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REVIEW: QUANTIFYING RESILIENCE

Quantifying spatial resilience

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Summary

1. Anthropogenic stressors affect the ecosystems upon which humanity relies. In some cases when resilience is exceeded, relatively small linear changes in stressors can cause relatively abrupt and nonlinear changes in ecosystems.

2. Ecological regime shifts occur when resilience is exceeded and ecosystems enter a new local equilibrium that differs in its structure and function from the previous state. Ecological resilience, the amount of disturbance that a system can withstand before it shifts into an alternative stability domain, is an important framework for understanding and managing ecological systems subject to collapse and reorganization.

3. Recently, interest in the influence of spatial characteristics of landscapes on resilience has increased. Understanding how spatial structure and variation in relevant variables in landscapes affects resilience to disturbance will assist with resilience quantification, and with local and regional management.

4. *Synthesis and applications.* We review the history and current status of spatial resilience in the research literature, expand upon existing literature to develop a more operational definition of spatial resilience, introduce additional elements of a spatial analytical approach to understanding resilience, present a framework for resilience operationalization and provide an overview of critical knowledge and technology gaps that should be addressed for the advancement of spatial resilience theory and its applications to management and conservation.

Key-words: alternative states, cross-scale ecology, landscape ecology, regime shift, resilience, spatial ecology, spatial regime

Introduction

Basic changes in the structure–process relationships in ecosystems are termed ecological regime shifts and occur when an ecosystem enters a new local equilibrium, or stable state, that differs in its structure and function from the previous state. Ecological resilience, the amount of disturbance a system can withstand before shifting into an alternative stability domain (Holling 1973), is an impor-

tant framework for understanding and managing ecological systems subject to regime changes (Gunderson, Allen & Holling 2010). When the resilience of an ecological system is exceeded, a regime shift occurs.

In social–ecological systems, people are often the primary drivers of ecological regime shifts. Anthropogenic stressors, including biological invasions, habitat loss and degradation, the emergence of novel diseases and climate change, affect ecosystems upon which humanity relies. In some cases, relatively small linear changes in these stressors cause relatively abrupt and large nonlinear changes in ecosystems (Scheffer *et al.* 2001). Transitions to novel, anthropogenically driven regimes, such as the conversion

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of rain forest to pasture, are typically characterized by reduced biodiversity and ecosystem services (Folke *et al.* 2002). The speed and nature of anthropogenically induced regime shifts are especially concerning in the light of the global scale at which their underlying driving forces now operate (Steffen *et al.* 2015).

Environmental change affects ecosystems and the landscapes in which they are embedded. Spatial heterogeneity in the location, manifestation of, and responses to environmental change makes spatially explicit approaches to management and conservation necessary. Spatial resilience, a crucial component of resilience theory, is at the forefront of attempts to operationalize and quantify resilience concepts in landscapes. Landscapes exhibit spatially and temporally complex dynamics, and attempts to understand pattern–process relationships in landscapes have led to rapid advances in ecological theory and application. The concept of spatial resilience represents the most recent conceptual advance that seeks to explain the resilience and transformability of heterogeneous and dynamic systems. Other recent developments include identifying leading indicators of critical spatial thresholds (Kéfi *et al.* 2014), assessing structural and functional spatial components of managed systems in relation to their resilience (Allen *et al.* 2014; Angeler *et al.* 2016), determining the role of connectivity, dispersal and other movements in conferring resilience (Underwood *et al.* 2009), assessing the relevance of network membership for node resilience and the relevance of node participation for network resilience (Keitt, Urban & Milne 1997; Moore, Grewar & Cumming 2016), evaluating the relationship of spatial landscape metrics to resilience (Cumming 2011b; Uden *et al.* 2014), and developing approaches for understanding cross-scale interactions in social–ecological systems (Cumming *et al.* 2015). Despite recent progress, ambiguity in definitions, information gaps and an overall lack of quantification and operationalization remain. In this manuscript, we: (i) review the history and current status of spatial resilience in the research literature, (ii) expand upon existing literature to develop a more operational definition of spatial resilience, (iii) provide an approach to quantifying spatial resilience that introduces a spatial analytical method for understanding resilience, (iv) provide a roadmap for the application of spatial resilience to ecosystem management and (v) discuss current gaps and opportunities related to the spatial resilience concept and its operationalization.

Terminology review and synthesis

Spatial resilience is a subset of resilience theory that has been defined in several ways. In studies of coral reef and rain forest disturbance, Nyström, Folke & Moberg (2000), Nyström & Folke (2001) and Elmqvist *et al.* (2001) introduced the term spatial resilience to refer to the importance of ecological legacies (i.e. species or habitat characteristics that persist after disturbance and provide ‘ecological

memory’ during reorganization) and connectivity among neighbouring systems for withstanding disturbances and avoiding regime shifts at broader spatial extents than individual focal systems. Ecological memory is expected to increase with geographical extent and to some degree with landscape heterogeneity and diversity (Berkes & Folke 2002), suggesting that fostering or actively conserving particular landscape features and structures may provide a means to enhance the ability of focal systems (e.g. protected areas) to absorb landscape disturbances such as climate change. In this context, spatial resilience is simply defined as ecological resilience at broader spatial scales (i.e. beyond local habitats) (Obura 2005), or more accurately, the ways in which broader-scale resilience affects local resilience and vice versa.

Nyström & Folke’s (2001) emphasis on resilience at spatial scales greater than the focal system has dominated subsequent spatial resilience references in research literature. For example, Bengtsson *et al.* (2003) focused on the importance of static and dynamic ecological reserves for developing spatial resilience against large-scale, long-term disturbances, and Folke (2006) emphasized the utility of spatial resilience for considering the influence of interactions among temporal scales, spatial scales and spatial heterogeneity on multi-stable behaviour (i.e. multiple basins of attraction) in ecosystems. Additional examples of the extension of Nyström & Folke’s (2001) definition are provided by Peterson (2002), Lundberg & Moberg (2003), Nyström *et al.* (2008), Welsh & Bellwood (2012a) and Cumming *et al.* (2013). Numerous other studies do not explicitly employ the term spatial resilience, but are still founded in Nyström & Folke’s (2001) definition of large-scale ecological memory and among-system connectivity as critical aspects of post-disturbance recovery and reorganization (e.g. van Nes & Scheffer 2005; and Gilmore *et al.* 2013).

Spatial resilience can also be more explicitly considered as the spatial arrangement of, differences in, and interactions among internal and external elements of a system (Cumming 2011a,b). System elements that are internal are those that are related to one another and/or interact with each other either structurally or functionally (or both) at the level of analysis defined by the investigator. Because interaction strengths often decay with distance in space and time, rather than being all-or-nothing, analyses may select a cut-off distance or time period over which to define study system boundaries. Thus, ‘internal’ may be defined in social, economic or ecological terms, by a geographical boundary (e.g. watershed or provincial boundary), by participation in a spatially segregated supply chain (e.g. timber is harvested in one location, cut in another, sold in another and bought in yet another) or by shared elements, such as the movements of individuals between habitat patches within a metapopulation at time-scales relevant to a single generation (Table 1). Peterson (2002) and Cumming *et al.* (2013) similarly consider resilience and spatial resilience in landscape contexts, and

Table 1. Internal and external components of spatial resilience (Cumming 2011b)

Internal elements	External elements
Internal arrangement of components	Context (area influencing system)
System morphology	System footprint (area influenced by system)
Number and nature of boundaries	Connectivity
Spatial variation in phase	Dispersal of organisms
Properties of location	Spatial feedbacks
	Spatial subsidies

Cumming (2011a,b) focus on the importance of asymmetries and gradients for resilience, and particularly on the relevance of gradients as drivers of social–ecological processes. Olds *et al.* (2012) view spatial resilience as an integration of resilience theory into the framework of landscape ecology, where resilience is made more tractable by utilizing location, context, connectivity and other landscape ecology concepts and metrics. Spatial resilience can therefore be more explicitly considered as an emergent property of the spatial arrangement, differences and interactions among internal elements of resilience (i.e. those within the focal system), external elements of resilience (i.e. those outside the focal system) and other spatially relevant aspects of resilience (e.g. adaptations to environmental change) (Cumming 2011a,b). External elements focus on how landscape metrics beyond the focal scale of analysis affect resilience (e.g. species migration and dispersal between habitat patches; hydrological connectivity between lakes), including spatial subsidies (e.g. sandstorms fertilizing low productivity soils elsewhere). Both internal and external components interact to affect the spatial feedbacks that either maintain a level of local stability within a landscape or push it into a different state.

Expanding and operationalizing spatial resilience

Based on current empirical and theoretical knowledge, a tractable ‘shorthand’ definition of spatial resilience is as follows: the contribution of spatial attributes to the feedbacks that generate resilience in ecosystems and other complex systems, and vice versa. This definition allows for the operationalization of spatial resilience in management, is consistent with the foundational aspects of resilience described by Nyström & Folke (2001) and Cumming (2011b) and builds upon the three spatially relevant aspects of complexity (i.e. asymmetries, networks and information processing) discussed by Norberg & Cumming (2008).

APPLICATIONS FROM COMPLEXITY THEORY

To operationalize and quantify spatial resilience, consideration of asymmetries, connectivity and information

processing is warranted (Cumming 2011b). Within complex systems, asymmetries are systematic heterogeneities, such as soil or climate conditions, that can create gradients in environmental and biotic variables and drive spatial feedbacks and processes that characterize the regime (or basin of attraction; processes and feedbacks that maintain dynamic states of systems) of distinct landscape units (e.g. ecozones, biogeographical regions and climate domains) (Norberg & Cumming 2008). Socio-economic asymmetries, such as urban to rural gradients, variations in access to public transport or spatial patterns in farming systems, can also drive processes in social–ecological systems.

Distinct landscape elements, such as habitat patches, are connected to one another by a variety of processes. They can be viewed as nodes in networks that are connected by movement, communication or other processes, such as nutrient exchanges. Network theory is useful in this context because it illustrates how spatial resilience can be influenced by the position of a system (e.g. a wetland or a city) and its connectivity within a network of similar systems (Uden *et al.* 2014). Network membership and position have implications for resilience at two scales, that of the individual node and that of the broader network. In fragmented ecosystems, for example, smaller patches with no obvious individual ecological significance may be important stepping stones for movement of organisms across landscapes (Urban & Keitt 2001).

Information processing in complex adaptive systems is related to information exchange within and across system elements. System elements can comprise habitat patches or communities of people or organisms; ecological patterns within and across these patches can be mediated by dispersing organisms or interconnected ecosystem processes; and social–ecological processes such as migration and communication are integral to socioeconomic dynamics. Thus, spatial elements of a system that relate to meta-community (Leibold *et al.* 2004) or meta-ecosystem (Loreau, Mouquet & Holt 2003) aspects can characterize information processing from a spatial resilience perspective. Furthermore, a basic tenet of information exchange among hierarchical levels is the constraint of lower levels by higher levels (Allen & Starr 1982). Higher levels establish boundaries within which lower levels are free to individualistically operate and simultaneously constrain even lower hierarchical levels. An initial application of this principle to spatial resilience is considering what surrounds the focal system— one of the major emphases of prior spatial resilience definitions. However, the main contribution of ‘thinking outside the focal system’ to spatial resilience has so far been in identifying subsidies that may be available for importation into the focal system during a post-disturbance reorganization phase. Essentially, this perspective relates to the lateral information flow among systems. As proposed by Bengtsson *et al.* (2003), a dynamic system of ecological reserves at multiple successional stages can help maximize ecological memory within

landscapes, so that in the wake of disturbance, ‘memories’ of various successional stages may contribute to reorganization. Such memories are not always ‘good’ from a management perspective; for example, the storage of phosphorus from past eutrophication events in the sediment of a lake or the continued presence of invasive species at other sites across a landscape can create an ecological debt that must be overcome before habitat quality can be restored.

In addition to the application of lateral information transfer, the vertical flow of information – as manifested in the surroundings of a focal system and the constraints they impose on its structure and function – is important for spatial resilience. For example, differences between the climatic conditions under which a system organized in the past and those under which it is forced to reorganize in the present could preclude the re-establishment of long-lived species (e.g. trees) or communities, despite the subsidization of their ‘memory’ from surrounding areas and past times. In this case, the spatial threshold that constrains system reorganization could be as simple as the elevation below which species can no longer persist in the long term, due to warmer conditions. Warmer temperatures may also increase the level of stress and decrease the resistance of tree species to diseases and pathogens, given that pests are not proportionately disadvantaged. This again illustrates how changing conditions in broader systems may establish sets of rules for future reorganization events.

Both temporary and longer-term thresholds are important elements of ecosystems (e.g. Hughes *et al.* 2013). In cases of long-term change, at some point the collapse of the existing system and its reorganization with different structures and functions becomes inevitable. The particular characteristics of the new system will depend on the new environmental conditions (i.e. vertical information flow or constraint), and on subsidies of ecological memory from within and outside the new system boundaries (i.e. lateral information flow). Detecting spatial thresholds illustrates how spatially relevant aspects of complexity can be applied to the operationalization of spatial resilience.

ECOLOGICAL MEMORY REVISITED

Measurement of ecological memory is an important aspect of spatial resilience, reflected, for example, in seed banks that allow grasslands to persist in the midst of intense and frequent disturbances (e.g. grazing, fire and drought) without experiencing major regime shifts. Alternatively, increasing propagule pressure from non-grassland species within a grassland system, coupled with long-term natural disturbance (e.g. fire) suppression, may push the system into a new state, as has been evidenced by the recent world-wide expansion of woody plants into grasslands (Naito & Cairns 2011). As historical disturbances are prevented from occurring at a natural range of variability, the resilience of the system is eroded and it nears

a regime shift threshold. In the case of woody plant invasion and expansion, the magnitude of the propagule pressure stressor is enhanced via a negative feedback loop as the number of seed-producing trees within and around the grassland increases. Crossing the threshold makes the transition from grassland to shrubland or woodland inevitable, perhaps even if the frequency of natural disturbance is returned to historical levels.

The roles of within- and among-system connectivity are critical to understanding ecological regime shifts and, therefore, resilience. Far-dispersing organisms may contribute more to the ecological memory of neighbouring systems, and thus, large-scale resilience, than shorter dispersers (Lundberg & Moberg 2003; Welsh & Bellwood 2012b). A common example of external subsidization is colonization of disturbed habitats by individuals originating from undisturbed patches (Bengtsson *et al.* 2003). Ecological memory and connectivity are critical determinants of the direction and duration of reorganization following disturbance. Greater functional connectivity among patches at different successional stages results in reorganization in natural landscapes that is faster and more predictable than in fragmented and anthropogenically altered landscapes (Nyström & Folke 2001; Bengtsson *et al.* 2003). However, isolation does not necessarily preclude reorganization following intense disturbance (Gilmour *et al.* 2013), and ‘isolation’ needs to be defined explicitly, as well as bounded in space and time. For example, as a result of habitat fragmentation, a species occupying a habitat patch may be structurally isolated from neighbouring patches and individuals; however, it may not be functionally (i.e. demographically) isolated if it can traverse the unsuitable habitat matrix between patches. Careful consideration of scale and species-specific dispersal ability is crucial when assessing disturbance impacts, connectivity, subsidies and other determinants of spatial resilience (Cumming 2011b).

Approaches to quantifying spatial resilience

EXTENDING ‘OF WHAT, TO WHAT’ TO SPATIAL RESILIENCE ASSESSMENTS

Resilience research leaped forward with the understanding that identifying the ‘of what’ and ‘to what’ of resilience is often a prerequisite for quantifying resilience (Carpenter *et al.* 2001). Measuring the resilience of *what* and *to what* requires consideration of process–structure–function interactions across multiple spatial and temporal scales. Without this context, resilience is often operationalized as a scale-invariant emergent property of ecological systems. Although useful for advancing resilience theory, the lack of spatial- and scale explicitness in this approach makes its contributions to site-specific and management-relevant resilience assessments challenging and ambiguous.

Detecting spatial patterns that are potentially relevant to resilience is a necessary step in assessing spatial

resilience. Detection of differences in resilience to disturbance among landscapes precedes explanation and understanding of the mechanisms responsible, as well as how spatial patterns may reflect system resilience. To quantify spatial resilience, we propose an extension of Carpenter *et al.*'s (2001) resilience quantification prerequisites to explicitly include spatial variability in both the system and disturbance under consideration, over a given time period (i.e. *the resilience of what, to what, given the spatial characteristics and variability of each, over a given time period*). This requires the consideration of numerous spatial elements of self-organization in complex ecological systems, including recognition of internal vs. external elements associated with scales of observation and system structure, the detection of spatial regimes which define the spatial boundaries of a system, understanding and identification of thresholds, which denote tipping points in the system beyond which abrupt change may occur, and development or use of new or emerging quantitative techniques. These basic spatial aspects of systems are quantifiable and provide insight into system structure and resilience. They are further described below.

It is important to emphasize emergence when incorporating spatial resilience into landscape ecology frameworks, because the extent of landscape analysis or intervention rarely coincides with the boundaries of complex social–ecological systems. Furthermore, any spatial analysis focused on quantifying resilience requires a temporal component, making static analyses or attempts to use management to freeze ecosystems in reference conditions insufficient. Ideally, resilience assessment data will contain multi-scale spatial and temporal observations to help guide multi-scale management decisions. The identification of internal elements at each scale, accompanied with the elucidation of external components and feedbacks operating at broader scales, is necessary for operationalizing multi-scale management.

Identifying spatial regimes of focal systems during the time period of interest is critical for assigning appropriate scale(s) and linking spatial resilience studies to spatial resilience management. This, in turn, necessitates the application of methods for delineating spatial regimes as an initial analytical step. Quantitative thresholds and the identification of tipping points within this multi-scale approach provide an impetus for management action (Twidwell *et al.* 2013a). Knowledge of thresholds and the identification of internal elements contributing to relatively lower resilience can help managers prioritize landscape interventions at appropriate scales. Similarly, knowledge of how differences in externalities that occur at broader scales and interact with internal elements can promote adaptive and flexible management strategies that embrace the potential for diverse response trajectories following intervention or disturbance. As currently implemented, haphazard geographical information system (GIS) analyses of spatial landscape components and their arrangement are unlikely to advance understanding of the

dynamic nature of focal systems. Moving forward, it is critical that we consider the ecological functions resulting from process–pattern relationships, as well as how spatial attributes of landscapes contribute to the resilience ‘of what’ and ‘to what’.

When considering the spatial aspects of system resilience, it is important to determine the key challenges and uncertainties to address with management interventions, as well as the scale(s) of the problem and realistic management implementation (Allen *et al.* 2011a; Cumming 2011b). Environmental problems with greater uncertainty and low controllability may require applied ecologists to employ scenario planning or other narrative approaches to address the key uncertainties related to the role of spatial resilience in the system. For environmental problems with greater controllability, adaptive management can enhance learning and foster increased awareness (Allen, Pope & Fontaine 2011b). Using these approaches to maintain and develop sustainable and resilient landscapes necessitates flexible and scale-appropriate management by governing institutions (Cumming *et al.* 2012). Landscape resilience is influenced by the degree of matching between the scale of human resource demands and the scale at which ecosystems provide them (Conroy *et al.* 2003; Maciejewski *et al.* 2015). Spatial scales of ecosystem service provisioning are more easily identified than those of human resource demands (Cumming *et al.* 2012).

DELINEATING INTERNAL AND EXTERNAL ELEMENTS

There are numerous internal and external ecosystem elements relevant for understanding the pattern–process–function relationships that determine spatial resilience (Table 1). Nyström *et al.* (2008) suggest analyses of spatial patterns of state shifts as a spatial resilience indicator. Many tools from landscape and community ecology can be used to assess internal and external ecosystem elements (Li & Wu 2004); however, our ability to interpret their outputs in the context of spatial resilience is limited. Some internal features of spatial resilience, including the arrangement of system components (e.g. patch arrangement), their morphology and system boundaries, as well as external components like context, can be readily assessed with remote sensing and GIS techniques. Many of these features require assessment over time to be useful. For example, the perimeter-to-edge ratio of a natural habitat in an urban space may be virtually meaningless on its own, but changes in perimeter-to-edge ratios over time can indicate shifts in the importance of edge effects (e.g. fire, predation, humidity) that may influence the resilience of ecological communities. Properties of local elements (e.g. habitat quality) – in terms of abiotic and biotic conditions – are captured through field sampling of variables of interest for assessing spatial resilience in the focal system (i.e. resilience of what). These variables may be related to water or soil properties, or to population, community or ecosystem processes. Many of these

variables are critical for the maintenance of robust ecological legacies.

DEFINING SPATIAL REGIMES

Spatial regimes are the spatial manifestation of social–ecological system boundaries, as well as spatial feedbacks resulting from the interaction of biotic and abiotic ecological system elements. They may not correspond perfectly with biophysical ecotones that can be detected through remote sensing, because the signatures of human land use and tenure rights may obscure ecotones in natural land cover, and changes in remotely sensed aspects of ecological systems (i.e. reflectance of vegetation) may lag behind other ecological aspects (e.g. species distributions or changes in nutrient flows). Spatial regime additionally refers to structure–process interactions, often through or mediated by animals interacting with plants and abiotic processes at discrete scales. Including the temporal dimension in spatial resilience assessments is crucial, especially for determining internal properties such as the spatial variation or coherence of resilience attributes or other spatially relevant resilience aspects (e.g. environmental change adaptation). Analyses based on static maps provide only snapshots of dynamic system change. Ideally, data with both spatial and temporal axes, at multiple scales, are available to provide a more accurate picture of changing spatial resilience pattern; however, such data are rare.

Spatial regimes emphasize self-similarity in patterns, which should not be interpreted as static, given that landscape pattern varies with succession, other ecological dynamics and the human imprint on the landscape. Ecosystems, at least at the scales usually operationalized, correspond with spatial regimes. However, because ecological systems are often strongly ‘self-organizing’, temporal dynamics of changing patterns within a spatial regime are broadly predictable. For example, differences in albedo and fire tolerance between darker and lighter vegetation in boreal forests may influence heat exchange, convection patterns, lightning strikes, fire exposure and, ultimately, the composition of forest tree communities (Bonan, Chapin & Thompson 1995). In such self-organizing systems, significant deviation from expected pattern (e.g. spruce mortality driven by an outbreak of spruce budworm resulting not in regeneration of spruce or its precedents, but different vegetation) is evidence of a new spatial regime.

UNDERSTANDING SPATIAL THRESHOLDS AND CONNECTIVITY

We define an ecological threshold as the point at which there is an abrupt change in an ecosystem quality, property or phenomenon, or where small changes in one or more external conditions produce large and persistent responses in an ecosystem. Stated another way, an ecological threshold is an abrupt change with respect to an environmental factor or stressor, which strongly modifies a

defined system or community (Solheim *et al.* 2008). Climate change is one such linear change that can lead to the crossing of thresholds and entering of alternative regimes. Ocean acidification is a second example, where increased CO₂ levels may result in the rapid global decline of coral reefs (Hoegh-Guldberg *et al.* 2007).

Spatial thresholds are often discontinuities, rather than simply being nonlinear (i.e. curvilinear), in the statistical sense. Climate change is likely to interact with other major drivers of ecological and social processes, the cumulative effects of which are uncertain. If responses of the environment to stressors such as climate change are indeed nonlinear, then humanity needs to first recognize and understand thresholds, and then either manage to enhance resilience or assist system transformation, so that new systems provide the maximum number of possible benefits. It is usually in humanity’s best interest to maintain and enhance resilience and to avoid crossing critical thresholds, because the post-transition states of systems that presently provide arrays of ecosystem services are generally unpredictable and may provide fewer benefits.

Thresholds played an important role in the development of the field of landscape ecology. For example, a contagious process such as fire can travel across a uniform landscape; however, this is not necessarily the case in a fragmented landscape. There exists a threshold of fragmentation, the percolation threshold (Keitt, Urban & Milne 1997), above which processes can span an entire landscape, but below which they cannot. This has relevance to the management of natural resources in the face of global change, because landscape connectivity is critical to the movement of animals and processes across landscapes. Maintaining some level of connectivity is critical under uncertain and changing conditions because it allows for adaptive responses in terms of movements, while preventing harmful contagious processes (e.g. hot fires and pathogen outbreaks) from affecting large portions of landscapes. Percolation thresholds are also important because they are amenable to remote sensing and quantification with GIS. Many other types of landscape thresholds exist, but those related to among-patch connectivity are of special interest, due to the effects of global change. Connectivity can be physical, as addressed by percolation theory, or virtual, as addressed by functional connectivity.

Functional connectivity is a species-specific measure that is directly related to the dispersal distance of an animal, with patches within dispersal distance being functionally connected. Fragmentation and the patch loss can affect the persistence of populations by reducing the habitat area available to them or preventing their among-patch movements in response to changing conditions. Alternatively, disturbances like disease may spread rapidly through a highly connected system. As a result of these simultaneous benefits and costs, it is hypothesized that intermediate levels of connectivity – and related modularity [i.e. metric that measures the separation of networks into smaller, connected clusters (Newman 2006)] – confer

ecological systems with high resilience (Cumming 2011b). Connectivity and spatial subsidies can be modelled using techniques from metacommunity and metaecosystems ecology, or network theory. Requisite levels of connectivity can be context specific and are highly contingent upon the resilience of 'what to what'.

NEW AND EMERGING QUANTITATIVE APPROACHES

Although there has been progress in quantifying spatial resilience, new approaches to understanding the relationships among spatial structure and resilience are needed. Göthe *et al.* (2014) utilize multi-scale spatial modelling to assess spatial structure in functional group distributions of stream benthic invertebrates. Their approach uses the predictions of the cross-scale resilience model (Peterson, Allen & Holling 1998; this model posits that the distribution of ecological functions within and across scales is non-random, and helps confer resilience) in an explicitly spatial context. That is, spatial modelling is able to discern independent patterns in the spatial distribution of species within a community. These patterns can arise from biogeographical signals at broad spatial scales, or more narrow patterns, for example, those that might occur within headwater streams of a single catchment. Studying how functional traits of species are distributed within and across detected spatial patterns promotes assessments of spatial resilience by identifying spatial scales at which anthropogenic impacts may be most pronounced. For example, a landscape is likely less resilient if only a few spatial scales with low redundancy of functional traits are detected, relative to other landscapes that display patterns at multiple scales and possess a host of diversity and redundancy in functional traits within and across scales. Multi-scale spatial modelling can also be used to identify species that exhibit stochastic dynamics (i.e. species that are not correlated with spatial patterns) (Angeler *et al.* 2015). Stochastic species can play an important role in the 'adaptive capacity' of ecosystems by increasing their ability to adapt to change without undergoing catastrophic regime shifts (Baho *et al.* 2014).

Network theory may also be adapted and used to quantify spatial resilience. Particular configurations of nodes and links can be recognized and related to resilience-related processes (Bodin & Tengö 2012), which in turn can be used to track changes in resilience in networks where nodes have geographical locations. Such approaches have particular relevance to conservation biogeography, although several analytical challenges remain before they can be widely applied (Cumming *et al.* 2010). This possibility is discussed in more detail in Moore, Grewar & Cumming (2016) and the references therein.

EXAMPLE FROM RANGELANDS

The sagebrush steppe ecosystem of North America provides an example of ecosystem dependence on spatial

resilience. Wyoming big sagebrush *Artemisia tridentata* does not resprout following fire (i.e. it is fire-intolerant). Yet, sagebrush occurs in an ecosystem with a long co-evolutionary history of fire (Miller & Rose 1999; Mensing, Livingston & Barker 2006). The ability of sagebrush to persist in the presence of high fire return intervals therefore depends on its ability to escape fire (West & Hassan 1985; Pyke 2011), opportunities which occur as a result of discontinuous surface fuel distributions and patterns of fire spread (Miller & Heyerdahl 2008). Where cheatgrass *Bromus tectorum* has invaded, the spatial structure of landscapes is fundamentally altered, so that the distribution of fuel is more spatially continuous. The loss of discontinuous surface fuel structure and absence of large fuel gaps fosters larger, more continuous fires that reduce the potential for sagebrush to escape fire damage and mortality (Keane *et al.* 2009; Balch *et al.* 2013). This reduction in the resilience of the sagebrush steppe to fire is induced by changes in the spatial attributes of the system as a consequence of biological invasion by a non-native species. The overwhelming response of applied ecologists to the loss of resilience has been to eliminate fire from the sagebrush ecosystem (Bukowski & Baker 2013), even in areas where cheatgrass has not yet invaded. This attempt to 'freeze' the distribution of sagebrush is incapable of managing for pattern-process interactions at scales necessary for the conservation of many plant and animal species (Miller & Tausch 2000). Moreover, many sagebrush ecosystems are likely to be transformed to juniper *Juniperus* spp. woodlands in the absence of fire (Miller & Rose 1999). This example demonstrates how ecosystem management efforts are trading one problem for another by not considering the functional contribution of spatial attributes and spatially contagious processes to ecological resilience. We contend that operationalization of spatial resilience has the potential to resolve conflicts surrounding these types of debates in applied ecology. Recent evidence supports our argument, demonstrating clear differences in spatial resilience and resistance of sagebrush communities to fire and invasion, respectively (Chambers *et al.* 2014). This example reinforces the fact that ecological systems can rarely be satisfactorily assessed or understood without explicit consideration of the social (human) element. It also illustrates that reversion to an original desired state may be extremely difficult, as is the case with acidified lakes (Baho *et al.* 2014); however, a resilience focus may help managers realistically assess this, and focus more explicitly on the trade-offs between one system and another, given management.

EXAMPLE FROM INVASION BIOLOGY

Another example of spatial resilience is provided in the ongoing spread of the invasive emerald ash borer *Agrilus planipennis* in North America. The introduction of this insect from Asia permitted it to disperse beyond its natu-

ral ability, and in doing so escape the constraints that shaped its native range. The characteristics of this invader, coupled with the lack of environmental constraints, its continued natural and human-assisted spread, the high susceptibility of ash trees and the clustered distribution of ash trees in anthropogenic landscapes, make it one of the most noticeable, concerning, uncontrollable and costly insect outbreaks on the North American continent (Kovacs *et al.* 2010). Spatial characteristics of the ‘of what’ and ‘to what’ contribute to this vulnerability, at multiple spatial scales.

Individual ash tree resilience to ash borer invasion may be related to tree health and manifested by time taken for structural or functional changes to occur in infected trees. A healthy tree can be defined as one that possesses a high level of structural connectivity among its internal components (e.g. phloem and xylem), as well as spreading roots and leaf-covered branches. Structural connectivity among these physical components allows for the efficient capture and transport of water and nutrients (i.e. essential functions) that gives trees a degree of natural resistance to invasion. Insect boring decreases structural connectivity among tree components, which decreases tree health and inhibits the functions of water and nutrient transport, thereby decreasing resistance to additional boring (i.e. negative feedback). Eventually, intratree structural changes translate into exterior structural and functional changes. Root, branch and leaf death – which all result from boring – decrease the capacity of the tree to obtain water and nutrients. To account for these losses, trees respond with epicormic sprouting (i.e. growth of leaves from buds on the tree trunk) – structural changes aimed at maintaining the essential functions of transpiration and photosynthesis. These responses may allow some trees to persist, but many eventually perish from girdling or other complete breakdowns of structure and function. Relative levels of individual tree resilience may be inferred from the time it takes for structural changes to occur, with less resilient trees exhibiting changes quicker.

Spatial patterns of spread may indicate resilience at multiple scales. At the intratree scale, one spatial indicator involves the degree of order in the spatial boring patterns of individual emerald ash borers. In areas with relatively high resistance to boring – and high structural connectivity among tree components – the spatial pattern of boring has a high degree of order, represented as a tight zigzag (Fig. 1). This is because areas of the trunk alongside those already bored have reduced structural connectivity, which translates into reduced water and nutrient transport potential, which translates into decreased resistance to additional boring. In effect, the emerald ash borer is constrained in its movements by the resistance of the tree. Over time, as trees experience sustained and increasing levels of stress from boring, their resistances to additional boring decreases. As the constraining effect of tree resis-



Fig. 1. Zigzag pattern of emerald ash borer boring beneath the bark of an otherwise healthy ash tree. Image courtesy of Troy Kimoto, Canadian Food Inspection Agency, Bugwood.org.



Fig. 2. Seemingly random pattern of emerald ash borer boring beneath the bark of an ash tree with a relatively low level of resistance to the insect. Image courtesy of Troy Kimoto, Canadian Food Inspection Agency, Bugwood.org.

tance decreases, the boring pattern of the ash borer transitions from the tight zigzag pattern, to more free-ranging and apparently random paths (Fig. 2). At greater scales, emerald ash borers disperse naturally and anthropogenically from infected to uninfected trees in the surrounding landscape.

Table 2. A roadmap for operationalizing spatial resilience

Criteria/measure	Description
Identify system and disturbance	Critical first step in a spatial resilience assessment, identifying the resilience <i>of what, to what</i>
Define spatial regimes/boundaries	Determine spatial regimes, which define system spatial limits and emphasize self-similarity in patterns that give rise to spatial manifestations of system boundaries
Delineate internal vs. external elements	Identify internal and external elements associated with scale of analysis (refer to Table 1). Known data should be gathered at this point
Quantify local diversity and complexity	Assess local measure of diversity and complexity, as well as metrics such as patch diversity, class diversity, topographic variability and related metrics from landscape ecology
Identify thresholds and/or state transitions	Quantify magnitudes of processes that cause abrupt changes in ecological response dynamics. Quantify divergent system trajectories across internal and/or external elements to a given perturbation; for example, internal asymmetries leading to an alternative state change in one location but not another, given the same perturbation, is indicative of differences in relative resilience that manifest in space (assuming constant external influence)
Identify ecological networks and functional connectivity	Consider and characterize influence of networks and functional connectivity in system, and opportunities for manipulating connectivity or network function Nodes typically comprised of discrete elements like towns, individuals, protected areas or computer terminals. Links capture the connections of nodes to one another and include infrastructure, personal interactions, organismal movement or energy exchange
Assess permeability	Not all patches and landscapes are equivalently permeable, and assessing barriers and bridges to the movements of processes and organisms is important
Identify information processing across internal and external components	Identify information exchange within and across internal and external elements, and how they influence steps linking stimulus/perturbation to response capacity
Characterize ecological memory	Determine antecedent conditions or states and their capacity to influence present or future states, conditions or ecological responses

Gaps and opportunities in understanding spatial resilience

Ultimately, to advance understanding of spatial resilience, applied ecologists are encouraged to consider relationships within landscapes between resilience and internal and external spatial components of systems under management, to identify boundaries of functional scaling domains via spatial regime detection and to identify spatial thresholds and tipping points associated with the internal and external processes driving spatial patterns (Table 2). There are several constraints that might impede such evaluations. First, monitoring is required to assess whether environmental change manifests in measurable changes in spatial attributes that promote regime shifts. Spatial regime detection is currently limited and in need of new approaches. Quantifying thresholds that are meaningful to natural resource management is often difficult. Magnitudes and fluxes of biophysical processes are not commonly used to derive threshold dynamics and emergent spatial patterns (Twidwell *et al.* 2013a). Thresholds are also dynamic and can be multiple in nature (Cumming *et al.* 2012).

There are clear gaps in our knowledge and technology that need to be addressed for the advancement of spatial resilience theory and its application. Although we are in the era of 'big data', we rarely have data of sufficient temporal and spatial extent or resolution for comprehensively understanding system dynamics – this is especially true for temporal data.

The concept and quantification of spatial regimes is emerging and not fully developed. Although advancing,

knowledge and quantification of coupled spatiotemporal patterns and the processes or dynamics that drive patterns within a regime over time are limited. The lack of coupled spatiotemporal data and understanding at appropriate scales can make it difficult to establish whether regimes readily identifiable with quantitative techniques are relatively stable or in transition. For example, Lake Michigan, USA, is very different biophysically, chemically, and the species composition and abundance is fundamentally altered from its pre-European state, but its large size and ongoing biological invasions make it impossible to know whether it is in a new ecological state or a slow transition (Spanbauer *et al.* 2014).

We are also in a period of rapid global social and ecological change. The lack of longitudinal data at fine scales for spatial aspects of landscapes makes it difficult to identify current regimes: that is, the world is changing so quickly, and it is difficult to know whether we are observing transient dynamics. Additionally, although the idea of detecting early warning metrics for regime change has received much attention (Kéfi *et al.* 2014), few indicators are robust. Early warning indicators are especially poorly developed for spatial data. Yet, most management goals, reflecting the certainty of the laws upon which they are based, have been established on the assumption that ecological systems are static (Garmestani, Allen & Harm-Benson 2013; Garmestani & Allen 2014). Managers, however, understand that they are working with ecological systems that are dynamic and subject to regime shifts.

The spatial resilience concept is an important framework within which to understand global change impacts.

Managing for spatial resilience seeks to strategically intervene in landscapes, in order to build or maintain resilience and avoid thresholds wherever possible. However, social elements can prevent managers from being adaptive and incorporating resilience management. As a result, most management interventions occur at relatively small spatial scales and are logistically incapable of managing for broader spatial contexts (Twidwell, Allred & Fuhlendorf 2013b). Without continued progress towards an interdisciplinary social–ecological purview of process–pattern relationships in nature and better matching of social governance with natural resource management, applied ecologists are unlikely to adjust management practice scales to increase system resilience to broad-scale disturbance events.

Conclusion

Spatial resilience is at the forefront of attempts to operationalize the resilience concept in real-world landscapes, a development that is much needed, given the consequences of ongoing global change. We have reviewed, synthesized and extended past definitions and uses of spatial resilience, in order to further our understanding of spatial resilience and its potential applications to social–ecological system management. We have also provided suggestions for spatial resilience operationalization and identified existing knowledge and technology gaps, the filling of which will advance the utility of spatial resilience assessment and management frameworks in the future.

Ecological memory and among-system connectivity – the foci of most past spatial resilience assessments – are certainly vital aspects of spatial resilience, because they influence post-disturbance reorganization. However, the consideration of other aspects of hierarchy theory and complexity theory, such as top–down environmental constraints (i.e. vertical information flows), the detection of spatial regimes and thresholds, environmental asymmetries and information processing, is useful for continuing to develop and operationalize spatial resilience frameworks. Also relevant is the utilization – and in some cases, development – of modelling techniques that allow for the delineation of focal system boundaries and the differentiation of their internal and external components. Finally, obtaining long-term, spatially explicit data will be vital for the quantification of spatial resilience in dynamic focal systems that continue to be affected by global change. In essence, the spatial aspects of the ‘of what’ and ‘to what’ in resilience assessments must continue to be explored. The aggregation and dissemination of this information will spur and assist future spatial resilience studies.

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Data accessibility

Data have not been archived because this article does not contain data.

References

- Allen, C.R., Pope, K. & Fontaine, T.J. (2011b) Adaptive management for a turbulent future. *Journal of Environmental Management*, **92**, 1339–1345.
- Allen, T.F.H. & Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago, IL, USA.
- Allen, C.R., Cumming, G.S., Garmestani, A., Taylor, P.D. & Walker, B. (2011a) Managing for resilience. *Wildlife Biology*, **17**, 337–349.
- Allen, C.R., Angeler, D.G., Garmestani, A.S., Gunderson, L.H. & Holling, C.S. (2014) Panarchy: theory and application. *Ecosystems*, **17**, 578–589.
- Angeler, D.G., Allen, C.R., Uden, D.R. & Johnson, R.K. (2015) Spatial scaling patterns and functional redundancies in a changing boreal lake landscape. *Ecosystems*, **18**, 889–902.
- Angeler, D.G., Allen, C.R., Barichievy, C., Eason, T., Garmestani, A.S., Graham, N.A.J. *et al.* (2016) Management applications of discontinuity theory. *Journal of Applied Ecology*, in press. doi:10.1111/1365-2664.12494.
- Baho, D.L., Drakare, S., Johnson, C.R., Allen, C.R. & Angeler, D.G. (2014) Similar resilience characteristics in lakes with different management practices. *PLoS ONE*, **9**(3), e91881. doi:10.1371/journal.pone.0091881.
- Balch, J.K., Bradley, B.A., D'Antonio, C.M. & Gómez-Dans, J. (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*, **19**, 173–183.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. (2003) Reserves, resilience and dynamic landscapes. *Ambio*, **32**, 389–396.
- Berkes, F. & Folke, C. (2002) Back to the future: ecosystem dynamics and local knowledge. *Panarchy: Understanding Transformations in Human and Natural Systems* (eds L. Gunderson & C.S. Holling), pp. 121–146. Island Press, Washington, D.C.
- Bodin, Ö. & Tengö, M. (2012) Disentangling intangible social–ecological systems. *Global Environmental Change*, **22**, 430–439.
- Bonan, G.B., Chapin, F.S. & Thompson, S.L. (1995) Boreal forest and tundra ecosystems as components of the climate system. *Climatic Change*, **29**, 145–167.
- Bukowski, B.E. & Baker, W.L. (2013) Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. *Ecological Applications*, **23**, 546–564.
- Carpenter, S., Walker, B., Anderies, J.M. & Abel, N. (2001) From metaphor to measurement: resilience of what to what? *Ecosystems*, **4**, 765–781.
- Chambers, J.C., Miller, R.F., Board, D.I., Pyke, D.A., Roundy, B.A., Grace, J.B., Schupp, E.W. & Tausch, R.J. (2014) Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. *Rangeland Ecology and Management*, **67**, 440–454.
- Conroy, M.J., Allen, C.R., Peterson, J.T., Pritchard, L. Jr & Moore, C.T. (2003) Landscape change in the southern piedmont: challenges, solutions, and uncertainty across scales. *Conservation Ecology*, **8**, 3.
- Cumming, G.S. (2011a) Spatial resilience: integrating landscape ecology, resilience, and sustainability. *Landscape Ecology*, **26**, 899–909.
- Cumming, G.S. (2011b) *Spatial Resilience in Social-Ecological Systems*. Springer, Dordrecht, The Netherlands.
- Cumming, G.S., Bodin, O., Ernstson, H. & Elmqvist, T. (2010) Network analysis in conservation biogeography: challenges and opportunities. *Diversity and Distributions*, **16**, 414–425.
- Cumming, G.S., Southworth, J., Rondon, X.J. & Marsik, M. (2012) Spatial complexity in fragmenting Amazonian rainforests: do feedbacks from edge effects push forests towards an ecological threshold? *Ecological Complexity*, **11**, 67–74.

- Cumming, G.S., Olsson, P., Chapin, F.S. III & Holling, C.S. (2013) Resilience, experimentation, and scale mismatches in social-ecological landscapes. *Landscape Ecology*, **28**, 1139–1150.
- Cumming, G.S., Allen, C.R., Ban, N.C., Biggs, D., Biggs, H.C., Cumming, D.H.M. *et al.* (2015) Understanding protected area resilience: a multi-scale, social-ecological approach. *Ecological Applications*, **25**, 299–319.
- Elmqvist, T., Wall, M., Berggren, A.L., Blix, L., Fritioff, A. & Rinman, U. (2001) Tropical forest reorganization after fire and cyclone disturbance in Samoa: remnant trees as biological legacies. *Conservation Ecology*, **5**, 10.
- Folke, C. (2006) Resilience: the emergence of a perspective for social-ecological systems analysis. *Global Environmental Change*, **16**, 253–267.
- Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C.S. & Walker, B. (2002) Resilience and sustainable development: building adaptive capacity in a world of transformations. *Ambio*, **31**, 437–440.
- Garrestani, A. & Allen, C.R. (2014) *Social – Ecological Resilience and Law*. University of Columbia Press, New York, NY.
- Garrestani, A.S., Allen, C.R. & Harm-Benson, M. (2013) Can law foster social-ecological resilience. *Ecology and Society*, **18**, 37.
- 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.
- Göthe, E., Sandin, L., Allen, C.R. & Angeler, D.G. (2014) Quantifying spatial scaling patterns and their local and regional correlates in headwater streams: implications for resilience. *Ecology & Society*, **19**, 15.
- Gunderson, L.H., Allen, C.R. & Holling, C.S. (2010) *Foundations of Ecological Resilience*. Island Press, New York, NY.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E. *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.
- Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**, 1–23.
- Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. & van Nes, E.H. (2013) Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology and Evolution*, **28**, 149–155.
- Keane, R.E., Agee, J.K., Fule, P., Keeley, J.E., Key, C., Kitchen, S.G. *et al.* (2009) Ecological effects of large fires on US landscapes: benefit or catastrophe? *International Journal of Wildland Fire*, **17**, 696–712.
- Kéfi, S., Guttal, V., Brock, W.A., Carpenter, S.R., Ellison, A.M., Livina, V.N. *et al.* (2014) Early warning signals of ecological transitions: methods for spatial patterns. *PLoS ONE*, **9**, e92097. doi:10.1371/journal.pone.0092097.
- Keitt, T.H., Urban, D.L. & Milne, B.T. (1997) Detecting critical scales in fragmented landscapes. *Conservation Ecology*, **1**, 4.
- Kovacs, K.F., Haight, R.C., McCullough, D.G., Mercader, R.J., Siegert, N.W. & Liebold, A.M. (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics*, **69**, 569–578.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F. *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.
- Li, H. & Wu, J. (2004) Use and misuse of landscape indices. *Landscape Ecology*, **19**, 389–399.
- Loreau, M., Mouquet, N. & Holt, R.D. (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, **6**, 673–679.
- Lundberg, J. & Moberg, F. (2003) Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems*, **6**, 87–98.
- Maciejewski, K., de Vos, A., Cumming, G.S., Moore, C. & Biggs, D. (2015) Cross-scale feedbacks and scale mismatches as influences on cultural services and the resilience of protected areas. *Ecological Applications*, **25**, 11–23.
- Mensing, S., Livingstone, S. & Barker, P. (2006) Long-term fire history in Great Basin sagebrush reconstructed from macroscopic charcoal in spring sediments, Newark Valley, Nevada. *Western North American Naturalist*, **66**, 64–77.
- Mercader, R.J., Siegert, N.W., Liebold, A.M. & McCullough, D.G. (2009) Dispersal of the emerald ash borer, *Agrilus planipennis*, in newly-colonized sites. *Agricultural and Forest Entomology*, **11**, 421–424.
- Miller, R.F. & Heyerdahl, E.K. (2008) Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from California, USA. *International Journal of Wildland Fire*, **17**, 245–254.
- Miller, R.F. & Rose, J.A. (1999) Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management*, **52**, 550–559.
- Miller, R. F. & Tausch, R.J. (2000) The role of fire in pinyon and juniper woodlands: a descriptive analysis. *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species* (eds K.E.M. Galley & T.P. Wilson), pp. 15–30. Tall Timbers Research Station, Miscellaneous Publication No. 11, Tallahassee, Florida, USA.
- Moore, C., Grewar, J. & Cumming, G.S. (2016) Quantifying network resilience: comparison before and after a major perturbation shows strengths and limitations of network metrics. *Journal of Applied Ecology*, doi:10.1111/1365-2664.12486.
- Naito, A.T. & Cairns, D.M. (2011) Patterns and processes of global shrub expansion. *Progress in Physical Geography*, **35**, 423–442.
- van Nes, E.H. & Scheffer, M. (2005) Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology*, **86**, 1797–1807.
- Newman, M.E.J. (2006) Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, **103**, 8577–8582.
- Norberg, J. & Cumming, G.S., eds. (2008) *Complexity Theory for a Sustainable Future*. Columbia University Press, New York, NY, USA.
- Nyström, M. & Folke, C. (2001) Spatial resilience of coral reefs. *Ecosystems*, **4**, 406–417.
- Nyström, M., Folke, C. & Moberg, F. (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution*, **15**, 413–417.
- Nyström, M., Graham, N.A.J., Norström, A.V. & Lokrantz, J. (2008) Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs*, **27**, 795–809.
- Obura, D.O. (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuarine, Coastal and Shelf Science*, **63**, 353–372.
- Olds, A.D., Pitt, K.A., Maxwell, P.S. & Connolly, R.M. (2012) Synergistic effects of reserves and connectivity on ecological resilience. *Journal of Applied Ecology*, **49**, 1195–1203.
- Peterson, G.D. (2002) Estimating resilience across landscapes. *Conservation Ecology*, **6**, 17.
- Peterson, G., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity and scale. *Ecosystems*, **1**, 6–18.
- Pickett, T.A., Kolasa, J. & Jones, C.G. (2007) *Ecological Understanding: The Nature of Theory and the Theory of Nature*. Elsevier/Academic Press, Amsterdam.
- Pyke, D.A. (2011) Restoring and rehabilitating sagebrush habitats. *Studies in Avian Biology*, **38**, 531–548.
- Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.
- Solheim, A.L., Rekolainen, S., Moe, S.J., Carvalho, L., Phillips, G., Ptacnik, R. *et al.* (2008) Ecological threshold responses in European lakes and their applicability for the Water Framework Directive (WFD) implementation: synthesis of lakes results from the REBECCA project. *Aquatic Ecology*, **42**, 317–334.
- Spanbauer, T.L., Allen, C.R., Angeler, D.G., Eason, T., Nash, K.L., Fritz, S.C. & Stone, J.R. (2014) Prolonged instability prior to a regime shift. *PLoS ONE*, **9**, e108936.
- Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M. *et al.* (2015) Planetary boundaries: guiding human development on a changing planet. *Science*, **347**, 736.
- Twidwell, D., Allred, B.W. & Fuhlendorf, S.D. (2013b) National-scale assessment of ecological content in the world's largest land management framework. *Ecosphere*, **4**, art94.
- Twidwell, D., Fuhlendorf, S.D., Taylor, C.A. Jr & Rogers, W.E. (2013a) Refining thresholds in coupled fire-vegetation models to improve management of encroaching woody plants in grasslands. *Journal of Applied Ecology*, **50**, 603–613.
- Uden, D.R., Hellman, M.L., Angeler, D.G. & Allen, C.R. (2014) The role of reserves and anthropogenic habitats for functional connectivity and resilience of ephemeral wetlands. *Ecological Applications*, **24**, 1569–1582.
- Underwood, J.N., Smith, L.D., van Oppen, M.J.H. & Gilmour, J.P. (2009) Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecological Applications*, **19**, 18–29.
- Urban, D. & Keitt, T. (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology*, **82**, 1205–1218.
- Welsh, J.Q. & Bellwood, D.R. (2012a) How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. *Coral Reefs*, **31**, 991–1003.
- Welsh, J.Q. & Bellwood, D.R. (2012b) Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs*, **31**, 55–65.
- West, N.E. & Hassan, M.A. (1985) Recovery of sagebrush-grass vegetation following wildfire. *Journal of Range Management*, **38**, 131–134.

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