturbance state means that a resistance–resilience framework provides particularly useful insights for managing ecological systems that are subject to anthropogenic disturbance. A common conservation goal in such systems is to minimize change to an ecological unit as a result of a disturbance or, if it is altered, to return rapidly it to its initial pre-disturbance state.

How does a resistance–resilience framework advance understanding?

The key role of resistance

Discerning the different roles that resistance and resilience play brings a more complete understanding of ecological responses to disturbance. However, in many situations only resistance can be considered because anthropogenic disturbances often are not released [18]. Unlike pulse disturbances (e.g., floods, fires) that eventually relax [25], many 'press' disturbances (e.g., regional-scale land clearing for agriculture, urbanization) and some ramp disturbances (e.g., climate change) persist or increase in their intensity through time (Figure 1). Resistance offers a conceptual means to understand different types of persistent disturbance and seek common mechanisms that enhance persistence. A narrow focus on resilience, or a fusion of resistance and resilience, can limit the opportunity for conservation

Box 1. Measuring resistance and resilience

Measures of resistance and resilience represent changes in ecological units over time, with 'before' compared with 'during' (or immediately after for pulse disturbances), and 'during' compared with 'following' the relaxation of the disturbance, respectively. Such measures can be changes in absolute values (e.g., number of species a community loses or gains) or proportional values (e.g., percentage of species lost or gained). A limitation with absolute measures of change is that they are influenced strongly by the initial state of the system [47]. The number of species a community can lose during a disturbance is related to the initial number of species, and thus communities with more species initially can lose more species [47]; this applies to other community measures such as biomass [16]. While this can be controlled in small-scale experimental or laboratory studies [5], it is not the case for studies at landscape or regional scales. Therefore, measures of proportional change often complement changes in absolute values because the former helps to account for the often-strong effect of existing disturbance gradients on ecological units.

Using the resistance–resilience framework, a simple measure of resistance is the proportion of a variable (S; e.g., species richness, population size, body mass) retained during disturbance. Resistance is the percent change from before (T1) to the end (T2) a disturbance = S_{T2}/S_{T1}. To calculate resilience, a third measurement following the relaxation of the disturbance (T3) is needed, providing a 'net change' = S_{T3}/S_{T1} (Figure I). From this, the resilience of an ecological unit can be calculated as resilience = $(S_{T3}/S_{T1}) - (S_{T2}/S_{T1})$.

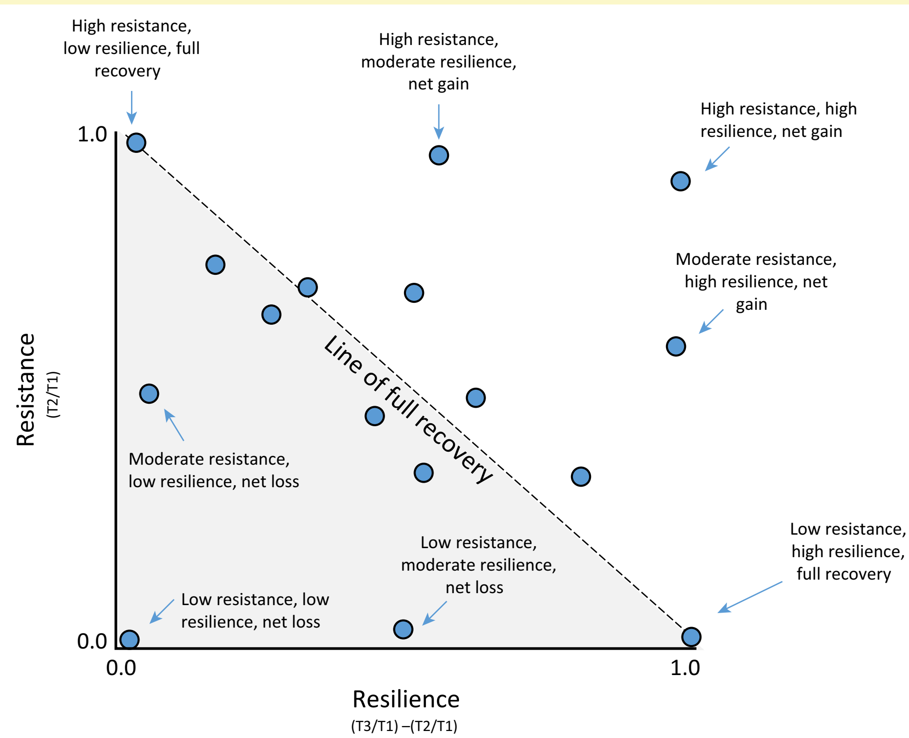

Figure I. Plotting values for resistance and resilience provides a visual representation of the magnitude of decline of a quantity (distance from line of full recovery) and the degree to which net change results from resistance, resilience, or both. Net loss indicates an ecological unit (e.g., community species richness) was reduced during the disturbance, whereas a net gain shows that the unit increased.