



Perspective

Resilience in ecology: Abstraction, distraction, or where the action is?



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ABSTRACT

Increasingly, the success of management interventions aimed at biodiversity conservation are viewed as being dependent on the 'resilience' of the system. Although the term 'resilience' is increasingly used by policy makers and environmental managers, the concept of 'resilience' remains vague, varied and difficult to quantify. Here we clarify what this concept means from an ecological perspective, and how it can be measured and applied to ecosystem management. We argue that thresholds of disturbance are central to measuring resilience. Thresholds are important because they offer a means to quantify how much disturbance an ecosystem can absorb before switching to another state, and so indicate whether intervention might be necessary to promote the recovery of the pre-disturbance state. We distinguish between helpful resilience, where resilience helps recovery, and unhelpful resilience where it does not, signalling the presence of a threshold and the need for intervention. Data to determine thresholds are not always available and so we consider the potential for indices of functional diversity to act as proxy measures of resilience. We also consider the contributions of connectivity and scale to resilience and how to incorporate these factors into management. We argue that linking thresholds to functional diversity indices may improve our ability to predict the resilience of ecosystems to future, potentially novel, disturbances according to their spatial and temporal scales of influence. Throughout, we provide guidance for the application of the resilience concept to ecosystem management. In doing so, we confirm its usefulness for improving biodiversity conservation in our rapidly changing world.

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1. Introduction

Resilience is a term used in a wide array of contexts, from human health and psychology through sociology to materials science and, of course, ecology and conservation biology. Resilience was introduced to the ecological literature with a lucid definition regarding the persistence of relationships within an ecosystem after disturbance, and is a measure of the ability of ecosystems to absorb changes of state variables, driving variables, and parameters, and still persist (Holling, 1973; Table 1). By this definition, resilience is of great importance for ecosystem management because it helps to predict ‘recovery’ after disturbance (Table 1). Despite this historically clear and straight-forward definition, the concept has, over the years, become increasingly vague, often used as a hook to attract an audience rather than being a truly meaningful concept driving research or informing ecosystem management (Brand and Jax, 2007; Myers-Smith et al., 2012). Yet, in spite of conceptual vagueness, its intuitive appeal is evident in its widespread adoption in policy and management documents (e.g., Benson and Garmestani, 2011). In this context, resilience is seen as an ecosystem property important for maintaining desired ecosystem states (Gunderson et al., 2010; Walker and Salt, 2012). However, more clarity around the concept is needed in order to meaningfully apply it in a management context (Beisner, 2012).

Two of the most highly cited papers in the ecological literature on resilience define the term differently. Holling (1973), as above, describes resilience as the capacity of an ecosystem to tolerate disturbance without switching to a qualitatively different state that is controlled by a different set of processes. Pimm (1984), however, defines it in terms of the time taken to return to the pre-disturbance state. These different forms of resilience are often referred to as ecological and engineering resilience, respectively (Gunderson et al., 2010), although usage is not consistent either

in policy or the ecological literature. For example, ecological literature on coral reef resilience to disturbance defines resilience in terms of recovery time (i.e., engineering resilience; Hoegh-Guldberg et al., 2007), ecological resilience (Hughes et al., 2007) and more recently, defines resilience as a two part process of ‘resistance’ and ‘recovery’ (Côté and Darling, 2010; McClanahan et al., 2012). Here, we refer to Holling’s definition as ‘resilience’ and Pimm’s definition as ‘recovery’, to reduce confusion about these important concepts.

In a management context, the most pressing questions concerning resilience are these—how much disturbance can an ecosystem absorb before switching to another state? Where is the threshold associated with the switch between ecosystem states? And will ecosystems recover from disturbance without intervention? Both resilience and recovery are important for answering these questions. If assessed quantitatively, resilience should help managers decide whether or not intervention will be required to push a system back towards the pre-disturbance state. Equally, assessments of recovery that are context specific (i.e., of a particular ecosystem to a particular disturbance) could be used to predict a time-frame for the return of a pre-disturbance state.

Here, we focus on resilience in the context of managing and predicting return to a pre-disturbance state, or a state that is similar to the pre-disturbance state in terms of species composition and/or function, because these states are often desirable from a management perspective (Ruiz-Jaen and Aide, 2005; Hallett et al., 2013). First, we discuss how to measure resilience to disturbance as defined by Holling (1973). Second, we distinguish between situations in which resilience of an ecosystem can be used to achieve return to a pre-disturbance state (helpful resilience) and situations in which resilience might impede the achievement of this goal (unhelpful resilience). Third, we review the factors likely to contribute to resilience. Finally, we consider the options for manage-

Table 1
Glossary of key concepts.

Concept	Definition
Disturbance	Any process that effects ecosystem, community, or population structure, and/or individuals within a population either directly or indirectly via changes to the biophysical conditions (Hobbs and Huenneke, 1992 and references within). Short-term and longer-term disturbances are often referred to as ‘pulse’ and ‘press’ disturbances respectively (Bender et al., 1984) or ‘acute’ and ‘chronic’ disturbances (Connell, 1997)
Functional diversity	The value and range of functional traits of the organisms present in an ecosystem (Tilman, 2001). Functional traits determine an organism’s response to the environment and/or its effects on ecosystem functioning (Díaz and Cabido, 2001). Examples of individual functional traits that are used to calculate functional diversity include body size, dispersal characteristics, reproductive phenology, seed mass, etc. <i>Units of measurement:</i> response diversity and functional redundancy (refer to text for details)
Helpful resilience	Resilience that helps to maintain a pre-disturbance ecosystem state so that it does not cross a threshold. The trajectory of recovery for ecosystems with helpful resilience mirrors the post-disturbance trajectory (i.e., hysteresis is not evident, the ‘return’ and ‘outward’ trajectories match; Beisner et al., 2003; Suding and Hobbs, 2009)
Recovery	The time taken for an ecosystem to return to its pre-disturbance state after a disturbance (Pimm, 1984). <i>Units of measurement:</i> time
Resilience	The ability of an ecosystem to absorb changes of state variables, driving variables, and parameters, that is, to persist after disturbance (Holling, 1973). Also referred to as ‘ecological resilience’ or ‘Holling’s resilience’ and often confused with ‘resistance’. <i>Units of measurement:</i> intensity of disturbance associated with a switch between states (i.e., the threshold; Connell and Sousa, 1983) coupled with data to document the switch (e.g., ecosystem attributes such as species composition)
Resistance	Degree to which a variable is changed following a disturbance (Pimm, 1984). <i>Units of measurement:</i> measure of one or more ecosystem state variables (e.g., species composition) before and after disturbance. Measuring resistance does not require knowledge of system specific thresholds
Threshold	Point at which a small change environmental conditions, associated with disturbance, leads to a switch between ecosystem states (Suding and Hobbs, 2009)
Unhelpful resilience	Resilience that helps to maintain an ecosystem in a degraded state following a disturbance. Requires management intervention to assist the return of the historic pre-disturbance state due to the presence of a threshold. May be associated with hysteresis

ment and predicting resilience to future (potentially novel) disturbances. Resilience is the focus but recovery is discussed too, in the context of time scales for management.

2. Measuring resilience: the importance of thresholds

Making the concept of resilience operational to management requires finding ways to quantitatively measure it. The approach to measurement that is consistent with Holling's definition involves determining the location of thresholds of disturbance associated with ecosystem change (Suding and Hobbs, 2009; Table 1). Interestingly, the threshold concept is usually allied with resilience in the literature, whichever resilience definition is adopted, reflecting a clear general understanding of the threshold concept and consensus as to its importance for measuring resilience (e.g., Suding and Hobbs, 2009; Côté and Darling, 2010; McClanahan et al., 2011; Walker and Salt, 2012). Locating thresholds requires experimental or observational data on disturbances associated with switches between ecosystem states, and if possible, information on whether the recovery pathway is likely to be the same or different to the pathway that led to the switch. The former situation can signal reversible change whereas the latter may indicate irreversible change (i.e., hysteresis; Suding and Hobbs, 2009). Ultimately, identifying indicators of an impending threshold would allow time for intervention to prevent a switch to an undesirable ecosystem state, though few such indicators exist for the complex ecosystems found in nature (Biggs et al., 2009; Scheffer et al., 2012).

Experimental tests of resilience can involve applying discrete (i.e., in time and space) disturbances of increasing intensity to identify the intensity of disturbance required to switch ecosystems between alternative states (i.e., the threshold; Connell and Sousa, 1983). Such an experimental approach has been used to identify the threshold in abundances of top predators in a freshwater lake associated with a switch from a food web dominated by planktivorous fishes to one dominated by piscivorous fishes (Carpenter et al., 2011). Similarly, broad-scale observational and experimental data were used to locate the threshold in simulated ice-scour disturbance associated with a switch from rock weed stands to mussel beds in intertidal marine ecosystems (Petraitis et al., 2009). More recently, experimental data on juniper mortality coupled with models of fire ecology and fire physics were used to locate the threshold in fire intensity associated with the encroachment of woody juniper into grasslands (Twidwell et al., 2013). Beyond these few examples, experimental tests of thresholds associated with disturbances are rare, particularly for terrestrial ecosystems.

Experimental tests of resilience are rare, at least in part, because of simple logistical reasons. In particular, the requirement for experimentally simulated disturbances to be of a similar spatial extent to natural disturbances precludes experimentally identifying thresholds for many pulse disturbances (e.g., logging, invasion fronts, changes in hydrology, etc.) let alone long-term and large-scale press disturbances such as climate change (Connell and Sousa, 1983; Table 1). Additionally, the need to track recovery time beyond average generation times (Connell and Sousa, 1983) largely inhibits the study of communities of slow-growing, long-lived organisms, such as forests and deep-sea communities. Therefore, experimental data are likely to be skewed towards the measurement of responses of short-lived organisms to small-scale pulse disturbances in microcosms (Standish, Shackelford and Hobbs, unpublished data). Given these practical limitations of manipulative experiments, we need a different approach to measuring the resilience of ecosystems to the global changes that currently threaten their persistence (Sala et al., 2000).

Observational data can be used to identify thresholds by retrospective analysis of disturbances associated with observed switches between ecosystem states. This approach, though correl-

ative in nature, can be used to assess resilience to both press and pulse disturbance. For example, van der Heide et al. (2007) used historical maps of seagrass beds and a long-term data set of water quality to estimate the level of turbidity associated with the switch from a seagrass-dominated state to a bare state that occurred in the Dutch Wadden Sea in the 1930s. In another example, Blarquez and Carcaillet (2010) reconstructed fire histories and vegetation dynamics of subalpine ecosystems using charcoal and plant macro-remains present in 8000-year old lake sediments to estimate the fire frequency associated with a switch between ecosystem states dominated by fire-sensitive and fire-tolerant species. These retrospective analyses helped to identify potential management interventions for seagrass recovery and the likely consequences of projected increases in fire frequency on contemporary subalpine ecosystems. A disadvantage of this approach is that it is retrospective and thus cannot be used to predict resilience to unmeasured or novel disturbances.

Often managers are faced with making decisions in the absence of any experimental data on thresholds of disturbance. In these cases, a potential approach involves assessing ecosystem dynamics after the removal of a disturbance whereby the lack of return of the pre-disturbance state might indicate the presence of a threshold. This approach cannot identify where the threshold lies but it can provide information about which types of intervention are insufficient to switch the ecosystem back to the pre-disturbance state. For example, the persistence of a degraded post-disturbance vegetation state after the removal of livestock has been used to infer the presence of thresholds associated with livestock grazing (Westoby et al., 1989; for other examples refer to the thresholds database published by the Resilience Alliance and Santa Fe Institute (2004)). Recovery assessments can be informative in this context because they can help to judge whether the time that has elapsed since the removal of the disturbance is approaching that of recovery for similar ecosystems and disturbance types, and therefore whether the return of the pre-disturbance state is potentially imminent. Thus, while recovery assessments and/or observations of ecosystem dynamics after the removal of disturbance do not provide definitive evidence for the existence of a threshold (or a quantitative measure of resilience), these assessments can signal the requirement for management interventions to assist the return of the pre-disturbance state.

3. Helpful and unhelpful resilience

Though resilience is used almost uniformly in the management literature to refer the ability of an ecosystem to resist transition to an alternative state or recover without intervention, resilience is, in reality a positive or a negative property of ecosystems depending on their state of degradation (Fig. 1). Indeed, ecosystem states that have been degraded by human activities can have the same, or even greater, levels of resilience to disturbance compared with less degraded ecosystems (e.g., Troell and Pihl, 2005; Côté and Darling, 2010; Gunderson et al., 2010). Here, we introduce the term 'unhelpful resilience' to describe these cases where degraded or altered ecosystems do not return to the historic pre-disturbance state without assistance (Table 1). In contrast, the (unassisted) return of a pre-disturbance state indicates the presence of 'helpful resilience'—as the threshold has not been crossed and thus management intervention is not required (Table 1). Given the current focus on resilience as a beneficial property of ecosystems, it is important to emphasise that resilience is not always desirable from a management perspective. Thus, when identifying approaches to quantifying thresholds of disturbance, it is important to consider whether or not helpful or unhelpful resilience might affect the options for management. Specifically, degraded ecosystems may

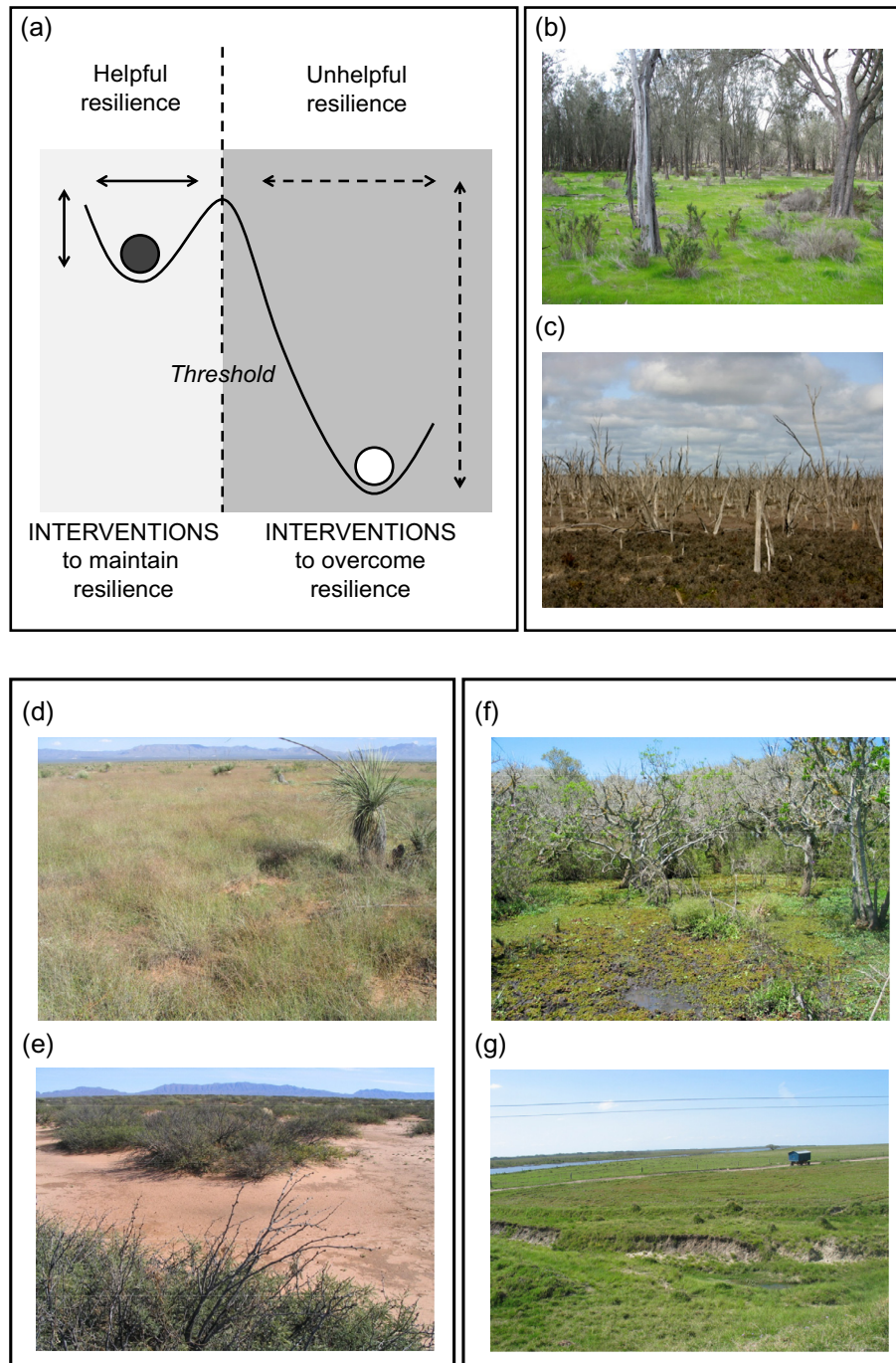


Fig. 1. Theoretical expectations for how disturbance may force a switch between two ecosystem states (depicted as balls) (a). One state is degraded (white-filled ball) and one is not (black-filled ball), which represents the pre-disturbance or desirable state. The resilience of the states to disturbance is proportional to the width and depth of the cups. Lake Toolibin (b) is a wetland in the wheatbelt of Western Australia which is threatened by salinization (Wallace, 2003). Lake Toolibin represents the black-filled ball in panel (a), apparently resilient, but threatened by saline inundation. Lake Taarblen (c) is an adjacent lake affected by salinization in the 1950s, which resulted in the death of all the canopy trees and the development of a low, relatively uniform cover of halophytes. The process of salinization arises in these landscapes from a hydrological imbalance caused by extensive vegetation clearing and subsequent rise of saline water tables (Cramer and Hobbs, 2002). Lake Taarblen represents the white-filled ball in panel (a), unhelpfully resilient. Lake Taarblen has undergone a state change and cannot be returned to its former state without unrealistically extensive and expensive intervention. Conversely, management of Lake Toolibin to maintain its condition, despite ongoing broad-scale drivers pushing it towards the degraded state, includes electric pumps to divert saline water around the lake (local action) and the planting of perennial vegetation to lower groundwater levels (landscape-scale actions; George et al., 2005; Wallace, 2003). Panels (d and e) are desirable and degraded ecosystems states of semiarid grassland in south-western New Mexico (Bestelmeyer et al., 2011, 2013; refer to text for details). Panels (f and g) are the desirable and degraded ecosystem states of restingia flooded forests in Rio Grande do Sul, Brazil. These coastal forests (f) have been heavily degraded by deforestation, livestock grazing and changes in hydrology associated with agricultural production and urbanization. Panel (g) depicts the result of these drivers of change: resilient semi-managed swampy grasslands. Photo credits: M.M. Mayfield (b, f and g); R.J. Hobbs (c); B.T. Bestelmeyer (d and e).

require complex, and often prolonged, intervention to rebuild the ecological interactions that are required for return of the pre-disturbance state and ultimately, the return of helpful resilience (Fig. 2).

There are other reasons why the distinction between helpful and unhelpful resilience could be important for ecosystem management. First, the distinction is a reminder that resilience is a means of, rather than an end to, management. Most often, the goal

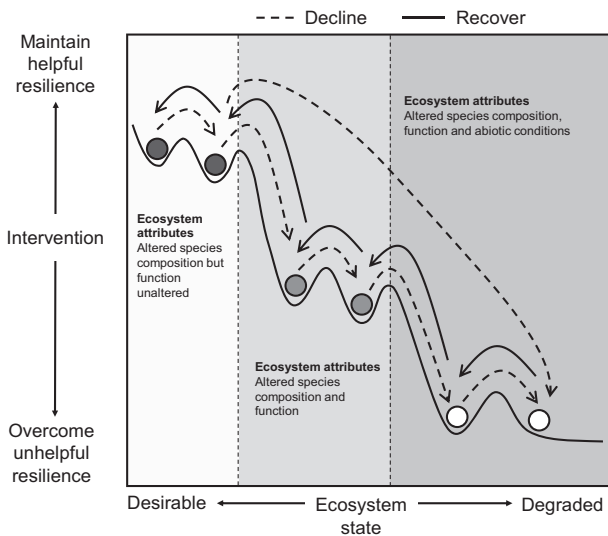


Fig. 2. An expanded version of Fig. 1 illustrating the possible spectrum of ecosystem states, their likely responses to disturbance (i.e., decline or recovery), and the corresponding options for their management. Note that pathways of decline and recovery can differ in the case of hysteresis (Suding and Hobbs, 2009) and this figure presents representative pathways only. Ecosystem attributes can indicate whether the state is desirable (i.e., historic pre-disturbance) or degraded, and experimental or observational data can indicate the presence of thresholds (upright dashed lines).

of management is to maintain a system in a particular state or to return it to that state—not simply to create a resilient ecosystem without reference to this goal (Ruiz-Jaen and Aide, 2005; Hallett et al., 2013). Understanding whether or not resilience is acting in a helpful or unhelpful capacity is likely to assist efforts to achieve management goals based on the return of the pre-disturbance state. This understanding remains relevant even if there is a shift away from strict use of the pre-disturbance state as the reference for management goals (Hobbs et al., 2010). In particular, the goal for disturbance-driven ecosystems may be the maintenance of processes that promote ecosystem recovery after disturbance (DeAngelis and Waterhouse, 1987). Additionally, distinguishing between helpful and unhelpful resilience may aid a more accurate estimation of the financial cost of restoring pre-disturbance ecosystem states, leading to a better understanding of the likely returns on investment or again, perhaps a re-valuation of the pre-disturbance state as the management goal. Lastly, society may be over-emphasizing the loss of (helpful) resilience and ignoring the importance of unhelpful resilience in preventing goals from being reached.

4. Predicting and managing resilience to disturbance

As we discussed earlier, thresholds of disturbance are important for measuring resilience but ultimately, managers need to be able to measure and predict ecosystem resilience to current as well as to future, potentially novel, disturbances. Thresholds are likely to move as ecosystems evolve, particularly in response to ongoing global changes, which makes it difficult to predict the location of thresholds to future disturbances, especially if these disturbances are novel. Therefore, we need additional or proxy measures of resilience to disturbance.

Contributing to the difficulty in measuring and predicting resilience is the complex interplay of ecological, geographical, local environmental and large-scale environmental factors involved in ecosystem responses to disturbance. For instance, population turnover times, connectivity, and the scale and intensity of disturbance are just a few of the factors likely to be important for determining

resilience and specifically, the trajectory and speed of return following disturbance (Connell and Sousa, 1983; van Nes and Scheffer, 2005; Thrush et al., 2008). Though we have a long way to go before we understand all of these complexities, in this section we consider the contribution of functional diversity, connectivity, and scale to resilience. We are primarily interested in predicting and managing helpful resilience, which we simply term resilience as per the common usage.

4.1. Functional diversity

Increasingly, trait-based approaches are recognised for improving our understanding of ecosystem dynamics because they offer a more mechanistic understanding of ecosystems than stand-alone patterns of species diversity (Lavorel and Garnier, 2002; Suding et al., 2008). In particular, trait-based measures of ‘functional diversity’ (Table 1) have recently become central to the discussion of ecosystem resilience to disturbance (e.g., Peterson et al., 1998; Van Ruijven and Berendse, 2010; Laliberté et al., 2010; Mouillot et al., 2013). We discuss the theory and the evidence available to test the contribution of functional diversity to resilience, and specifically, the potential for indices of functional diversity to act as proxy measures of resilience.

Multi-trait indices of functional diversity are likely to be more useful than approaches focused on individual traits for understanding resilience because such indices capture a more comprehensive picture of the complex ecological processes maintaining ecosystem states. When examined individually, traits may only provide information about a single ecosystem function, while combined they provide information about ecological strategies that are representative (or not) of particular ecosystem states. For example, information on whether species fix nitrogen or not, how their seeds are dispersed and how tall they grow, all contribute to ecological understanding of an ecosystem (Weiher et al., 1999). Logically too, these indices should be calculated using combinations of functional traits that are relevant to the disturbance for which resilience is being assessed. The literature on trait selection for the study of thresholds and ecosystem recovery is reasonably well developed for terrestrial plant communities (Lavorel and Garnier, 2002; Funk et al., 2008; Cadotte et al., 2011), but remains largely unexplored for aquatic ecosystems and for animal communities in general (but see D’agata et al., 2014).

Several multi-trait indices of functional diversity have emerged recently (Mouillot et al., 2013). Two of these indices that have particular relevance as contributors to resilience are functional redundancy and response diversity. Functional redundancy is measured as the number of species contributing similarly to an ecosystem function or functional group (Walker, 1992). Response diversity is a measure of how functionally similar species respond differently to disturbance (Elmqvist et al., 2003). Field studies reveal clear evidence for a loss of functional redundancy in degraded systems (Balvanera et al., 2006; Flynn et al., 2009; Laliberté et al., 2010; Graham et al., 2013), which offers some support for the theory that suggests functional redundancy contributes to resilience. Tools for measuring functional redundancy are well developed (Laliberté and Legendre, 2010; Laliberté et al., 2010) making it tractable to measure its contribution to resilience for a range of ecosystems and types of disturbance. Response diversity has not received as much attention as functional redundancy, perhaps in part because it is difficult to measure (Mori et al., 2013). Modelling time-series data of species abundances offers one approach to estimating response diversity (Ives et al., 2003) and has been used to estimate response diversity of herbivorous coral-reef fishes to (unmeasured) environmental fluctuations (Thibaut et al., 2012). Multivariate analyses offer another approach to estimating response diversity. Laliberté et al. (2010) used a multivariate

analysis of a global dataset of plant communities to first define functional groups on the basis of effect traits, and then estimate response diversity to increasing land-use intensity as the multivariate within-group dispersion in response trait space. Using these approaches to measure ecosystem states before and after disturbance will improve our mechanistic understanding of the link between functional diversity and resilience.

4.2. Connectivity

Connectivity is the movement of matter and species in landscapes and is widely recognised for its contribution to resilience (Nystrom and Folke, 2001; Lundberg and Moberg, 2003; Heller and Zavaleta, 2009). Broadly, connectivity is a function of the amount, quality and spatial arrangement of habitat patches, and the factors that influence the movement of species (and matter) across landscapes (Hodgson et al., 2009). In modern, human-modified landscapes, connectivity is a particularly important consideration for managing resilience to disturbance, and may contribute most to resilience when patches are heterogeneous and therefore respond differently to a disturbance (e.g., Adam et al., 2011). Generally, increasing the scale of landscape degradation increases the probability that individual patches embedded in the landscape matrix will remain in a degraded state, through reduced abiotic and biotic connectivity among patches. For example, a recent review of rangeland management in the United States and elsewhere highlighted a preference among mammals and birds for rangeland matrices with habitat heterogeneity, which means they are unlikely to move through degraded, homogenous rangelands (Fuhendorf et al., 2012). In another example, mountain-ash eucalypt forests in eastern Australia tended not to recover from large-scale fire disturbance in landscapes where logging had reduced the cover of old-growth forest compared with its historical cover (Lindenmayer et al., 2010). Similarly, the loss of connectivity to source populations has been shown to contribute to the limited return of native vegetation to old-fields around the world (Cramer et al., 2008).

Conversely, landscapes that are less modified by human activity are more likely to retain landscape heterogeneity and connectivity among patches, which is likely to positively impact the resilience of ecosystems to disturbance within such landscapes. For instance, woodland ecosystems are more likely to recover after patch-level disturbances such as mining compared with their recovery from large-scale disturbances such as agriculture (McIntyre and Hobbs, 1999). In another example, the resilience of coral reefs in marine reserves in eastern Australia was attributed to connectivity to both mangroves that act as nurseries and foraging habitat for the herbivorous reef fish that prevent the switch to an algae-dominated state and to coral reefs where fishing was excluded (Olds et al., 2012). In this and other examples, it is not connectivity per se that helps determine resilience but connectivity among patches which are heterogeneous with respect to the prevailing management regime or their responses to disturbance events (Adam et al., 2011). More broadly, maintaining or increasing connectivity and the availability of alternative environments (i.e., landscape heterogeneity) are often suggested as a means to maintain the resilience of native ecosystems to climate change (Heller and Zavaleta, 2009; McClanahan et al., 2012; Prober et al., 2012).

The movement of matter, rather than species, can influence the resilience of ecosystems to disturbance too. Like species, the movement of matter can be influenced by patch and landscape features. For example, in a study of cloud formation, the authors found fewer clouds tended to form over a modified agricultural landscape compared with the adjacent landscape of intact native vegetation, and attributed this result to the darker colour and increased roughness of the native vegetation promoting the convective mixing nec-

essary for cloud formation (Lyons, 2002). The consequent reduction in rainfall is likely to influence the ability of native vegetation in the modified landscape to recover from disturbances such as fire and grazing (Prober and Smith, 2009). The movement of water in rivers can similarly affect the resilience of river ecosystems to disturbances such as floods and drought. Specifically, lateral water flow, and extensive hydrologic connectivity between the river and its floodplain groundwater system, creates the conditions necessary for the development of refugia that are important for the recovery of river ecosystems to disturbance (Sedell et al., 1990). Dams that isolate a river from its watershed or the removal of riparian vegetation can reduce the availability of refugia, and consequently a first-step for management is to focus on the protection or creation of refugia, for example by re-instigating low rates of water flow (Sedell et al., 1990; Lake, 2003). Taken together, understanding the importance of biotic and abiotic connectivity to resilience will help to inform management interventions.

4.3. Scale

As discussed above the temporal and spatial components of disturbance are important for determining resilience. In both cases, the scale of the disturbance across space and time is central to these relationships. There are other ways, however, in which scale might also contribute to resilience. For example, response diversity is predicted to increase when a given function is fulfilled by species operating at different scales because species' perception of, and responses to, their environment are scale dependent (Elmqvist et al., 2003). In theory, response diversity can be estimated by the mean number of scales at which functional groups are represented (averaged across all functional groups; Allen et al., 2005). Fischer et al. (2007) used this measure to estimate response diversity of forest and woodland bird communities in fragmented agricultural landscapes and concluded that their 'relative ecological resilience' was reduced due to the selective extinction of particular body mass and functional groups. Thus, integrating scaling and trait-based approaches might offer a means to predict resilience (Allen et al., 2005; Kerckhoff and Enquist, 2007; Nash et al., 2014).

Ultimately, an approach that combines spatial and temporal scaling with trait indices and measures of connectivity, may offer the best way forward for predicting resilience. For example, an ecosystem with high functional redundancy and extensive connectivity across scales will be much more likely to be resilient to moderate habitat degradation and fragmentation compared to an adjacent ecosystem with low functional redundancy and limited connectivity across scales. Though this example is a simplistic extreme, it illustrates that if used consistently, these combined data would vastly improve our ability to predict resilience and so inform management. Where possible, linking these data to known thresholds is likely to provide the most information about resilience (Table 2).

The contribution of scale to resilience has important implications for management. While it is often possible to maintain or restore a pre-disturbance state via local-scale interventions, managing resilience becomes increasingly more difficult as the scale of interventions required increases (Fig. 2). For example, local-scale intervention to reduce heavy grazing, particularly during drought conditions, can help prevent a shift from a grassland state to a shrubland state in Chihuahuan semiarid grasslands (Bestelmeyer et al., 2011). Additionally, reducing pollution and overfishing at a local scale were suggested to be important factors contributing to coral reef resilience following the recovery of an isolated reef from a bleaching event (Gilmour et al., 2013). Sea level rises that trigger switches from floodplain forests to marsh communities in the coastal wetlands of the Gulf of Mexico (Shirley and Battaglia, 2006), however, are too large to manage with local or even regional interventions. This does not, however, mean these systems are

Table 2

A synthetic overview of the application of the resilience concept to management. Suggestions for research are listed, along with management options, both of which depend on the scale of disturbance and the availability of data to locate the threshold. Linking known thresholds to proxies measures of resilience (i.e., indices of functional diversity), and incorporating measures of connectivity and scale, will improve our ability to predict resilience to future disturbances of the same type and may be of use for predicting resilience to novel disturbances of similar spatial and temporal scales.

Disturbances of increasing scale	Threshold	Research	Management
Short-term small-scale e.g., fire	known	Study contribution of connectivity, functional diversity and scale	Local intervention e.g., manage fire frequency, increase functional diversity
	unknown	Manipulative experiments to identify threshold	
Short-term large-scale e.g., hurricane	known	Study contribution of connectivity, functional diversity and scale	Regional intervention e.g., targeted species conservation, increase connectivity
	unknown		
Long-term small-scale e.g., grazing	known	Study contribution of connectivity, functional diversity and scale	Local intervention e.g., manage grazing intensity
	unknown	Observational experiments to identify threshold	
Long-term large scale e.g., climate change	known	Study contribution of connectivity, functional diversity and scale	Regional intervention e.g., assisted migration, re-assess goals
	unknown		

beyond help. In cases of large-scale pulse and press disturbances (like climate change) there is the potential to use novel approaches to management that overcome issues of scale. For example, assisted migration is a controversial management response to climate change (Hewitt et al., 2011) that is only just beginning to be explored. More research is needed to appreciate whether or not the novel ecosystem that results from assisted migration is desirable both in the context of managing for resilience and more generally, given the risk of an adverse outcome for the recipient ecosystem.

5. Conclusion

The idea that ecosystems can return to a pre-disturbance state after human-mediated disturbances, either with or without our help, is a compelling one. Central to directing this process is the concept of resilience. The resilience concept offers a means for helping us to understand how ecosystems respond to disturbance and therefore its intuitive appeal is well deserved. The primary task ahead for ecologists is to improve our understanding of how the concept can be applied to ecosystem management. We offer these key insights for achieving this goal:

1. Thresholds are central to the measurement of resilience. Direct experimental data on thresholds are too difficult to obtain in most cases but observational data from ecosystems in different states of degradation can be used effectively to direct management decisions and priorities. In particular, these data may help predict the response of ecosystems to future disturbance events of a similar nature.
2. Distinguishing between helpful and unhelpful resilience can clarify how the concept can contribute to management, and specifically, whether or not management intervention is required for the return of the pre-disturbance state.

3. Functional redundancy and response diversity show promise as proxy measures of resilience. Critically, these properties are amenable to management should further research confirm this idea. For example, there is the potential to maximize both functional redundancy and response diversity in rangelands by maintaining assemblages of both rare and common species, which contribute similarly to ecosystem productivity and have a diversity of responses to grazing disturbance (Walker et al., 1999).
4. Available evidence suggests connectivity and scale contribute to resilience. Management should aim to improve connectivity so that species can recolonize after disturbance, thus giving ecosystems greater potential to recover from future disturbances. Addressing scale in combination with functional diversity might offer an effective approach to management, for example, by restoring the size distribution of fauna in ecosystems to increase resilience to future disturbances.
5. Approaches to management vary depending on the scale of disturbance and the availability of data to determine the location of thresholds. Ultimately, linking known thresholds to measures of functional diversity, connectivity and scale will improve our ability to predict and to manage resilience (Table 2).

Although we have focused primarily on ecosystems here, we recognise the importance of the broader social-ecological systems approach to resilience as well. However, embedded in this broader scheme must be a clear understanding of what resilience means in an ecological context. Moving from abstraction to action requires the measurement of resilience to match its definition. Only then will we have a clear understanding of the intervention required to manage ecosystems as they respond to the variety of disturbances that characterise our rapidly changing world.

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References

- Adam, T.C., Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Edmunds, P.J., Carpenter, R.C., Bernardi, G., 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS One* 6 (8), e23717.
- Allen, C.R., Gunderson, L., Johnson, A.R., 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8, 958–966.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Beisner, B.E., 2012. The shifting states of resilience: easier to define than to measure. *Ideas Ecol. Evol.* 5, 57–62.
- Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Front. Ecol. Environ.* 1, 376–382.
- Bender, E.A., Case, T.J., Gilpin, M.E., 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65, 1–13.
- Benson, M.H., Garmestani, A.S., 2011. Can we manage for resilience? The integration of resilience thinking into natural resource management in the United States. *Environ. Manage.* 48, 392–399.
- Bestelmeyer, B.T., Goolsby, D.P., Archer, S.R., 2011. Spatial patterns in state-and-transition models: a missing link to land management? *J. Appl. Ecol.* 48, 746–757.
- Bestelmeyer, B.T., Duniway, M.C., James, D.K., Burkett, L.M., Havstad, K.M., 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. *Ecol. Lett.* 16, 339–345.
- Biggs, R., Carpenter, S.R., Brock, W.A., 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proc. Natl. Acad. Sci. USA* 106, 826–831.
- Blarquez, O., Carcaillet, C., 2010. Fire, fuel composition and resilience threshold in subalpine ecosystems. *PLoS One* 5 (8), e12480.
- Brand, F.S., Jax, K., 2007. Focusing meaning(s) of resilience: resilience as a descriptive concept and a boundary object. *Ecol. Soc.* 12, 23. <<http://www.ecologyandsociety.org/vol12/iss1/art23/>>.
- Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087.
- Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., Coloso, J., Hodgson, J.R., Kitchell, J.F., Seekell, D.A., Smith, L., Weidel, B., 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332, 1079–1082.
- Connell, J.H., 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* 16, S101–S113.
- Connell, J.H., Sousa, W.P., 1983. On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121, 789–824.
- Côté, I.M., Darling, E.S., 2010. Rethinking ecosystem resilience in the face of climate change. *PLoS Biol.* 8, e1000438.
- Cramer, V.A., Hobbs, R.J., 2002. Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: impacts and possible management responses. *Aust. Ecol.* 27, 546–564.
- Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends Ecol. Evol.* 23, 104–112.
- D'agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., David R. Bellwood, D.R., Cinner, J.E., Cowman, P.F., Kronen, M., Pinca, S., Vigliola, L., 2014. Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Curr. Biol.* 24, 555–560.
- DeAngelis, D.L., Waterhouse, J.C., 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* 57, 1–21.
- Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* 1, 488–494.
- Fischer, J., Lindenmayer, D.B., Blomberg, S.P., Montague-Drake, R., Felton, A., Stein, J.A., 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10, 964–974.
- Flynn, D.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Trautman Richers, B., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* 12, 22–33.
- Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., Limb, R.F., Bidwell, T.G., 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecol. Manage.* 65, 579–589.
- Funk, J.L., Cleland, E.E., Suding, K.N., Zavaleta, E.S., 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol. Evol.* 23, 695–703.
- George, R., Dongramaci, S., Wyland, J., Lacey, P., 2005. Protecting stranded biodiversity using groundwater pumps and surface water engineering at Lake Toolibin, Western Australia. *Aust. J. Water Resour.* 9, 119–128.
- Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H., Pratchett, M.S., 2013. Recovery of an isolated coral reef system following severe disturbance. *Science* 340, 69–71.
- Graham, N.A.J., Bellwood, D.R., Cinner, J.E., Hughes, T.P., Norström, A.V., Nyström, M., 2013. Managing resilience to reverse phase shifts in coral reefs. *Front. Ecol. Environ.* <http://dx.doi.org/10.1890/120305>.
- Gunderson, L.H., Allen, C.R., Holling, C.S. (Eds.), 2010. *Foundations of Ecological Resilience*. Island Press.
- Hallett, L.M., Diver, S., Eitzel, M., Olson, J., Ramage, B.S., Sardinas, H., Statman-Weil, Z., Suding, K.N., 2013. Do we practice what we preach? Goal setting for ecological restoration. *Restor. Ecol.* 21, 312–319.
- Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.* 142, 14–32.
- Hewitt, N., Klenk, N., Smith, A.L., Bazely, D.R., Yan, N., Wood, S., MacLellan, J.L., Lipsig-Mumme, C., Henriques, I., 2011. Taking stock of the assisted migration debate. *Biol. Conserv.* 144, 2560–2572.
- Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* 6, 324–333.
- Hobbs, R.J., Cole, D.N., Yung, L., Zavaleta, E.S., Aplet, G.H., Chapin, F.S., Landres, P.B., Parsons, D.J., Stephenson, N.L., White, P.S., Graber, D.M., Higgs, E.S., Millar, C.I., Randall, J.M., Tonnessen, K.A., Woodley, S., 2010. Guiding concepts for park and wilderness stewardship in an era of global environmental change. *Front. Ecol. Environ.* 8, 483–490.
- Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. *J. Appl. Ecol.* 46, 964–969.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N.C., Eakin, M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., Hatziaelos, M.E., 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschanivskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360–365.
- Ives, A.R., Dennis, B., Cottingham, K.L., Carpenter, S.R., 2003. Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.* 73, 301–330.
- Kerkhoff, A.J., Enquist, B.J., 2007. The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *Bioscience* 57, 489–499.
- Lake, P.S., 2003. Ecological effects of perturbation by drought in flowing waters. *Freshwater Biol.* 48, 1161–1172.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305.
- Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Sánchez Merlos, D., Vesik, P.A., Mayfield, M.M., 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.* 13, 76–86.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
- Lindenmayer, D.B., Hobbs, R.J., Likens, G.E., Krebs, C.J., Banks, S.C., 2010. Newly discovered landscape traps produce regime shifts in wet forests. *Proc. Natl. Acad. Sci. USA* 108, 15887–15891.
- Lundberg, J., Moberg, F., 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6, 87–98.
- Lyons, T.J., 2002. Clouds prefer native vegetation. *Meteorol. Atmos. Phys.* 80, 131–140.
- McClanahan, T.R., Graham, N.A.J., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H., Wilson, S.K., 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proc. Natl. Acad. Sci. USA* 108, 17230–17233.
- McClanahan, T.R., Donner, S.D., Maynard, J.A., MacNeil, M.A., Graham, N.A.J., Maina, J., Baker, A.C., Alemu, J.B., Beger, M., Campbell, S.J., Darling, E.S., Eakin, M., Heron, S.F., Jupiter, S.D., Lundquist, C.J., McLeod, E., Mumby, P.J., Paddock, M.J., Selig, E.R., van Woestik, R., 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS One* 7 (8), e42884.
- McIntyre, S., Hobbs, R.J., 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conserv. Biol.* 13, 1282–1292.
- Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. *Biol. Rev.* 88, 349–364.
- Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbance. *Trends Ecol. Evol.* 28, 167–177.
- Myers-Smith, I.H., Trefry, S.A., Swarbrick, V.J., 2012. Resilience: easy to use but hard to define. *Ideas Ecol. Evol.* 5, 44–53.

- Nash, K.L., Allen, C.R., Angeler, D.G., Barichievy, C., Eason, T., Garmestani, A.S., Graham, N.A.J., Granholm, D., Knutson, M., Nelson, J., Nyström, M., Stow, C.A., Sundstrom, S.M., 2014. Discontinuities, cross-scale patterns, and the organization of ecosystems. *Ecology* 95, 654–667.
- Nyström, M., Folke, C., 2001. Spatial resilience of coral reefs. *Ecosystems* 4, 406–417.
- Olds, A.D., Pitt, K.A., Maxwell, P.S., Connolly, R.M., 2012. Synergistic effects of reserves and connectivity on ecological resilience. *J. Appl. Ecol.* 49, 1195–1203.
- Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1, 6–18.
- Petraitis, P.S., Methratta, E.T., Rhile, E.C., Vidargas, N.A., Dudgeon, S.R., 2009. Experimental confirmation of multiple community states in a marine ecosystem. *Oecologia* 161, 139–148.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. *Nature* 307, 321–326.
- Prober, S.M., Smith, F.P., 2009. Enhancing biodiversity persistence in intensively used agricultural landscapes: a synthesis of 30 years of research in the Western Australian wheatbelt. *Agric. Ecosyst. Environ.* 132, 173–191.
- Prober, S.M., Thiele, K.R., Rundel, P.W., Byrne, M., Christidis, L., Gosper, C.R., O'Connor, M.H., Grierson, P.F., Macfarlane, C., Scott, J.K., Standish, R.J., Stock, W.D., van Etten, E.J.B., Wardell-Johnson, G.W., Watson, A., 2012. Facilitating adaptation of biodiversity to climate change: a conceptual framework applied to the world's largest Mediterranean-climate woodland. *Clim. Change* 110, 227–248.
- Resilience Alliance and Santa Fe Institute, 2004. Thresholds and alternate states in ecological and social-ecological systems. *Resilience Alliance*. <<http://www.resalliance.org/index.php?id=183>>, (accessed 24.06.13).
- Ruiz-Jaen, M.C., Aide, T.M., 2005. Restoration success: how is it being measured? *Restor. Ecol.* 13, 569–577.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., LeRoy Poff, N., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W.A., Dakos, V., van de Koppel, J., van de Leemput, I.A., Levin, S.A., van Nes, E.H., Pascual, M., Vandermeer, J., 2012. Anticipating critical transitions. *Science* 338, 344–348.
- Sedell, J.R., Reeves, G.H., Haver, F.R., Stanford, J.A., Hawkins, C.P., 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environ. Manage.* 14, 711–724.
- Shirley, L.J., Battaglia, L.L., 2006. Assessing vegetation change in coastal marsh-forest transitions along the northern Gulf of Mexico using National Wetlands Inventory data. *Wetlands* 26, 1057–1070.
- Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. *Trends Ecol. Evol.* 24, 271–279.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.* 14, 1125–1140.
- Thibaut, L.M., Connolly, S.R., Sweatman, H.P.A., 2012. Diversity and stability of herbivorous fishes on coral reefs. *Ecology* 93, 891–901.
- Thrush, S.F., Halliday, J., Hewitt, J.E., Lohrer, A.M., 2008. The effects of habitat loss, fragmentation, and community homogenization on resilience in estuaries. *Ecol. Appl.* 18, 12–21.
- Tilman, D., 2001. Functional diversity. In: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*, vol. 3. Academic Press, pp. 109–120.
- Troell, M., Pihl, L., Ronnback, P., Wennhage, H., Soderqvist, T.S., Kautsky, N., 2005. Regime shifts and ecosystem services in Swedish coastal soft bottom habitats: when resilience is undesirable. *Ecol. Soc.* 10, 30. <<http://www.ecologyandsociety.org/vol10/iss1/art30/>>.
- Twidwell, D., Fuhlendorf, S.D., Taylor, C.A., Rogers, W.E., 2013. Refining thresholds in coupled fire-vegetation models to improve management of encroaching woody plants in grasslands. *J. Appl. Ecol.* 50, 603–613.
- van der Heide, T., van Nes, E., Geerling, G., Smolders, A., Bouma, T., van Katwijk, M., 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. *Ecosystems* 10, 1311–1322.
- van Nes, E.H., Scheffer, M., 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* 86, 1797–1807.
- Van Ruijven, J., Berendse, F., 2010. Diversity enhances community recovery, but not resistance, after drought. *J. Ecol.* 98, 81–86.
- Walker, B.H., 1992. Biodiversity and ecological redundancy. *Conserv. Biol.* 6, 18–23.
- Walker, B.H., Salt, D.A., 2012. *Resilience Practice: Building Capacity to Absorb Disturbance and Maintain Function*. Island Press.
- Walker, B.H., Kinzig, A., Langridge, J., 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113.
- Wallace, K.J., 2003. Lake Toolibin: working together. *Pac. Conserv. Biol.* 9, 51–57.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., Eriksson, O., 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *J. Veg. Sci.* 10, 609–620.
- Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. *J. Range Manage.* 42, 266–274.