

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

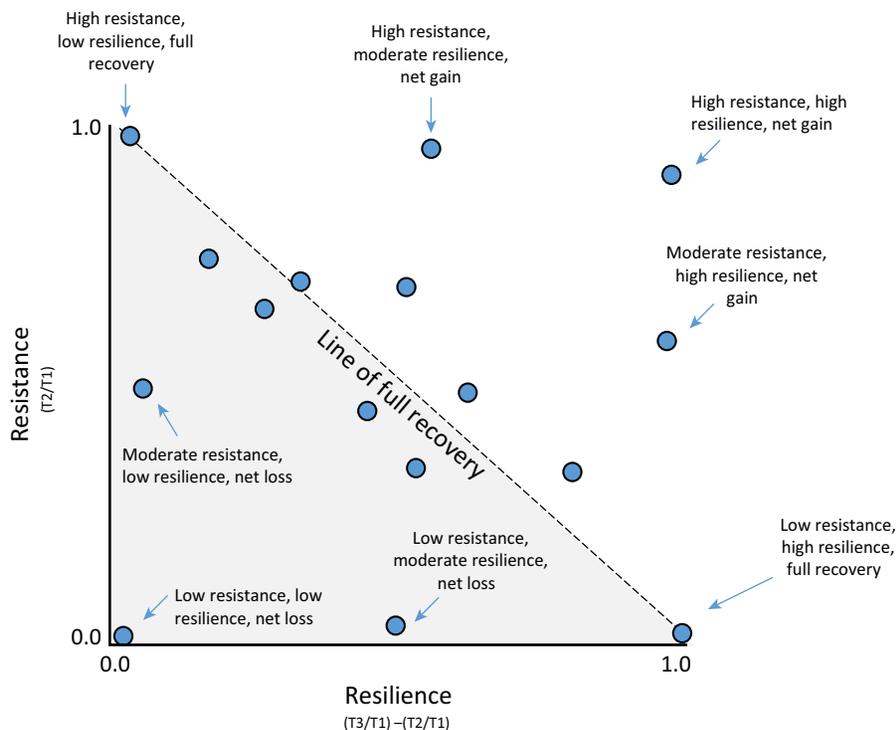
Discerning the different roles that resistance and resilience play brings a more complete understanding of ecological responses to disturbance. However, in many situations only resistance can be considered because anthropogenic disturbances often are not released [18]. Unlike pulse disturbances (e.g., 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

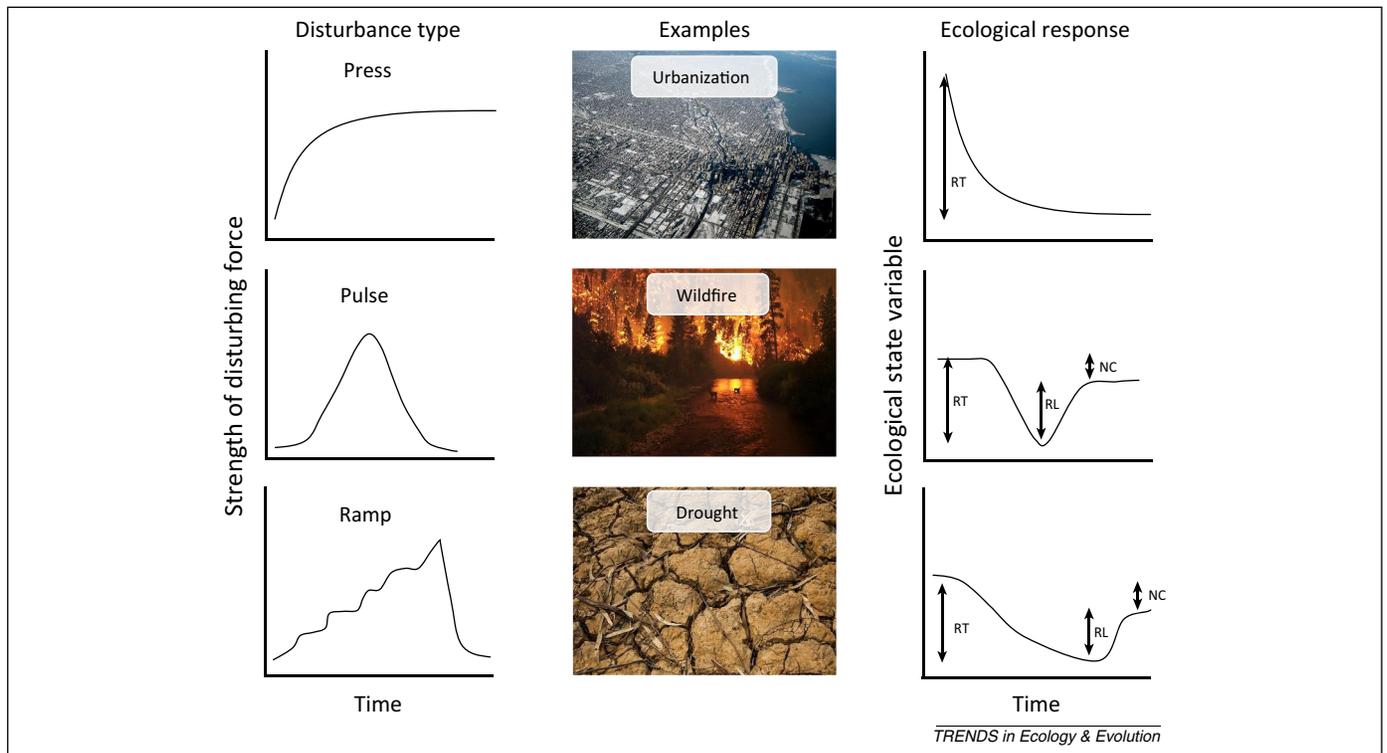
Measures of resistance and resilience represent changes in ecological units over time, with ‘before’ compared with ‘during’ (or immediately after for pulse disturbances), and ‘during’ compared with ‘following’ the relaxation of the disturbance, respectively. Such measures can be changes in absolute values (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 ( $T_1$ ) to the end ( $T_2$ ) a disturbance =  $S_{T_2}/S_{T_1}$ . To calculate resilience, a third measurement following the relaxation of the disturbance ( $T_3$ ) is needed, providing a ‘net change’ =  $S_{T_3}/S_{T_1}$  (Figure 1). From this, the resilience of an ecological unit can be calculated as resilience =  $(S_{T_3}/S_{T_1}) - (S_{T_2}/S_{T_1})$ .



**Figure 1.** 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.



**Figure 1.** Types of disturbances, the ecological responses they engender, and measurement of resistance (RT), resilience (RL), and net change (NC) within the resistance-resilience framework. Modified from Lake [58]. Urbanization: Wiki commons image, license details [https://commons.wikimedia.org/wiki/File:Chicago\\_Downtown\\_Aerial\\_View.jpg](https://commons.wikimedia.org/wiki/File:Chicago_Downtown_Aerial_View.jpg); Wildfire: Wiki commons image, license details [https://commons.wikimedia.org/wiki/File:Deerfire\\_high\\_res\\_edit.jpg](https://commons.wikimedia.org/wiki/File:Deerfire_high_res_edit.jpg); Drought: Wiki commons image, license details [https://commons.wikimedia.org/wiki/File:Cracked\\_ground\\_151.jpg](https://commons.wikimedia.org/wiki/File:Cracked_ground_151.jpg).

biologists to gain insights into how to promote resistance to persistent disturbance [18].

Identifying the determinants of resistance in the face of a persistent disturbance is particularly valuable for conservation management [26]. For instance, invasion ecology has provided many ideas about the ability of biotic communities to ‘resist’ ongoing species invasion [26,27]. For example, biotic communities with diverse functional groups have been shown to be more resistant to the spread of invasive species [28]. Similarly, the field of landscape ecology has shown that the properties of agricultural land mosaics, such as the spatial arrangement or composition of remnant vegetation, can affect the capacity of species to persist within the landscape decades after the disturbance was initiated [29,30]. Such knowledge feeds directly into conservation management by revealing management actions that can promote resistance in the face of persistent disturbances [26].

#### *Intrinsic attributes associated with resistance and resilience*

Intrinsic attributes refer to the characteristics of an ecological unit that are distinct from the characteristics of its environmental setting (‘extrinsic attributes’, see below). Examples include the physiological and behavioral traits of individuals, the size or age-structure of populations, species richness, evenness or diversity of communities and of the energy and nutrient dynamics in ecosystems. It is widely recognized that such intrinsic attributes can influence the resistance and resilience of ecological units to

disturbance [31–33]. Ecological traits, for example, often are used to explain or predict responses of species to disturbances [34,35]. However, few studies have distinguished between the intrinsic attributes of ecological units that help them to persist during a disturbance (‘resistance traits’) from those that enable recovery following its relaxation (‘resilience traits’) [36,37]. Failure to differentiate in this way obscures relationships between intrinsic attributes and disturbance-induced ecological change because ecological change is more than the sum of its parts. A given decline in an ecological unit over the course of disturbance can be due to a loss of resistance only, resilience only, or combinations in between those two extremes (see Insights into long-term change in biodiversity).

Attributes that confer a high level of resistance to a given disturbance are those that facilitate tolerance to the disturbance or that allow adaptation. For individual species, this might include physiological or behavioral plasticity [36,38]. By contrast, attributes associated with resilience often relate more strongly to recolonization (e.g., dispersal, mobility) and reproduction or rapid regrowth *in situ* (e.g., high reproductive rates, resprouting [39,40]). For example, heat tolerance in corals is an important trait modulating resistance to climate pressures, while recruitment rates are more important for resilience [41]. An improved understanding of the traits associated with either resistance or resilience will help to identify the mechanisms that underpin such responses [42], while also improving the capacity of scientists to predict those units (e.g., species, communities) most vulnerable to a given disturbance [34,43].

### Extrinsic factors that determine resistance and resilience

Extrinsic attributes are those characteristics of the environment in which the ecological unit is embedded. For individuals, this might be the density of intraspecific competitors, whereas for a community it might relate to abiotic conditions in the ecosystem (e.g., soil moisture). Such factors might explain variation in resistance and resilience among otherwise ecologically similar units (i.e., ecological units with similar intrinsic attributes). For example, during a severe drought in south-eastern Australia, Selwood *et al.* [44] and Haslem *et al.* [45] showed that the resistance of bird communities to drought was affected by environmental variables (vegetation type and the extent of tree cover, respectively). These findings suggest that extrinsic factors amenable to conservation management (either through habitat restoration or protection) modulate resistance and resilience.

### Mechanisms that confer resistance and resilience

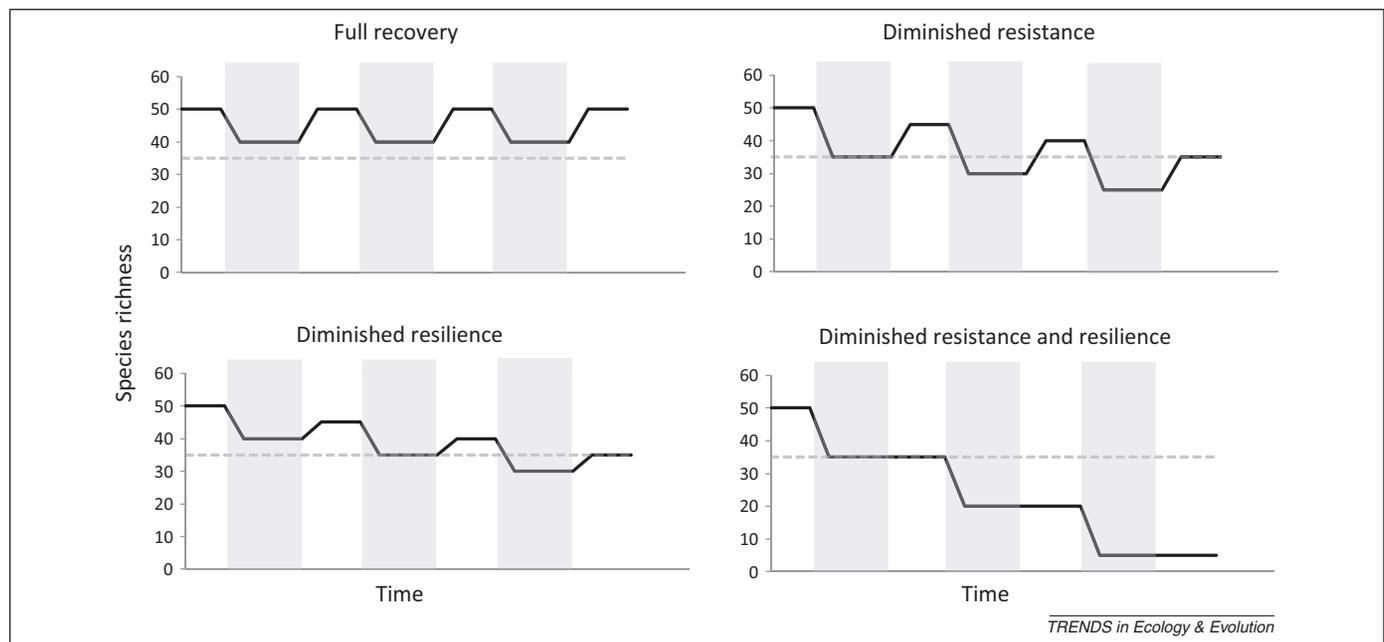
In many cases, the extrinsic factors that influence resistance and resilience will be tightly linked because they arise from a common mechanism. For instance, the ‘climate refuge’ concept is linked to both resistance and resilience [44]. Microclimates that are buffered from climatic extremes allow individuals to survive, or allow continued recruitment at the local scale, such that such locations have higher resistance to drought. Following the end of drought, the resistant populations provide a source for recolonization of the broader landscape, thereby enhancing resilience. In this way, refugia can operate across spatial scales to enhance both resistance and resilience of biota to a large-scale disturbance.

However, there is not always a strong link between the determinants of resistance and resilience, suggesting that the mechanisms that underpin each can differ. The resistance of forests to wind-throw was related to disturbance intensity (negatively) and to the initial biotic conditions (herb cover and biomass, positively), whereas resilience was influenced by light availability at the forest floor [46]. The resistance of intertidal macroalgal communities to experimental heat-stress was affected largely by prior abundance (i.e., cover) of dominant species, whereas resilience was influenced more strongly by the degree of heating and by species composition [47]. In both cases, resistance was affected by prior reserves (e.g., biomass) while resilience was determined by the availability of resources following the relaxation of the disturbance.

If the factors that influence resistance and resilience differ, then management actions to enhance them must also differ. In such circumstances, conservation management in response to environmental change might entail a complementary strategy aimed at enhancing both resistance and resilience, or a decision to give priority to one over the other. This choice might be dictated by which of the two is of greater importance for longer-term conservation (see ‘Insights into longer-term change’).

### Relationships between resistance and resilience inform post-disturbance condition

Plotting the relationship between resistance and resilience can help to identify the post-disturbance state of an ecological unit (e.g., ‘net gain’ or ‘net loss’ of a measure); and, importantly, whether that state is the result of a loss of resistance, a loss of resilience or both (see Figure I in Box 1).



**Figure 2.** An illustration of how long-term change in an ecological unit, in this example change in species richness in a community, can result from a loss of either resistance or resilience. Gray strips indicate the duration of the disturbance events (e.g., flooding events), respectively, and the solid black line represents species richness over time; (i) a community with resistance and resilience that is equal, such that species richness declines but recovers fully following the release of the disturbance; (ii) a community for which resistance is diminished, such that the community loses more species during disturbance events than it gains between successive disturbances, leading to long-term decline; (iii) a community for which resilience is diminished, leading to less recovery following each disturbance event, and resulting in long-term decline. Note that net change (i.e., total change following the release of the disturbance, as compared with prior) in the community measure is the same regardless of whether resistance or resilience has been diminished (indicated by a dashed gray line). (iv) A community with both diminished resistance and resilience such that each successive disturbance removes a fraction of the community without recovery.

This allows the identification of units (e.g., species, communities) that might require management intervention and the type of intervention required.

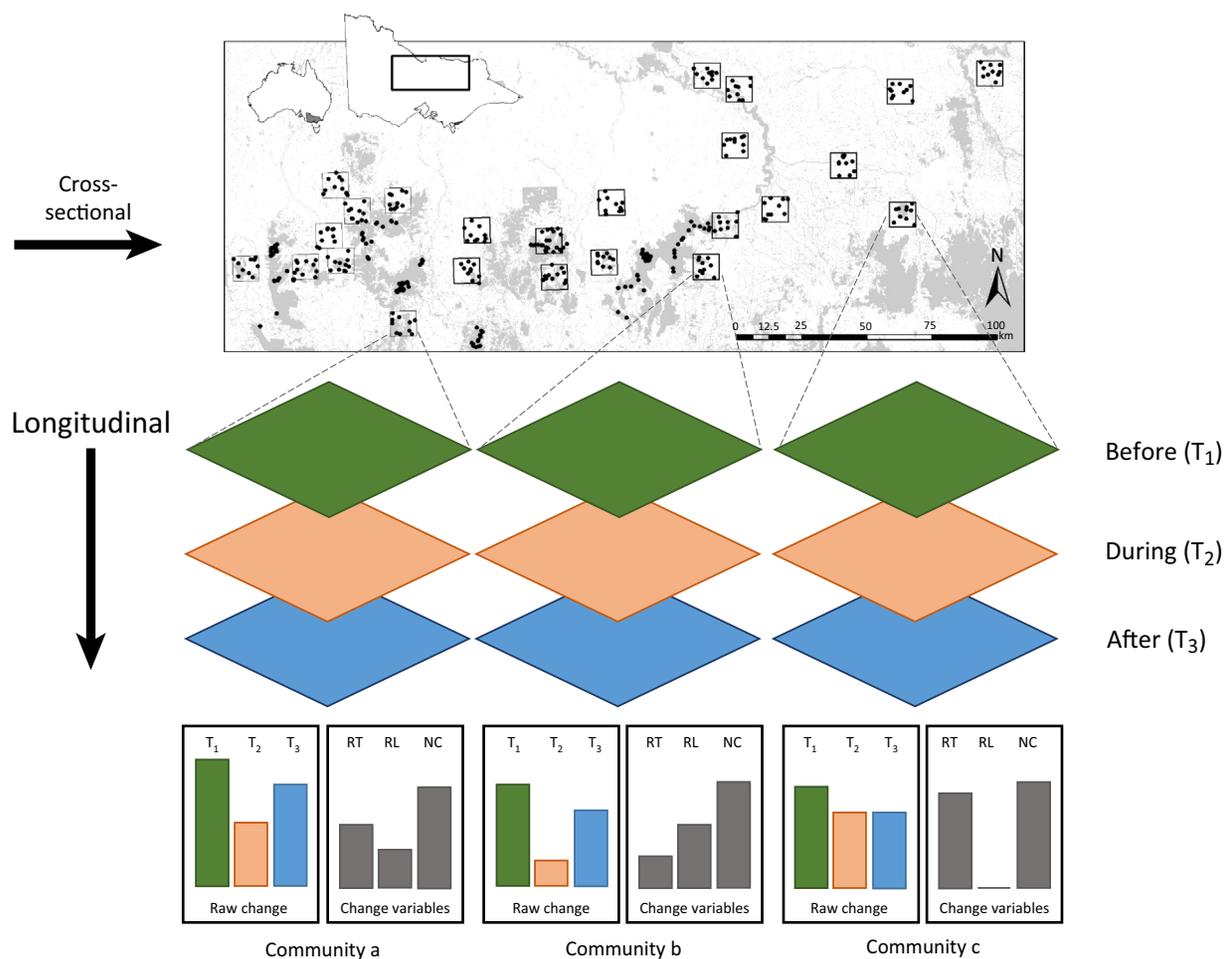
Three types of relationships between resistance and resilience are conceivable in ecological communities, as an example. First, there might be an inverse relationship in which the community with lowest resistance (e.g., loses most species) has the highest resilience (e.g., gains most species) following the end of the disturbance [48]. This relationship implies a return towards initial conditions

(see **Figure I** in **Box 1**). Second, there might be no consistent relationship between measures of resistance and resilience among communities [46]. Such an outcome might occur if there is an inconsistent relationship between mechanisms that govern resistance and resilience, respectively. Third, measures of resistance and resilience might have a positive relationship, which would indicate substantial losses or gains in the community (depending on which side of the line of full recovery the data points lie; see **Figure I** in **Box 1**). If a community has both low resistance and low resilience to

### Box 2. Identifying the determinants of resistance and resilience

The resistance–resilience framework allows one to identify factors that determine the resistance and resilience of an ecological unit, such as a community, to a disturbance. To do so, resistance and resilience must be measured in multiple locations that capture gradients of interest (**Figure I**) [5], by sampling the community before, during, and after the disturbance. Key gradients of interests include (i) variation in legacies from previous disturbances (e.g., from past land clearing or fire events) and (ii) variation in environmental parameters such as rainfall and soil fertility. Many ecosystems are exposed to multiple interacting disturbances, such that the resistance and resilience of the biota to a given

disturbance might be amplified or diminished by existing disturbance processes [45,59]. Resistance and resilience are likely to vary along natural environmental gradients [44]. Some areas can be buffered from disturbance more than their surroundings, thereby providing a more stable environment. Such areas ('refugia' [60]) can enhance the resistance of communities to disturbance by promoting *in situ* persistence, and enhance resilience by providing colonists for surrounding areas after the pressure is released. Characteristics of the disturbance process itself, which can also vary spatially (e.g., disturbance intensity, frequency), are also relevant.



**Figure I.** An example of how longitudinal monitoring data can be used to directly model resistance and resilience in relation to environmental variables. In this example, study landscapes (squares) have been selected to capture a gradient in wooded vegetation cover (light gray). Sampling of a hypothetical community in each landscape occurs before (green bars), during (orange bars), and after (blue bars) the release of a disturbance (e.g., drought), and the proportional change in values (e.g., species richness) is used to calculate resistance (RT), resilience (RS), and net change (NC). In this example, although net change is the same for all three hypothetical communities, they differ by: (i) the pre-disturbance state of the community [initial raw values (e.g., species richness) are higher for a than for b or c]; and (ii) the degree to which net change is attributable to resistance or resilience (e.g., community b has low resistance but high resilience, whereas community c has high resistance but low resilience). Species-specific results from this study have been published elsewhere [34]. RT, RL, and NC are calculated as per **Box 1**.

a particular disturbance, the result is a substantial net loss for the community [49], and might signify that the system is entering an alternative ecological state [50]. This might occur when a common mechanism that led to the initial decline then prevents recovery once the disturbance has been released, or if the decline was sufficiently great to eliminate the reserves necessary for recovery.

#### *Insights into long-term change in biodiversity*

When an ecological unit – for example an ecological community – experiences periodic disturbance (e.g., frequent fires, recurrent hurricanes), it might show a gradual but long-term shift in community structure, such as loss of species [51]. Such change is particularly likely when a community is subject to multiple disturbances that interact at different temporal scales, for example when drought events (multi-year) occur in fragmented landscapes (subject to decades or centuries of disturbance). In such cases, disturbances can interact to reduce the capacity of communities to resist or recover following the relaxation of a given disturbance [51,52].

Treating resistance and resilience as separate components of the response to disturbance helps to ascertain their relative contributions to longer-term change [48]. Communities might have a similar amount of net change when comparing community measures before and after disturbance, but this can be achieved by experiencing different patterns of resistance and resilience (Figure 2). Changes can be due to a loss of resistance, a loss of resilience, or both. If the loss of resistance or resilience is not reversed, then each successive disturbance will remove another fraction of the community, resulting in a pattern of long-term decline. When the mechanisms that determine resistance and resilience differ, it is important to know the extent to which negative net change has resulted from diminished resistance (e.g., reduced

survivorship) or diminished resilience (e.g., incapacity to breed successfully) because this will help in planning actions to arrest decline.

#### *Policy relevance, science communication, and measurement*

In addition to providing new insights into ecological change, the resistance–resilience framework has advantages from a policy and science communication perspective. First, the underpinning concepts align with common usage of these terms (i.e., resistance as ‘holding out’ and resilience as the ability to ‘bounce back’). This means that measures of the resistance and resilience of a population, community, or ecosystem to anthropogenic pressures can be readily communicated to a broad audience of stakeholders, including decision makers, conservation groups, and the general public. Second, the resistance–resilience framework proposes direct measures of resistance and resilience that are simple and interpretable measures of ecological change. Coupled with an understanding of the mechanisms of change, this can assist researchers and conservation managers to assess the effects of disturbances, the value of management interventions, and the success or failure of those interventions and policies. Third, this framework promotes the need to manage before, and not only after, the occurrence of disturbances to improve the ongoing persistence of biota (i.e., pro-active as well as reactive management, rather than the common approach of only addressing the latter). This is particularly relevant for planned disturbance events, such as the use of prescribed fire.

#### *Researching resistance and resilience*

The methods by which we can determine the factors that influence resistance and resilience come from the usual arsenal of the scientific method (e.g., laboratory

### **Box 3. Caveats and limitations of the resistance–resilience framework**

There are some important issues that need to be considered when applying the resistance–resilience framework.

#### *Getting the baseline correct*

The resistance–resilience framework is based on the pre-disturbance state of an ecological unit, and is only relevant where change from that state is of interest. Not all ecological change, even disturbance-induced change, is necessarily undesirable. It is important that the pre-disturbance state of the community is described adequately by the variables for which resistance and resilience will be measured, and that sampling is sufficient to establish a baseline against which change can be assessed.

#### *Resistance and resilience are broad measures*

Resistance and resilience are general measures of disturbance-induced ecological change, and are intended to be calculated for disturbances that differ in scale and type (i.e., pulse, press, and ramp). Resistance and resilience complement but do not replace more mechanistic frameworks for understanding ecological responses to particular disturbance types (e.g., succession in fire ecology, state-and-transition models in response to grazing).

#### *Resistance and resilience of what?*

Researchers and managers must carefully choose the variables for which measures of resistance and resilience are taken [61]. Some variables describing an ecological unit may display high resistance or resilience, while other variables describing the same unit may show

otherwise. Therefore, deciding on the suite of variables necessary to adequately represent ecological change is a crucial step in applying the resistance–resilience framework. There are possible perverse outcomes from applying the resistance–resilience framework if variables are ‘cherry-picked’ to reflect high or low resistance and resilience rather than being variables that fundamentally characterize change in the ecological unit.

#### *Latent resilience*

Resilience, when measured in the field, is affected by the initial change that an ecological unit experiences. Given that resilience is the ‘bounce back’, it is partially determined by how much change was initially experienced (i.e., resistance). Ecological units that are highly resistant may show limited resilience, not because they lack resilience *per se* but because there is little ‘room’ for recovery. Therefore, ecological units that show high resistance and low resilience ought to be viewed differently from those that show low resistance and low resilience.

#### *Resistance and resilience are scale-dependent*

Considerations of scale – both temporal and spatial – must underlie the construction and interpretation of the measurement of resistance and resilience. High resistance in a variable at one scale may not be evident at other scales. The choice of appropriate spatial scales should be informed by the scale of the disturbance process, the likely scales of the ecological responses, and by the scale of conservation management.

experiments [53], field experiments [54], and field survey programs [55]). If we focus on management-relevant units (populations, communities, ecosystems, and landscapes), then the spatial and temporal scale of these units makes natural experiments combined with long-term monitoring and statistical approaches the most feasible, owing to the difficulty in undertaking controlled experiments at such large spatial scales [5].

Identifying the relationships between resistance, resilience, and intrinsic or extrinsic variables can be achieved through a combination of longitudinal and cross-sectional data (Box 2). The magnitude of change in an ecological unit through time (longitudinal data) can be compared among multiple sites that vary spatially in their extrinsic attributes (cross-sectional data), such that attributes that influence the rate of change can be identified [5,54] (Box 2). This approach allows researchers to answer the important question ‘which environmental factors influence resistance and resilience to this particular disturbance?’ Such knowledge offers an opportunity for managers to intervene with on-ground actions to maintain or enhance the resistance and resilience of an ecological unit of concern.

The measurement of resistance and resilience can allow spatially explicit models of resistance and resilience to be built for a particular type of disturbance and mapped across landscapes to highlight areas of high or low resistance and resilience, which would induce different management actions depending on location. Further, quantitative tools (e.g., zonation [56]) can be used to identify areas of high priority for protection or restoration aimed at enhancing resistance or resilience, in conjunction with constraints such as planning for human infrastructure and other development [57]. These approaches depend on variation in resistance and resilience being relatable to spatial data, such as remotely sensed vegetation patterns. Recent work at the community and species levels indicate that this is often the case [44,45,55].

### Concluding remarks

A growing number of policy documents and strategies advocate a need to ‘manage for resilience’ or ‘enhance

resilience’ [7–9], but there is a lack of clarity concerning measures that can be used to determine the success or failure of such objectives. Although the framework we propose has limitations (Box 3), and gaps in our knowledge remain (Box 4), we argue that the resistance–resilience framework can assist managers and researchers to better understand how systems change during disturbance by recognizing the distinct components of change (resistance, resilience) that can be measured in ecological units of direct relevance to management (e.g., populations, communities, ecosystems). Armed with such knowledge, managers will be better placed to develop plans for actions to conserve global biodiversity in the 21st century, even in the face of disturbances that might be beyond their immediate control.

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### Box 4. Outstanding questions

- Which environmental factors enhance the resistance of ecological units to persistent disturbances, including press disturbances such as land clearing, urbanization, and invasion of species, as well as ramping disturbances such as climate change?
- How similar are the factors that determine resistance and resilience, respectively, of ecological communities, and in what ways are they linked?
- Are there commonalities among the determinants and underlying mechanisms of resistance and resilience among different ecosystems?
- What are the intrinsic attributes of individuals, populations, communities, and ecosystems that confer resistance and resilience?
- To what degree are species’ traits that are associated with resistance or resilience similar among ecosystems and for different types of disturbance?
- Are long-term changes in ecological units in the face of disturbances due mainly to a loss of resistance, loss of resilience, or loss of both? Can long-term declines be reduced by focusing on alleviating only one of resistance or resilience?

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