ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Bounded ranges of variation as a framework for future conservation and fire management

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Alterations in natural fire patterns have negatively affected fire-prone ecosystems in many ways. The historical range of variability (HRV) concept evolved as a management target for natural vegetation composition and fire regimes in fire-prone ecosystems. HRV-based management inherently assumes that ecosystem resilience is reflected in observed ranges of past vegetation and fire dynamics, typically without knowledge of where thresholds exist beyond these dynamics. Given uncertainty in future conditions, some have argued that HRV may not adequately reflect ecosystem resilience to future fire activity. We suggest a refinement that includes concepts from the thresholds of potential concern (TPC) framework, which emphasizes tipping points at the extremes of ecosystem dynamics and other socially unacceptable outcomes. We propose bounded ranges of variation (BRV), an approach focused on building resilience by using historical information, but also by identifying socio-ecological thresholds to avoid and associated management action triggers. Here, we examine nonnative species and carbon sequestration as examples of how the BRV framework could be used in the context of conservation and fire management.

Keywords: conservation planning; disturbance ecology; fire ecology and management; historical range of variation; ecosystem thresholds; resilience and climate change

Introduction

Reference conditions have traditionally formed the basis for evaluating the current state of contemporary ecosystems and setting management goals. Given this need, much effort has been directed toward explicitly characterizing the stochastic nature of ecosystem dynamics. One widely used approach, often called the historical range of variability (HRV) framework, has focused on quantifying the range of variation that a set of ecological patterns or processes may naturally exhibit over a given historical period.[1–12] While many interpretations of HRV exist, the framework is based on the premise that retaining key ranges of variability in many ecosystem components can provide guidance concerning how ecosystems may respond to different types of human activities or natural disturbances like fire. Retaining this variability is also seen as crucial to maintaining ecological resilience.[13]

As we enter a period when climate change may seriously threaten ecosystem resilience, HRV is being utilized in novel approaches to identify ecological vulnerabilities and evaluate adaptation strategies for conservation.[14] At the same time, there appears to be a movement away from the use of HRV for fire-related issues in the United States. Some have suggested alternative adaptive strategies and the creation of landscape heterogeneity in vegetation structure and composition to facilitate future resilience, instead of aiming for conditions based on the past.[15–17] Although it is likely that future environmental conditions could be quite different from those forming the basis of HRV, proponents of HRV have argued that it may still provide the most viable framework for future fire management and that trying to manage without a historical reference framework is a risky prospect. Underlying this debate is the need for a deeper understanding of resilience

itself: the capacity of a system to accommodate a range of disturbances or state changes while retaining essential (or desired) structure and function.

Here, we propose a refinement of the HRV concept, drawing from decision-making frameworks across fire-prone parts of the world outside the United States. In particular, we borrow from an approach that emphasizes threshold-based dynamics to avoid key thresholds of potential concern (TPC), beyond which more drastic actions would have to be initiated to maintain desired system functioning.[18] We propose a *bounded ranges of variation* (BRV) framework, which accommodates socio-ecological thresholds and the need for landscape heterogeneity to increase future resilience. The BRV framework retains a basis in HRV, given that there is still much to learn about interactions between past fire regimes and ecosystem resilience.[19–21] We finish by describing how BRV may lend itself to different ecosystem management priorities, including carbon sequestration and controlling invasive species.

Historical range of variability, resilience, and thresholds

Whether baseline conditions for characterizing HRV reflect a reconstruction of past fire regimes (Fig. 1A) or past composition of vegetation mosaics (Fig. 1B), HRV typically aims to capture natural ecosystem functioning before modern human perturbations. For fire management, HRV would provide guidance on how to restore or emulate natural fire-related patterns in space and time. Note that Figure 1 depicts a more predictable (e.g., Gaussian, homogeneous) set of landscape dynamics than may have been typical in many areas.[16] It may also be difficult to establish meaningful and stable estimates of HRV from available records, given rates of ecosystem dynamics in relation to past climatic variation.[22] Regardless, an assumption in management using HRV is that ecosystems should be resilient to environmental fluctuations experienced over a reference period, or ecosystem integrity would not have persisted through these fluctuations.

In many ways, linking HRV and ecosystem function requires a somewhat Clementsian notion of ecosystem-as-organism, relying on a simplified view of ecosystem complexity and quasi-equilibrium states.[23] For example, evaluating vegetation patch composition with long-term landscape averages in mind[24, 25] is analogous to the shifting-mosaic steady
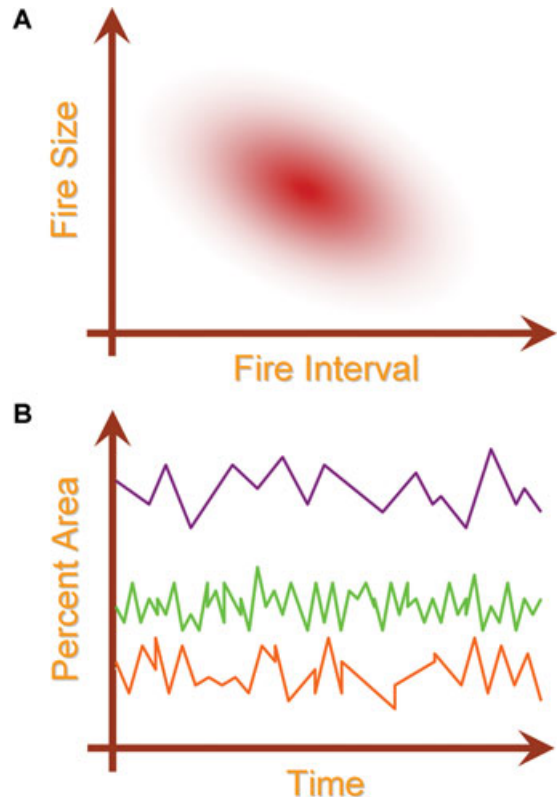

Figure 1. Alternative data sources for characterizing HRV. (A) A stylized range of past area burned and fire frequencies in an ecosystem. (B) A hypothetical time series of patch dynamics on a landscape, which contains three different (by color) vegetation types that fluctuate in how much of the landscape they occupy. Statistical measures of both central tendency and variation could be applied to describe HRV in either context.

state,[26] an early and equilibrium-oriented example of HRV. Although one chooses the spatial and temporal scales to characterize an ecosystem and its HRV, and this choice does not necessarily assume an equilibrium, the concept of resilience suggests the existence of a meta-stable state from which the ecosystem departs and to which it can return.[27] Whether an ecosystem exhibits dynamic equilibrium conditions will depend on the disturbance and recovery processes in question, but also the length of the historical reference period.[28] Given appropriate scales of space and time, it is nonetheless reasonable to relate HRV to some level of ecosystem persistence, stability, and resilience.

Ecological resilience is a measure of the capacity of a system to cope with disturbance and undergo change while retaining similar structure and

function.[29–31] As resilience declines, it should take progressively milder disturbances to push the system into a different state (also termed *regime* or *basin of attraction*[32]). Here, the extremity of a disturbance, such as fire, is linked directly to HRV, as a potential deviation from natural fire patterns may cause transition to a different state. Because crossing this threshold can result in rapid and substantial changes in structure and function, one goal of management can be to increase resilience within particular basins of attraction, assuming the conditions defining basins are themselves somewhat stable (e.g., fire, herbivory, and rainfall causing regime shifts between vegetation states[33]).

Theoretically, these concepts assume expectations of equilibrium dynamics: within a state or regime the system tends toward a certain composition or landscape mosaic (e.g., a ball tending to settle at a bottom of a basin), similar to climatic-climax succession models. However, they also encompass an expectation of the ability of the system to adapt to a certain degree of variability (e.g., the ball can move within the bounds of the basin when pushed), complementary to the concept of HRV and the importance of landscape heterogeneity. Beyond those limits (the edge of the basin), the system moves toward a different eventual configuration (e.g., a ball passing into a new basin). The resulting differences in structure and function occur due to the development of different feedbacks among components of the system and with the biophysical environment. For example, some fire-prone systems naturally have alternative plant community states that tend to persist, such as shrubland and forest patches maintained by differing pyrogenic feedbacks on the same landscape.[34, 35]

Measurement of ecological resilience is notoriously difficult,[36] in part because it depends on at least four factors: the existence of multiple states or basins of attraction, characterization of the different states, characterization of the deviation of a disturbance regime (trigger) from the natural disturbance regime, and the influence of additional factors that may change the shape of the basin of attraction. First, it should not be expected that all systems exhibit threshold dynamics; changes may be smoothly reversible within a single basin of attraction.[37] Concepts of resilience are therefore predominately applicable where there are alternate states. In these cases, management decisions must reflect the pos-

sibility of hysteretic effects (i.e., the effects of a past condition) that can make a shift from one to the other difficult or even impossible to reverse. Inside a single basin of attraction, recovery should be more straightforward (although it could still be slow) if the disturbance regime is returned to within HRV.

State variables are most often characterized by the dominance of different functional groups such as algal versus coral domination in coral reefs[38] and grass versus woody domination,[39] key species such as seagrass presence versus absence,[40] or key processes such as phosphorus to nitrogen limitation in lakes.[41] Landscape-scale dynamics, such as the HRV of different vegetation patches, are less commonly used state variables, but are certainly applicable to fire management.[24, 25] All these measurements essentially describe a key system component, and they reflect the important feedbacks that change across thresholds. In some cases, crossing a threshold brings about a sudden, sharp, and dramatic change in the responding state variables, as in the shift from clear to turbid water in lake systems.[41] In other cases, although the dynamics and feedbacks of the system have flipped from one attractor to another, the transition in the state variables is more gradual, such as the change from a grassy to a shrub-dominated rangeland.[42] The speed of transition in state variables often reflects time lags associated with species life histories or legacies in ecosystem processes, which must be reflected in appropriate temporal scales used to characterize HRV.[22] One critical but often hard-to-test factor is that shifts in state variables persist for at least one complete turnover of the population.[43]
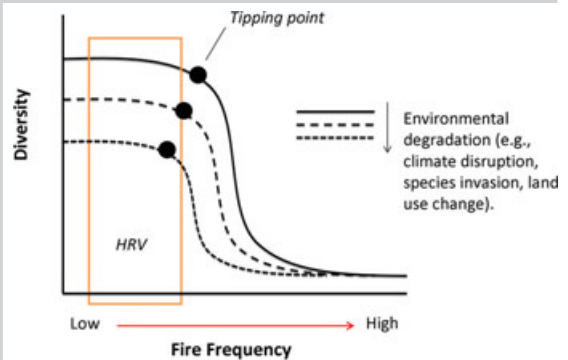
Meaningful measurements of ecosystem conditions must relate to changes in the key disturbance triggers that fundamentally alter important feedbacks. Here, such deviations constitute thresholds, which are sometimes implied in the application of HRV but seldom identified. For example, resilience is expected to depend on maintaining sources of regeneration or adaptation (see Box 1).[44] Maintaining seed sources and seed banks is thus critical for recovery and can affect the likelihood of thresholds being crossed. This aspect of resilience requires a landscape or regional perspective in management, because ensuring that species from adjacent areas can colonize is essential. Undesirable connectivity must also be considered, as it could allow the colonization of invasive or other species that may affect

Box 1. Diversity and resilience.

Functional diversity should relate to ecological resilience and disturbance HRV. Loss of a major functional group, such as apex predators, other consumers, or benthic filter-feeders, may cause drastic alterations in ecosystem functioning.[46–48] For example, overhunting and use of fire by humans some 30,000–40,000 years ago is thought to have caused a widespread and irreversible shift that resulted in an ecosystem of fire and fire-dominated plants.[49] Similarly, in systems that lack a specific functional group, the addition of just one species may dramatically change the structure and functioning of ecosystems.[39,50]

How species respond to disturbance (functional response) relative to how they affect function (functional effect) may be critical to ecosystem resilience;[46,51,52] this has been called response diversity[53] to environmental change among species that contribute to the same ecosystem function. By this logic, landscape and genetic diversity should also be important to resilience at some scale.[54]

While diversity in general can relate to resilience, some have distinguished between real and apparent redundancy.[30] More species do not lead to increased system performance where there is real functional redundancy (similar functional effect traits[55]). Furthermore, if this set of functionally redundant species does not exhibit any response diversity, they would not contribute to resilience. However, there has been little empirical work to determine whether these aspects of functional diversity can be

The upper response curve represents a functioning ecosystem state that is resilient (flat portion) to a range of fire frequencies within HRV; however, higher fire frequencies can lead to a threshold transition to a much less diverse ecosystem. Given a loss of diversity due to environmental degradation (shift to lower response curves), the ecosystem may be closer to a threshold transition point, even if fire frequencies are within HRV (lowest curve).

consistently determined a priori or how they relate to HRV; certainly, a conservative strategy would be to maintain high diversity at multiple levels, assuming that this taxonomic diversity will relate to functional diversity.

ecosystem function in undesirable ways, causing system reorganization and a breakdown in system-level processes following disturbance. Before system-level resilience can be understood, the boundary of the desirable basin of attraction must be defined, providing a metric against which the current system state is evaluated.

The capacity of a system to cope with a disturbance is related to more than just the component states and disturbance trigger. Other factors, such as climate and species pool limitations, can change the shape of the basin of attraction and thus affect adaptive capacity (i.e., the ability to avoid threshold transitions). Scale is an essential consideration,[45] as many important feedbacks occur across scales, such as dispersal connectivity and recovery. In ad-

dition, thresholds can be expected to occur at some scales but not others; for instance, recovery within a patch type might follow very different dynamics than patches across a landscape. The importance of landscape heterogeneity and its HRV emphasizes the interactions between these scales.

Challenges of implementing HRV

Once HRV has been characterized, it must be applied. Several examples are presented in recent reviews of HRV.[11,12] The most straightforward implementation has been to use a measure of deviation from the mean as a management guideline. While this may be helpful for comparing current and historical time series, a potentially risky assumption here is that distance from the mean is an isotropic

risk in terms of ecological destabilization. In other words, avoiding both the left and right tails of the distribution in question (e.g., fires that are too small or too large) is implied as equally important, and this may not always be true.[56]

Other dangers in applying HRV include focusing only on one or a few parameters (e.g., fire frequency in Fig. 1A) or over-emphasizing measures of central tendency (e.g., mean patch composition in Fig. 1B). The U.S. LANDFIRE Program, for instance, used an average fire return interval from HRV to characterize how many multiples of this interval may have been missed in different ecosystems, to identify areas most in need of potential fuel treatments.[57] In contrast, some applications have gone to much greater lengths to characterize HRV of multiple patterns and processes for ecosystem management,[58,59] but this is not the norm. Regardless, some distillation of HRV complexity should be expected in its application to conservation and management problems. A key hurdle is interpreting the ecological meaning of the parameter space characterizing HRV and how it actually links to ecosystem resilience.

One of the largest threats to the relevance of HRV in ecosystem restoration and conservation is the possible emergence of no analogue or novel future conditions.[15,60–62] In such cases, past dynamics certainly could have less to offer in guiding future ecosystem management. It is important, however, to consider which pattern or process will potentially be unique. Are we concerned with climate norms, a top-down set of influences that are exogenous to a given ecosystem? Or are we concerned about soil moisture availability in an ecosystem, fine-scale patterns that can be constrained by abiotic characteristics of the landscape itself? Alternatively, the focus may be species assemblages, the patch mosaic of vegetation types, or fire regimes, all of which emerge as a result of cross-scale interactions and may therefore show some inertia in the face of climate change. Until there is compelling evidence for no analogue fire regimes in future climate scenarios, HRV for fire characteristics should remain relevant in ecosystem management (see Box 2).

It is worth noting that those advocating a move away from using HRV[15–17] also emphasize the heterogeneity of forest composition and pattern as a primary mechanism for facilitating resilience to climate change, arguing that such complexity was the norm for many prehistoric mixed conifer forests.

Therefore, relatively high landscape-scale heterogeneity is likely within the bounds of HRV and is a desirable characteristic, despite the difficulty it poses for specific management prescriptions. As opposed to disregarding HRV, a goal should be to develop methods and tools that more fully utilize HRV in landscape-scale planning and management.[63]

Specifying boundaries in HRV

Although the U.S. literature has addressed thresholds and ranges of variation in ecosystem dynamics,[13,37,42,66–69] to our knowledge, none have suggested the potential merger of HRV with a threshold-based framework. Conceptually, the closest to this merger may be the call for characterizing bounded variation[42] or the acceptable range of variation[66] in ecosystem dynamics. In contrast, some HRV-related concepts have been integrated in a TPC context,[70,71] although a lack of information about historical ecosystem dynamics has probably limited their application.

TPCs were originally envisioned as warning signs of unacceptable environmental change in national parks of South Africa, described as "upper and lower levels of change in selected biotic and abiotic variables."[18] These management thresholds are intended to precede and avoid ecological threshold responses. Because TPCs represent management decision points, fraught with imperfect information and evolving needs, the TPC framework has been refined to incorporate adaptive management.[72–75] In essence, the TPC approach reduces the probability of a system state change by anticipating the boundaries of the desired basin of attraction, including both physical and biological processes and feedbacks between the two.[37] Management triggers can incorporate more species- or process-specific information when knowledge of particular ecological thresholds is available. From this understanding comes a defined set of system parameters to assess the current state condition, relative to the desired distance from different thresholds.[18] Outside of South Africa, the TPC framework has been applied to ecosystem management in fire-prone parts of Australia.[76]

For fire-related conservation issues, concepts from TPC can inform HRV-based management in important ways. Incorporation of thresholds and basins of attraction in HRV, with the express goal

Box 2. No analogue fire activity in the future?

Because fire is affected by vegetation and productivity patterns that are partially constrained by topography, shifts in fire regimes may be less pronounced than those in coarse-scale climate parameters. The choice of downscaling approach is therefore important to realistically capture future climate-driven processes. The most common approach has been statistical downscaling, in which projections are interpolated and calibrated against local weather station data; the resulting spatial scale is often relatively coarse (e.g., tens of km). Process-based models can also be driven by coarse-scale climate variables, simulating fine-scale and topographically influenced micro-climate or water availability predictions.[55,64]

Future fire probabilities in California, for example, have been projected using fine-scaled eco-hydrology model outputs driven by different climate change scenarios.[65] Comparing a warmer–drier future with one representing a warmer–wetter future, the figure here shows that shifts in fire frequencies should be expected across nearly all elevations and time periods in a topographically complex region. Even so, most cases still show substantial overlap between current and future fire probabilities. Therefore, future no analogue fire frequencies could be relatively uncommon.
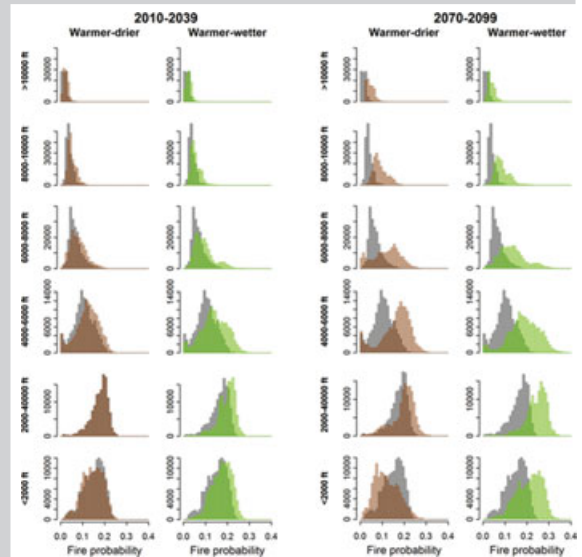
The area examined here covers several dozen vegetation types and life history strategies across ∼ 20,000 km^2 in the southern half of the Sierra Nevada Mountain ecoregion in California. The gray backdrop distribution of fire probabilities in each elevation class represents modeled baseline historical frequencies in the 1971–2000 period, and the colored distributions indicate shifts under future climate scenarios.

of managing resilient systems, can be considered bounds in our BRV approach. Rather than managing around observed system conditions, BRV accommodates the full range of possible conditions, recognizing the potential for a fire event that is in the unobserved tails of the distribution (e.g., very small or very large fires). Rare events such as large or very severe fires are often out of human control, yet some can facilitate landscape heterogeneity.[21] Therefore, while these events may be uncharacteristic and a significant departure from the mean, some may be acceptable or even desired if they do not approach a management boundary that precedes an ecological threshold.

Specifying boundaries for the application of BRV requires identification of the potential range of alternative states or losses (e.g., functionality or local extirpations), along with quantification of the

threshold level of disturbances causing undesirable changes. Such undesirable changes can also include human preferences and perceptions of what is unacceptable, resulting in systems of socio-ecological boundaries.[77] Although it is unlikely that precise disturbance characteristics associated with ecological threshold transitions will be identifiable in many circumstances, general steps for an iterative implementation of BRV are provided below. By integrating monitoring, science, and adaptive management to refine unacceptable thresholds under a changing environment,[37,73,74] BRV could provide a framework that accommodates heterogeneity and natural variation, where resilience is still the primary goal.

BRV: fire and nonnative plants

Nonnative plants, and their potential to transform ecosystems,[80] provide an example of a change agent

that can push a system beyond an ecological threshold. The term *transformation* is used to imply a change in the dominant species present, the physical structure of the system, and the internal ecosystem processes resulting from and potentially reinforcing the compositional changes. Transformation is essentially passing beyond a TPC or out of a basin of attraction into a different and undesirable basin. The ability of the system to return to the prior basin and HRV is assumed to be low. Some of the most dramatic or rapidly occurring examples of transformation are alterations of fire regime caused by changes in fuel structure or distribution due to alien plant invasions.[39,81,82] Individual or multiple fires can trigger the transformation. Potential consequences for conservation include declines in native species cover and richness that are both short and long term,[83–86] loss of topsoil or carbon storage or other functions,[87,88] and loss of wildlife habitat.[89] Identifying boundaries and maintaining the system within BRV requires understanding the importance of environmental or disturbance regime thresholds to keep transforming invaders out of an ecosystem, as well as abundance thresholds of the invader beyond which the probability of ecosystem transformation is greatly enhanced. Thus the BRV for systems where invasive species are of concern should include both biotic (invader abundance) and abiotic (fire regime parameters) boundaries within which the desired system functions are maintained.

Currently, managers of many arid and semiarid ecosystems consider fire-promoting or fire-responsive alien species to be among their key management challenges. Most examples of changes in fire regime driven by alien plants have involved grasses, which appear to have dramatically increased the frequency[83,90] and intensity of fire.[86,91] There was also a recent study of shifts in the timing of fire as driven by the prevalence of alien fuels.[92] Few quantified examples exist of invasive species reducing the frequency or intensity of fire (but see Ref. 93) beyond a threshold such that ecosystem transformation occurs, although there are suggestions that many species have the potential to do so.[94]

Most studies of the relationship of nonnative species to fire do not evaluate thresholds of composition or process beyond which ecosystems would move out of a defined BRV or off of a trajectory that would keep them in a desired basin of attraction. Indeed, for most case studies evaluating invasive species and fire, the historical range of fire regime parameters of the system before invasion is unknown, but anecdotal evidence suggests that it is substantially outside the realm of the new fire regime that is being promoted by the invaders. For example, the annual Mediterranean grass *Bromus tectorum* (cheatgrass) has invaded the North American intermountain west where it is promoting frequent fire[83] to the detriment of native woody species cover.[95,96] While it has been demonstrated that individual fire events locally eliminate native woody species in this ecosystem (reviewed in Ref. 96), and recurrent fire at less than a five-year return interval further deplete native species,[83] neither the fire frequency required to maintain the cheatgrass-dominated state over decades nor the HRV of the desired condition are yet known. For cheatgrass in sagebrush ecosystems of the Great Basin, the desired condition is assumed to be one in which occasional (> 35-year return interval, see Ref. 96) fire could maintain a landscape balance between a more shrub-dominated (sagebrush) and more native perennial grass-dominated condition[97] with low cheatgrass abundance. Indeed, Baker[96] warns that fire return intervals for sagebrush-dominated ecosystems are likely very long, and thus cautions against using fire to try to keep senescent sagebrush systems from crossing thresholds of susceptibility to cheatgrass–fire transformation. A region-wide study is underway to evaluate thresholds of sagebrush, native perennial grass, and cheatgrass abundance within which fire can be used as a tool to maintain the system within a range of desired states (http://www.sagestep.org). This study is unique in its focus on what could be considered a TPC, although they do not use this terminology.

Since the impact of a species is a function of both its abundance and its unique per capita traits,[98] the latter in this case being fuel characteristics, it is possible to define on-the-ground thresholds of invader abundance that greatly increase the probability of the ecosystem moving to a new basin of attraction or to a potentially irreversible undesired condition. Likewise, it might also be possible to define environmental or disturbance regime BRV thresholds that limit invasion of the system by undesirable species. Such thresholds have been identified in a southeastern United States prairie ecosystem, where it was found that fire intervals of four years or less prohibited the establishment of an invasive shrub and

intervals above this allowed the invader to become abundant and resistant to fire mortality.[93] Careful research could therefore guide identification of other BRV thresholds for ecosystems invaded or being threatened by fire-associated exotic species.

Thresholds for fire-transformed areas at the landscape scale also deserve greater study. For example, the negative effects of sagebrush ecosystem fragmentation via cheatgrass and fire have been documented[89] for breeding passerine birds (also see Ref. 99). These studies suggest thresholds of landscape scale transformation beyond which certain species disappear from the habitat. Our framework of BRV would therefore provide a basis for managers to assess the extent to which maintaining or restoring patches of desired vegetation within a regional landscape is essential to species persistence within that region.

BRV: fire and carbon

Carbon sequestration in natural systems has gained considerable attention due to its mitigating effect on climate change. With this attention has come increasing pressure on land managers to account for the effects of management actions on carbon stocks and emissions. The relatively new emphasis on carbon is above and beyond typical ecosystem management concerns (e.g., habitat and water quality), which may be strongly affected by fire. This focus on carbon may also be seen as more of a socio-political priority, rather than one explicitly relating to an ecological tipping point, but it lends itself to BRV concepts in several ways.

The frequency of fire as a natural process ranges from frequent, in systems such as grasslands and dry forests, to infrequent, in systems such as temperate wet forests. Infrequent fire systems are characterized by a fire event resetting the successional stage of the system, often called crown fire or stand renewing if the dominant overstory canopy is consumed. From a carbon perspective, this results in a direct flux of carbon to the atmosphere during the combustion process and an indirect flux from the decomposition of fire-killed vegetation. The immediate effects are often characterized as the system transitioning from carbon sink to source. However, over a period of time encompassing the broader HRV, vegetation recovers and the system transitions back to a sink.[100] For frequent fire systems, mortality rates are lower, typically resulting in reduced indirect carbon emis-

sions compared to infrequent fire systems. Reduced mortality rates also allow the system to sequester the carbon emitted during the fire in a relatively short period of time.[101]

Because forests burn at varying intervals, the carbon stock and source-sink dynamics oscillate as a function of the frequency of disturbance, the primary difference being the amplitude of the oscillations.[102–105] Theoretically, the amount of carbon in a given forest could be maximized by eliminating disturbances, but this is unlikely to be indefinitely sustainable.[106] Fire exclusion in many forests with historically frequent fires has altered the vegetation structure in these ecosystems, resulting in a range of effects on carbon stocks.[105, 107–110] Regardless of the carbon-stock implications of fire-exclusion, the change in structure and associated fuel buildup has often pushed fire regimes from frequent, low-severity toward less frequent, high-severity fire, approaching what some would consider a TPC. Others might see this as typical of a naturally mixed-severity fire regime, although the extent to which this occurred prehistorically has yet to be determined.

Systematically restoring fire to many forest systems is typically achieved by targeting the mean structure associated with HRV through mechanical thinning and/or prescribed burning. These actions result in carbon removal (thinning) and emissions (burning, equipment, etc.), with the size of the carbon-stock reduction and emissions varying as a function of a number of factors, including treatment intensity.[104, 108, 111, 112] It has been argued that these treatments can yield a net carbon benefit because of the reduction in emissions and mortality associated with fire occurrence.[103, 113] However, some have argued that at the landscape scale, these treatments generally result in a net loss of carbon when compared to fire, because of the need to treat more land area than is potentially burned by wildfire.[104]

The concept of BRV thresholds in fire management can be applied to carbon storage in any fire-prone ecosystem, where the carbon stock in the system fluctuates across time and space as a function of the frequency and intensity of fire. In this context, a useful concept for framing the discussion is the carbon carrying capacity (CCC). The CCC of a system is the amount of carbon that can be stored in different age classes of vegetation under prevailing climatic and natural disturbance conditions, but

excluding anthropogenic disturbances.[114,115] This concept can serve as a benchmark against which the current carbon stock in a given location can be evaluated. Levels of carbon storage below CCC would reflect capacity lost due to past land use and management activities. Above the CCC would be a carbon saturation level prone to carbon emissions from the system given the occurrence of natural disturbances.[116]

In the case of fire and human intervention, a given ecosystem may be experiencing fires at a frequency higher or lower than the one under which it evolved. When fire is too frequent, serotinous, obligate seeding, and resprouting species can be negatively affected;[117] alternatively, when fire is too rare, community structure can be fundamentally altered resulting in a buildup of fuel and a fundamental shift in fire type.[118] Both ends of this spectrum could constitute boundaries for a particular ecosystem in a BRV framework. The implications of altered fire frequency range from substantial reductions in the carbon stock (e.g., grassland replacement of shrubland) with shortened fire intervals to substantial increases with lengthened fire intervals.[109,110,119] In cases where fire management for conservation seeks to reduce fire frequency to aid in ecosystem recovery, the potential exists for increasing the carbon stock closer to some natural carrying capacity. BRV thresholds and management triggers could therefore be identified based on ecological targets, carbon sequestration goals, and tradeoffs therein. For example, in systems where the goal is to restore fire as a more frequent process and the system is currently above the carbon carrying capacity, reductions in the carbon stock will be required.

The effectiveness of viewing the CCC of a natural system in the context of BRV is that it accounts for changes stemming from both climate and disturbance, shifts that may result in the range shifting upward or downward, expanding or contracting. An example where the range is likely to move up can be found in northeastern U.S. forests, where fire exclusion has caused a shift from open- to closed-canopy forest, resulting in mesofication of the system,[120] and climate change is projected to enhance future productivity.[121] The role of fire has diminished, and with predicted productivity increases, the upper range of carbon variation could potentially increase. Attempting to restore fire in these less flammable systems, simply because it has

been historically important (using HRV as the management target), could push carbon below a BRV threshold, as defined by prevailing climatic and natural disturbance conditions. In this case, crossing the BRV threshold for carbon (i.e., below the CCC of the system) may result in a shift in species composition (from more mesic to more xeric species), and it needs to be considered whether this also crosses a BRV threshold for ecosystem composition.

While, conceptually, the CCC can provide benchmarks for an appropriately sized carbon stock in a given system, it is imperative that we do not fall into the trap of having a single (or maximum) target carbon condition for every patch within the entire landscape, because it would neglect important ecosystem heterogeneity. The roles of disturbance variability and changing climate must be considered in defining an ecologically appropriate BRV for the carbon stock. As climate changes, system-level productivity is likely to be affected,[122] altering the amount of carbon that can be stored in the system, and fire frequency may change as temperature and precipitation change.[123–126] Accounting for multiple BRV thresholds can thus accommodate the role of both ecological disturbances and climate. Furthermore, understanding that desired carbon stocks will fluctuate and sometimes even conflict with conservation goals allows for tradeoffs in socio-ecological constraints, rather than seeking maximization of this one ecosystem service.

Implementation of BRV

Because historical dynamics of many ecosystems are only known for relatively short periods, and anticipating tipping points of change is difficult, the BRV framework we propose here will have to evolve as it is put into practice. It should be possible to adjust decision points that trigger management action as we learn more about the range of factors negatively affecting systems today and how they are likely to shift in the future (e.g., choosing a more conservative percentile in the tails of the distribution). This is especially true for our growing knowledge of ecological threshold dynamics,[37] but it also applies to shifting public perceptions of what types of changes are unacceptable.

The invasive species and carbon examples above examine the potential for using a BRV framework, but without the details of putting it into practice. To develop and implement BRV in a real-world
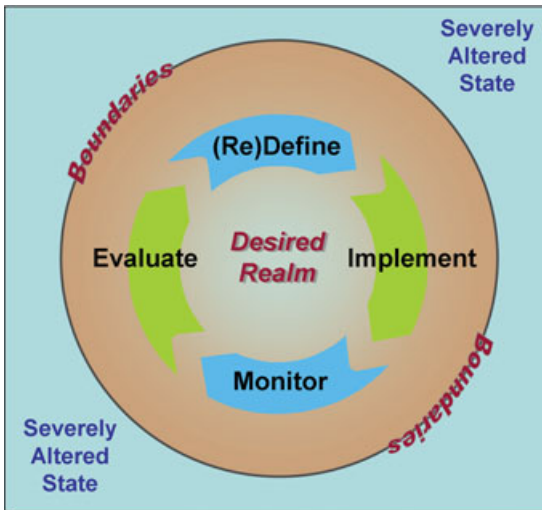
Figure 2. BRV and adaptive management. The traditional adaptive management feedback loop can be used to iteratively refine BRV by incorporating knowledge of desired heterogeneity in past landscape patterns and processes (HRV) and undesirable changes (TPC). Triggers for management activities would be identified at some distance in parameter space from the desired realm of dynamics, but prior to reaching boundaries.

setting, one would necessarily embed the framework in an adaptive feedback loop (Fig. 2). The traditional adaptive management cycle could thus emphasize ecosystem resilience and allow for entering into the BRV framework with limited knowledge through the following iterative stages: (1) *defining the context of the problem and desired future conditions*, including key drivers of change and potential future ranges of variation, measurable pattern/process targets and bounds for specific parameters, management triggers that precede bounds, feasible activities to achieve BRV goals, and experimental trials to confirm cause-effect relationships; (2) *implementing the plan* using passive landscape management to promote natural dynamics, active landscape management to facilitate desired heterogeneity, and active landscape management triggered to avoid severe alterations; (3) *monitoring outcomes of management and natural dynamics*, including actual management activities undertaken (versus planned), variation in key pattern/process metrics characterizing dynamics, and trends toward future management triggers; (4) *evaluating new information*, including causal links between management and landscape changes, observed natural stochasticity in dynamics, intended versus unin-

tended outcomes, and recent outside research on HRV and/or TPC in related systems; and (5) *beginning the process again* to refine and achieve BRV goals.

The up-front quantification of measurable pattern and process targets and bounds for specific parameters is admittedly challenging, and a review of the various methodologies used for each is beyond the scope of this paper. However, the previously cited HRV and TPC literature will provide useful guidance for this step, and a notable merger of approaches is described in Gillson and Duffin,[71] where a TPC for reductions in woody vegetation cover is evaluated in relation to fossil pollen records describing its HRV.

Where knowledge of ecosystem dynamics is lacking, simulation models are a valuable set of tools for predicting ecosystem states, trajectories, ranges of variation, and threshold transitions under various conditions.[127–129] In fact, simulation is one of the few approaches available for examining potential future scenarios and capturing rare occurrences of threshold dynamics. How tipping points in one ecosystem may relate to tipping points in another is also largely unknown. Simulation modeling thus allows for landscape-scale experiments to detect such thresholds in complex and stochastic systems.

While a fairly typical response to decision making under uncertainty is inaction and the call for more information, this is an increasingly futile option with regard to fire management and conservation. At a minimum, ranges of historical dynamics and potential thresholds may need to be hypothesized for BRV, based on knowledge of ecological tolerances for a few species, patterns, or processes (see Box 3). This provides a starting point for BRV, which can then be iteratively augmented with new information through time. In practice, the BRV framework should eventually result in a clear set of parameters for multiple ecosystem management goals, which would reflect the current ecosystem condition, distance from different thresholds, and management activities triggered to keep bounds from being crossed.
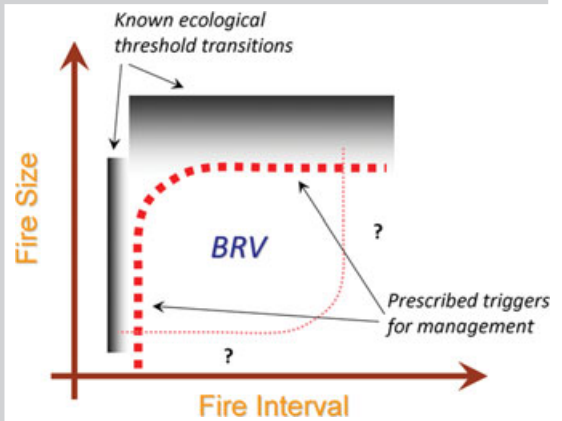
Concluding thoughts

Our goal has been to review current thinking on fire management and conservation, with an emphasis on maintaining inherent ecosystem resilience. In light of this goal, our contribution is oriented more

Box 3. Constructing BRV for chaparral shrublands

As a starting point for BRV, we use some of what is known about fire sizes and frequencies, as they relate to dominant chaparral shrubs and spawning habitat quality for a key anadromous fish.

Short fire-return intervals can restrict recruitment of plant species that recruit by seed, if they require a longer fire-free interval to reestablish a sufficient seed bank. Certain fire-dependent shrub species may thus be lost after frequent fires.[78] Environmental variation (e.g., precipitation gradients) can speed or slow the time to seed production, also affecting where a threshold in fire frequency exists. On the long interval extreme, these same species could conceivably be eliminated, as the seed bank dies off along with the parent plants in the absence of fire. The threshold on rapid fire frequencies is likely to be relatively sharp, whereas the long-interval extreme may be a more gradual system boundary. For chaparral shrublands of California, a short-interval threshold may exist in the ~ 15 year range; the long-interval extreme for chaparral, if it exists, is not known.

Small fires are not seen as a risk to many species. In contrast, large events can have severe effects on some ecosystems.[56] Great distances to unburned seed sources may result

For ecological thresholds at short fire intervals of ~ 15 years and large fire sizes ~ 68 km in width, one could identify boundaries for chaparral ecosystem dynamics, beyond which some management intervention should be considered. Overlain on HRV, such triggers would constitute outer edges of BRV. As more is learned about ecological responses (e.g., in parameter space), BRV can be adjusted accordingly.

from large fires, as well as other landscape-altering effects (e.g., debris flows). In chaparral shrublands, postfire seed dispersal is not limiting; however, effects of large fires on riparian areas can be substantial. Large fires and subsequent fine sediments can threaten endangered southern Steelhead, an anadromous fish species that spawns in creeks of chaparral-dominated landscapes. In key Steelhead conservation areas, management studies have thus used the 1000-year event (fires >68 km in width) as being events of concern.[79] The figure demonstrates the identification of these parameter space thresholds in HRV, along with the management triggers that precede them, constituting a minimal BRV framework for this system.

toward conserving ecosystems in some desired and historically relevant condition, rather than restoring badly degraded habitats or guiding new assemblages of species into novel ecosystems. To build on existing theory and management approaches, we have suggested the merger of two decision-making frameworks from different fire-prone parts of the world.

Although climate change will have diverse effects and sometimes result in novel distributions of fire,[130] future fire activity is likely to have substantial overlap with historical patterns, and many topographic microclimates should be maintained at fine scales.[131] HRV in fire therefore provides an ongoing and useful context for decision making. It is, however, the extremes that often matter most,[132] and this requires an emphasis on thresholds. Incorporating known or expected tipping points in key disturbance regime parameters is therefore an important contribution from the TPC framework, as is the inclusion of socially unacceptable levels of change. Social and ecological goals will, of course, be at odds sometimes, so these too may require trade-offs and value judgments.

The uncertainty of the future climate space for a given geographic location may at first make the

facilitation of system-level resilience seem intractable. However, the BRV concept, used as part of the decision matrix for managing under uncertainty, can provide assistance in allocating conservation resources. For multiple conservation areas, one could first assess system state within BRV and the associated risk of crossing some critical resilience threshold. The conservation priority of different areas, combined with knowledge of their BRV status, can then serve as a means for allocating scarce conservation resources to priority areas with the greatest capacity for resilience. Given the scarcity of conservation dollars and projected regional changes, the goal of restoring some ecosystems throughout the space they currently occupy may be unattainable. However, areas that have a high conservation priority (e.g., endemic populations present) and have yet to approach BRV thresholds (burned by uncharacteristically severe wildfire) could be selected as a target for resource investment to mitigate the risk that some conservation value will be lost due to a fire-driven change.

In some cases, the ecosystem management goal may be to appropriately target a preferred alternative state or basin of attraction outside BRV. In the context of fire management, a conservative approach might involve targeted fire-exclusion in a particular burned area to ensure an opportunity for colonization by new species likely to disperse into the area and survive under new conditions. Allowing natural colonization is likely to be most effective in areas where the candidate group of species is in relatively close proximity, such as along a steep elevation gradient. In areas where a desirable set of new candidate species is not in close proximity, this may require human intervention.[15,17] In a changing climate, however, which human intervention should be taken will depend on knowledge of a preferred alternative state (and the nearby basins of attraction). Therefore, decisions should link directly back to the historical range of ecosystem dynamics and the thresholds therein (i.e., BRV).

Although we have proposed the application of BRV in an adaptive management context above, BRV is currently more of a conceptual framework than one ready for widespread application. We have not directly addressed the issue of scale, and this will have to be explored in depth if BRV is to take hold in decision making. The patterns and processes in question would imply use over relatively broad landscape extents. Very localized and high-value conservation targets, such as iconic stands of certain trees or unique endemic habitats, should simply be preserved if possible. Over broader scales, landscape heterogeneity must provide some linkage to ecosystem resilience, both past and future. This heterogeneity is structured in space and time, however, and its most careful application will also incorporate ecological thresholds and the management triggers that should precede them.

Acknowledgments

Conflicts of interest

The authors declare no conflicts of interest.

References

1. Cissel, J.H., F.J. Swanson, W.A. McKee & A.L. Burditt. 1994. Using the past to plan the future in the Pacific Northwest. *J. For.* **92:** 30–46.

2. Kaufmann, M.R., R.T. Graham, D.A.J. Boyce, *et al.* 1994. *An Ecological Basis for Ecosystem Management.* Gen. Tech. Rep. RM 246. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.

3. Swanson, F.J., J.A. Jones, D.O. Wallin & J.H. Cissel. 1994. "Natural variability: implications for ecosystem management." In *Volume II: Ecosystem Management: Principles and Applications.* M.E. Jensen & P.S. Bourgeron, Eds: 80–94. Portland, OR: USDA Forest Service, Pacific Northwest Research Station.

4. Aplet, G. & W.S. Keeton. 1999. "Application of historical range of variability concepts to biodiversity conservation." In *Practical Approaches to the Conservation of Biological Diversity.* R.K. Baydack, H. Campa & J.B. Haufler, Eds.: 71–86. New York, NY: Island Press.

5. Landres, P.B., P. Morgan & F.J. Swanson. 1999. Overview and use of natural variability concepts in managing ecological systems. *Ecol. Appl.* **9:** 1179–1188.

6. Millar, C.I. & W.B. Woolfenden. 1999. The role of climate change in interpreting historical variability. *Ecol. Appl.* **9:** 1207–1216.

7. Swetnam, T.W., C.D. Allen & J.L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecol. Appl.* **9:** 1189–1206.

8. Egan, D. & E.A. Howell Eds., 2001. *The Historical Ecology Handbook: A Restorationist's Guide to Reference Ecosystems.* Washington, DC: Island Press.

9. Keane, R.E., R.A. Parsons & P.F. Hessburg. 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. *Ecol. Model.* **151:** 29–49.

10. Veblen, T.T. 2003. Historic range of variability of mountain forest ecosystems: concepts and applications. *For. Chron.* **79:** 223–226.

11. Keane, R.E., P.F. Hessburg, P.B. Landres & F.J. Swanson. 2009. The use of historical range and variability (HRV) in landscape management. *For. Ecol. Manag.* **258:** 1025–1037.

12. Romme, W.H.J., J.A. Wiens, & H.D. Safford. 2012. "Setting the stage: theoretical and conceptual background of historical range of variation." In *Historical Environmental Variation in Conservation and Natural Resource Management.* J.A. Wiens, G.D. Hayward, H.D. Safford & C.M. Giffen, Eds.: 3–18. Chichester: John Wiley and Sons, Ltd.

13. Holling, C.S. & G.K. Meffe. 1996. Command and control and the pathology of natural resource management. *Conserv. Biol.* **10:** 328–337.

14. Klausmeyer, K.R., M.R. Shaw, J.B. MacKenzie & D.R. Cameron. 2011. Landscape-scale indicators of biodiversity's vulnerability to climate change. *Ecosphere* **2:** art88.

15. Millar, C.I., N.L. Stephenson & S.L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* **17:** 2145–2151.

16. North, M., P. Stine, K. O'Hara, W. Zielinski & S. Stephens. 2009. *An Ecosystem Management Strategy for Sierran Mixed-Conifer Forests.* Gen. Tech. Rep. PSW-GTR-220. Albany, CA: USDA Forest Service, Pacific Southwest Research Station.

17. Stephens, S.L., C.I. Millar & B.M. Collins. 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. *Environ. Res. Lett.* **5:** 024003.

18. Rogers, K. & H.C. Biggs. 1999. Integrating indicators, endpoints and value systems in strategic management of the Kruger National Park. *Freshwater Biol.* **41:** 439–451.

19. Johnstone, J.F., F.S. Chapin, T.N. Hollingsworth, *et al.* 2010. Fire, climate change, and forest resilience in interior Alaska. *Canad. J. For. Res.* **40:** 1302–1312.

20. Kitzberger, T., E. Aráoz, J.H. Gowda, *et al.* 2012. Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems* **15:** 97–112.

21. Moritz, M.A., P.F. Hessburg & N.A. Povak. 2011. "Native fire regimes and landscape resilience." In *The Landscape Ecology of Fire.* Ecological Studies 213. D. McKenzie, C. Miller & D.A. Falk, Eds.: 51–86. Netherlands: Springer.

22. Whitlock, C., P.E. Higuera, D.B. McWethy & C.E. Briles. 2010. Paleoecological perspectives on fire ecology: revisiting the fire-regime concept. *Open Ecol. J.* **3:** 6–23.

23. De Leo, G.A. & S. Levin. 1997. The multifaceted aspects of ecosystem integrity. *Conserv. Ecol.* **1:** 3. http://www.consecol.org/vol1/iss1/art3/

24. Pratt, S.D., L. Holsinger & R.E. Keane. 2006. "Modeling historical reference conditions for vegetation and fire regimes using simulation modeling." In *The LANDFIRE Prototype Project: Nationally Consistent and Locally Relevant Geospatial Data for Wildland Fire Management.* M.G.

Rollins & C. Frame, Eds: 277–314. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

25. Keane, R.E., L.M. Holsinger, R.A. Parsons & K. Gray. 2008. Climate change effects on historical range and variability of two large landscapes in western Montana, USA. *For. Ecol. Manag.* **254:** 375–389.

26. Bormann, F.H. & G.E. Likens. 1979. *Pattern and Process in a Forested Ecosystem.* New York: Springer.

27. Wu, J. & O.L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Qtly. Rev. Biol.* **70:** 439–466.

28. McGarigal, K. & W.H. Romme. 2012. "Modeling historical range of variability at a range of scales: an example application." In *Historical Environmental Variation in Conservation and Natural Resource Management.* J.A. Wiens, G.D. Hayward, H.D. Safford & C.M. Giffen, Eds.: 128–146. Chichester: John Wiley and Sons, Ltd.

29. Holling, C.S. 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* **4:** 1–23.

30. Folke, C., S. Carpenter, B. Walker, *et al.* 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* **35:** 557–581.

31. Walker, B., A. Kinzig & J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2:** 95–113.

32. Scheffer, M. & S.R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18:** 648–656.

33. Anderies, J.M., M.A. Janssen & B.H. Walker. 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. *Ecosystems* **5:** 23–44.

34. Myers, R.L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. *Bull. Torrey Bot. Club* **112:** 241–252.

35. Odion, D.C., M.A. Moritz & D.A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. *J. Ecol.* **98:** 96–105.

36. Carpenter, S., B. Walker, J.M. Anderies & N. Abel. 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* **4:** 765–781.

37. Suding, K.N. & R.J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. *Trends Ecol. Evol.* **24:** 271–279.

38. Hughes, T.P., N.A.J. Graham, J.B.C. Jackson, *et al.* 2010. Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* **25:** 633–642.

39. D'Antonio, C.M. & P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **23:** 63–87.

40. van der Heide, T., E.H. van Nes, G.W. Geerling *et al.* 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. *Ecosystems* **10:** 1311–1322.

41. Carpenter, S.R., D. Ludwig & W.A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* **9:** 751–771.

42. White, P.S. & J.L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restor. Ecol.* **5:** 338–349.

43. Connell, J.H. & W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *Am. Nat.* **121:** 789–824.

44. Nystrom, M. & C. Folke. 2001. Spatial resilience of coral reefs. *Ecosystems* **4:** 406–417.

45. Peters, D.P.C., B.T. Bestelmeyer, J.E. Herrick, *et al.* 2006. Disentangling complex landscapes: new insights into arid and semiarid system dynamics. *BioScience* **56:** 491–501.

46. Chapin, F.S. & A.M. Starfield. 1997. Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Clim. Change* **35:** 449–461.

47. Duffy, J.E. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* **99:** 201–219.

48. Jackson, J.B.C. *et al.* 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293:** 629–638.

49. McWethy, D.B. *et al.* 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proc. Natl. Acad. Sci. USA* **107:** 21343–21348.

50. Chapin, F.S. *et al.* 2000. Consequences of changing biodiversity. *Nature* **405:** 234–242.

51. Norberg, J., D.P. Swaney, J. Dushoff, *et al.* 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proc. Natl. Acad. Sci. USA* **98:** 11376–11381.

52. Suding, K.N., I.W. Ashton, H. Bechtold, *et al.* 2008. Plant and microbe contribution to community resilience in a directionally changing environment. *Ecol. Monograp.* **78:** 313–329.

53. Elmqvist, T., C. Folke, M. Nystrom, *et al.* 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1:** 488–494.

54. Hilborn, R., T.P. Quinn, D.E. Schindler & D.E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. USA* **100:** 6564–6568.

55. Flint, L.E. & A.L. Flint. 2012. Downscaling future climate scenarios to fine scales for hydrologic and ecological modeling and analysis. *Ecol. Proces.* **1:** 1–15.

56. Romme, W.H., E.H. Everham, L.E. Frelich, *et al.* 1998. Are large infrequent disturbances qualitatively different from small frequent disturbances? *Ecosystems* **1:** 524–534.

57. Schmidt, K.M., J.P. Menakis, C.C. Hardy, *et al.* 2002. *Development of Coarse-Scale Spatial Data for Wildland Fire and Fuel Management.* Gen. Tech. Rep. RMRS-GTR-87. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

58. Hessburg, P.F., B.G. Smith & R.B. Salter. 1999. Detecting change in forest spatial patterns from reference conditions. *Ecol. Appl.* **9:** 1232–1252.

59. Gärtner, S., K.M. Reynolds, P.F. Hessburg, *et al.* 2008. Decision support for evaluating landscape departure and prioritizing forest management activities in a changing environment. *For. Ecol. Manag.* **256:** 1666–1676.

60. Williams, J.W. & S.T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5:** 475–482.

61. Seastedt, T.R., R.J. Hobbs & K.N. Suding. 2008. Management of novel ecosystems: are novel approaches required? *Front. Ecol. Environ.* **6:** 547–553.

62. Hiers, J.K., R.J. Mitchell, A. Barnett, *et al.* 2012. The dynamic reference concept: measuring restoration success in a rapidly changing no-analogue future. *Ecol. Restor.* **30:** 27–36.

63. Hessburg, P.F., K.M. Reynolds, R.B. Salter, *et al.* 2013. Landscape evaluation for restoration planning on the Okanogan-Wenatchee National Forest, USA. *Sustainability* **5:** 805–840.

64. Hannah, L., L. Flint, A. Syphard, *et al.* Fine-scale modeling of vegetation response to climate change. *Trends Ecol. Evol.* In review.

65. Krawchuk, M.A. & M.A. Moritz. 2012. *Fire and Climate Change in California.* California Energy Commission. Publication number: CEC-500-2012-026.

66. Parrish, J.D., D.P. Braun & R.S. Unnasch. 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience* **53:** 851–860.

67. Groffman, P.M. *et al.* 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* **9:** 1–13.

68. Martin, J., M.C. Runge, J.D. Nichols, *et al.* 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. *Ecol. Appl.* **19:** 1079–1090.

69. Samhouri, J.F., P.S. Levin & C.H. Ainsworth. 2010. Identifying thresholds for ecosystem-based management. *PLoS ONE* **5:** e8907.

70. Rogers, K.H. 2003. "Adopting a heterogeneity paradigm: implications for management of protected savannas." In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity.* du Toit, J.T., K.H. Rogers & H.C. Biggs, Eds.: 41–58. Washington, DC: Island Press.

71. Gillson, L. & K.I Duffin. 2007. Thresholds of potential concern as benchmarks in the management of African savannahs. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **362:** 309–319.

72. Biggs, H.C. & K.M. Rogers. 2003. "An adaptive system to link science, monitoring and management in practice." In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity.* du Toit, J.T., K.H. Rogers & H.C. Biggs, Eds.: 59–80. Washington, DC: Island Press.

73. van Wilgen, B.W., N. Govender & H.C. Biggs. 2007. The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. *Int. J. Wildland Fire* **16:** 519–530.

74. Roux, D. & L.C. Foxcroft. 2011. The development and application of Strategic Adaptive Management (SAM) within South African National Parks. *Koedoe* **53:**1049.

75. Van Wilgen, B.W., N. Govender, G.G. Forsyth & T. Kraaij. 2011. Towards adaptive fire management for biodiversity conservation: experience in South African National Parks. *Koedoe* **53:**982.

76. Chapple, R.S., D. Ramp, R.A. Bradstock, *et al.* 2011. Integrating science into management of ecosystems in the Greater Blue Mountains. *Environ. Manag.* **48:** 659–674.

77. Biggs, H., S. Ferreira, S. Freitag-Ronaldson & R. Grant-Biggs. 2011. Taking stock after a decade: does the 'thresholds of potential concern' concept need a socioecological revamp? *Koedoe* **53:** 1002.

78. Zedler, P.H., C.R. Gautier & G.S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* **64:** 809–818.

79. Boughton, D.A. *et al.* 2007. *Viability Criteria for Steelhead of the South-central and Southern California Coast.* NOAA Tech. Mem. Series Draft NOAA-TM-NMFS-SWFSC-407. Santa Cruz, CA: NMFS.

80. Richardson D.M., N. Allsopp, C.M. D'Antonio, *et al.* 2000. Plant invasions: the role of mutualisms. *Biol. Rev.* **75:** 65–93.

81. Rossitor, N.A., S.A. Setterfield, M.M. Douglas & L.B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Divers. Distrib.* **9:** 169–176.

82. Brooks, M.L., C.M. D'Antonio, D.M. Richardson, *et al.* 2004. Effects of invasive alien plants on fire regimes. *BioScience* **54:** 677–688.

83. Whisenant S.G. 1990. *Changing Fire Frequencies on Idaho's Snake River Plains: Ecological and Management Implications. Gen. Tech. Rep.* INT-276. Logan, UT: USDA Forest Service, Intermountain Research Center.

84. Hughes R.F., P.M. Vitousek & J.T. Tunison. 1991. Exotic grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology* **72:** 743–746.

85. D'Antonio, C.M., R.F. Hughes & J.T. Tunison. 2011. Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands. *Ecol. Appl.* **21:** 1617–1628.

86. Setterfield, S.A., N.A. Rossitor-Ranchor, L.B. Hutley, *et al.* 2010. Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australia savannas. *Divers. Distrib.* **16:** 854–861.

87. Obrist, D., E.H. Delucia & J.A. ARnone III. 2003. Consequences of wildfire on ecosystem CO2 and water vapour fluxes in the Great Basin. *Glob. Change Biol.* **9:** 563–574.

88. Bradley, B., R.A. Houghton, J.F. Mustard & S.P. Hamburg. 2006. Invasive grass reduces aboveground carbon stocks in shrublands of the western US. *Glob. Change Biol.* **12:** 1815–1822.

89. Knick, S. & J. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. *Conserv. Biol.* **9:** 1059–1071.

90. Tunsion, J.T., R. Loh & C.M. D'Antonio. 2001. "Fire, grass invasions and revegetation of burned areas in Hawaii Volcanoes National Park." In *Proceedings of the Invasive Species Workshop: The Role of Fire in the Controls and Spread of Invasive Species.* K.E. Galley & T.P. Wilson, Eds.: 122–131. Tall Timbers Research Station Publication No. 11, Lawrence Kansas: Allen Press.

91. Lippincott, C.L. 2000. Effects of *Imperata cylindrica* (L.) Beauv. (cogongrass) invasion on fire regime in Florida Sandhill (USA). *Nat. Areas J.* **20:** 140–149.

92. Balch, J.K., B.A. Bradley, C.M. D'Antonio & J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Glob. Change Biol.* **19:** 173–183.

93. Stevens, J.T. & B. Beckage. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). *New Phytol.* **184:** 365–375.

94. D'Antonio C.M. 2000. "Fire, plant invasions, and global changes." In *Invasive Species in a Changing World.* H.A. Mooney & R.J. Hobbs, Eds.: 65–93. Washington, DC: Island Press.

95. Knick, S. 1999. Requiem for an ecosystem. *Northwest Sci.* **73:** 53–57.

96. Baker, W.L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Soc. Bull.* **34:** 177–185.

97. D'Antonio, C.M., J.C. Chambers, R. Loh & J.T. Tunison. 2009. "Applying ecological concepts to the management of widespread grass invasions." In *Management of Invasive Weeds* Inderjit, Ed.: 123–149. New York: Springer.

98. Parker, I., D. Simberloff, W.M. Lonsdale, *et al.* 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invas.* **1:** 3–19.

99. Knick, S.T., D.S. Dobkin, J.T. Rotenberry, *et al.* 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* **105:** 611–634.

100. Kashian, D.M., W.H. Romme, D.B. Tinker, *et al.* 2006. Carbon storage on landscapes with stand-replacing fires. *BioScience* **56:** 598–606.

101. Hurteau, M.D. & M. North. 2010. Carbon recovery rates following different wildfire risk mitigation treatments. *For. Ecol. Manag.* **260:** 930–937.

102. Beringer, J., L.B. Hutley, N.J. Tapper & L.A. Cernusak. 2007. Savanna fires and their impact on net ecosystem productivity in North Australia. *Glob. Change Biol.* **13:** 990–1004.

103. Hurteau, M. & M. North. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Front. Ecol. Environ.* **7:** 409–414.

104. Mitchell, S.R., M.E. Harmon & K.E.B. O'Connell. 2009. Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. *Ecol. Appl.* **19:** 643–655.

105. Hurteau, M.D. & M.L. Brooks. 2011. Short- and long-term effects of fire on carbon in US dry temperate forest systems. *BioScience* **61:** 139–146.

106. Hudiburg, T., B. Law, D.P. Turner, *et al.* 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecol. Appl.* **19:** 163–180.

107. Fellows, A.W. & M.L. Goulden. 2008. Has fire suppression increased the amount of carbon stored in western U.S. forests? *Geophys. Res. Lett.* **35:** L12404.

108. North, M., M. Hurteau & J. Innes. 2009. Fire suppression and fuels treatment effects on mixed-conifer carbon stocks and emissions. *Ecol. Appl.* **19:** 1385–1396.

109. Hurteau, M.D., M.T. Stoddard & P.Z. Fule. 2011. The carbon costs of mitigating high-severity wildfire in southwestern ponderosa pine. *Glob. Change Biol.* **17:** 1516–1521.

110. Collins, B.M., R.G. Everett & S.L. Stephens. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* **2:** art51.

111. Finkral, A.J. & A.M. Evans. 2008. The effects of a thinning treatment on carbon stocks in a northern Arizona ponderosa pine forest. *For. Ecol. Manag.* **255:** 2743–2750.

112. Stephens, S.L., J.J. Moghaddas, B.R. Hartsough, *et al.* 2009. Fuel treatment effects on stand-level carbon pools, treatment-related emissions, and fire risk in a Sierra Nevada mixed-conifer forest. *Canad. J. For. Res.* **39:** 1538–1547.

113. Hurteau, M.D., G.W. Koch & B.A. Hungate. 2008. Carbon protection and fire risk reduction: toward a full accounting of forest carbon offsets. *Front. Ecol. Environ.* **6:** 493–498.

114. Gupta, R.K. & D.L.N. Rao. 1994. Potential of wastelands for sequestering carbon by reforestation. *Curr. Sci.* **66:** 378–380.

115. Keith, H., B.G. Mackey & D.B. Lindenmayer. 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl. Acad. Sci. USA* **106:** 11635–11640.

116. Moroni, M.T., T.H. Kelley & M.L. McLarin, 2010. Carbon in trees in Tasmanian State Forest. *Int. J. For. Res.* **25:**129–146.

117. Syphard, A.D., V.C. Radeloff, T.J. Hawbaker & S.I. Stewart. 2009. Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conserv. Biol.* **23:** 758–769.

118. Stephens, S.L. 1998. Evaluation of the effects of fuels treatments on potential fire behaviour in Sierra Nevada mixed-conifer forests. *For. Ecol. Manag.* **105:** 21–35.

119. Kaye, J.P., J. Romanya & V.R. Vallejo. 2010. Plant and soil carbon accumulation following fire in Mediterranean woodlands in Spain. *Oecologia* **164:** 533–543.

120. Nowacki, G.J. & M.D. Abrams. 2008. The demise of fire and "mesophication" of forest in the eastern Unted States. *BioScience* **58:** 123–138.

121. Campbell, J., D. Donato, D. Azuma & B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. *J. Geophys. Res.* **112:** G04014.

122. Beer, C. *et al.* 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* **329:** 834–838.

123. Westerling, A.L. & B.P. Bryant. 2008. Climate change and wildfire in California. *Clim. Change* **87**(Suppl. 1): S231–S249.

124. Krawchuk, M.A. & M.A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* **92:** 121–132.

125. Westerling, A.L., M.G. Turner, E.A.H. Smithwick, *et al.* 2011. Continued warming could transform greater Yellowstone fire regimes by mid-21st century. *Proc. Natl. Acad. Sci. USA* **108:** 13165–13170.

126. Moritz, M.A., M.-A. Parisien, E. Batllori, *et al.* 2012. Climate change and disruptions to global fire activity. *Ecosphere* **3:** 49.

127. Keane, R.E. & E. Karau. 2010. Evaluating the ecological benefits of wildfire by integrating fire and ecosystem simulation models. *Ecol. Model.* **221:** 1162–1172.

128. Scholes, R.J. & J.M. Kruger. 2011. A framework for deriving and triggering thresholds for management intervention in uncertain, varying and time-lagged systems. *Koedoe* **53:** 987.

129. Keane, R.E. 2012. "Creating historical range of variation (HRV) time series using landscape modeling: overview and issues." In *Historical Environmental Variation in Conservation and Natural Resource Management.* J.A. Wiens, G.D. Hayward, H.D. Safford & C.M. Giffen, Eds.: 113–127. Chichester: John Wiley and Sons, Ltd.

130. Krawchuk, M.A., M.A. Moritz, M.-A. Parisien, *et al.* 2009. Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE* **4:** e5102.

131. Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Change Biol.* **17:** 1022–1035.

132. Jentsch, A., J. Kreyling & C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. *Front. Ecol. Environ.* **5:** 365–374.