Rangeland Ecology & Management 70 (2017) 149–164

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Using Resilience and Resistance Concepts to Manage Persistent Threats to Sagebrush Ecosystems and Greater Sage-grouse

Jeanne C. Chambers [a,*], Jeremy D. Maestas [b], David A. Pyke [c], Chad S. Boyd [d], Mike Pellant [e], Amarina Wuenschel [f]

[a] Research Ecologist, US Forest Service, Rocky Mountain Research Station, Reno, NV 89509, USA
[b] Sagebrush Ecosystem Specialist, USDA Natural Resources Conservation Service, Redmond, OR 97756, USA
[c] Research Ecologist, US Geological Survey, Forest & Rangeland Ecosystem Science Center, Corvallis, OR 97331, USA
[d] Rangeland Ecologist, US Department of Agriculture—Agricultural Research Service, Burns, OR 97720, USA
[e] Rangeland Ecologist, USDI Bureau of Land Management, Boise, ID 83709, USA
[f] Presidential Management Fellow, US Forest Service, Rocky Mountain Regional Office, Golden, CO 80401, USA

ARTICLE INFO

Article history:
Received 1 February 2016
Received in revised form 7 August 2016
Accepted 9 August 2016

Key Words:
conifer expansion
conservation
invasive annual grasses
population persistence
soil temperature/moisture regimes
wildfire

ABSTRACT

Conservation of imperiled species often demands addressing a complex suite of threats that undermine species viability. Regulatory approaches, such as the US Endangered Species Act (1973), tend to focus on anthropogenic threats through adoption of policies and regulatory mechanisms. However, persistent ecosystem-based threats, such as invasive species and altered disturbance regimes, remain critical issues for most at-risk species considered to be conservation-reliant. We describe an approach for addressing persistent ecosystem threats to at-risk species based on ecological resilience and resistance concepts that is currently being used to conserve greater sage-grouse *(Centrocercus urophasianus)* and sagebrush ecosystems. The approach links biophysical indicators of ecosystem resilience and resistance with species-specific population and habitat requisites in a risk-based framework to identify priority areas for management and guide allocation of resources to manage persistent ecosystem-based threats. US federal land management and natural resource agencies have adopted this framework as a foundation for prioritizing sage-grouse conservation resources and determining effective restoration and management strategies. Because threats and strategies to address them cross-cut program areas, an integrated approach that includes wildland fire operations, postfire rehabilitation, fuels management, and habitat restoration is being used. We believe this approach is applicable to species conservation in other largely intact ecosystems with persistent, ecosystem-based threats.

Published by Elsevier Inc. on behalf of The Society for Range Management.

Introduction

Conservation of imperiled species worldwide often demands curtailing a complex suite of threats that undermine species viability. Regulatory approaches, such as the US Endangered Species Act of 1973 (ESA) (United States Government, 2002), provide necessary stopgap protection but are largely reactive. The focus tends to be on addressing anthropogenic threats through adoption of policies and regulatory mechanisms such as restricting hunting or banning harmful pesticides (Boyd et al., 2014). Persistent ecosystem-based threats, such as invasive species and altered disturbance regimes, remain chronic issues for most at-risk species considered to be conservation reliant and require sustained conservation effort (Scott et al., 2010; Goble et al., 2012). Creative solutions based on an understanding of ecosystem resilience can be used to integrate science, management, and policy and help ecologists embrace uncertainty, manage risk, and adapt in rapidly changing environments (Curtin and Parker, 2014; Pope et al., 2014; Angeler et al., 2016).

Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) is a high-profile species facing a myriad of anthropogenic and persistent ecosystem threats that has been considered for federal regulatory protections under the ESA multiple times (USFWS, 2015). Sage-grouse and more than 350 other species rely on sagebrush (*Artemisia* spp.) ecosystems (Suring et al., 2005). These ecosystems now comprise only about 59% of their historical area, and the primary patterns, processes, and components of many of these systems have been significantly altered since Euro-American settlement in the mid-1800s (Knick et al., 2011; Miller et al., 2011). Primary threats driving continued loss and fragmentation of sagebrush habitat include large-scale wildfire, invasion of exotic annual grasses, conifer expansion, energy development, conversion to cropland, and urban and exurban development (USFWS, 2013). In 2010, concern over sagebrush habitats and the potential for listing sage-grouse under the ESA set in motion sweeping federal and state land management plan changes and proactive conservation actions to address threats within the realm of management control

* Correspondence: Jeanne Chambers, US Forest Service, Rocky Mountain Research Station, 920 Valley Road, Reno, NV 89509, USA.
E-mail address: jchambers@fs.fed.us (J.C. Chambers).

http://dx.doi.org/10.1016/j.rama.2016.08.005
1550-7424/Published by Elsevier Inc. on behalf of The Society for Range Management.

(USFWS, 2015). In fall 2015, federal regulators determined that sage-grouse did not warrant protection under the ESA due to ongoing efforts to address threats but that the species status would be reevaluated again in 2020 (USFWS, 2015). Invasive species and altered fire regimes remain persistent challenges, and changes in precipitation coupled with increased temperatures due to climate change are already magnifying effects of these threats and adding urgency to implementing strategic solutions (Chambers and Pellant, 2008; Abatzoglou and Kolden, 2011; Bradley et al., 2016). For example, climate change is likely linked to recently observed "mega-fires" through an increased propensity for and severity of climatic extremes (Stephens et al., 2014).

Application of ecological resilience and resistance concepts to species and ecosystems of conservation concern has emerged as a unifying framework for managing persistent threats in a variety of ecosystems (Curtin and Parker, 2014; Pope et al., 2014; Angeler et al., 2016). We define resilience as the capacity of ecosystems to reorganize and regain their fundamental structure, processes, and functioning (i.e., to recover) when altered by stressors like drought and disturbances like inappropriate livestock grazing and altered fire regimes (Holling, 1973). Resistance is the capacity of ecosystems to retain their fundamental structure, processes, and functioning when exposed to stresses, disturbances, or invasive species (Folke et al., 2004). Resistance to invasion by nonnative plants is increasingly important in rangeland ecosystems; it is a function of the abiotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen, 2004). Because resilience and resistance are functions of the biophysical characteristics of ecosystems, they vary over environmental gradients, are quantifiable, and can be used to manage risks and predict outcomes of management decisions (Chambers et al., 2014a, 2014b; Allen et al., 2016; Angeler et al., 2016). Linking biophysical indicators of ecosystem resilience and resistance with species-specific population and habitat requisites can yield an ecologically based framework for managing complex ecosystem problems threatening at-risk species at multiple scales (Chambers et al., 2014c, in press).

Here we illustrate how resilience and resistance concepts are being operationalized to reduce impacts of persistent threats from invasive annual grasses and altered fire regimes on sagebrush ecosystems and sage-grouse, particularly in the western portion of the species range (i.e., Columbia Basin, Snake River Plain, and Northern and Southern Great Basin ecoregions; USEPA, 2016). We begin by describing persistent ecosystem and anthropogenic threats to sagebrush ecosystems and discussing the resilience and resistance of these ecosystems based on their biophysical characteristics and known responses to disturbances and management actions. We present objectives and management strategies to support resilience management in sagebrush ecosystems and then link our understanding of sagebrush ecosystem resilience and resistance with sage-grouse habitat requirements in a decision matrix that supports habitat management. Finally, we show how this framework can be used to identify priority areas for management and guide allocation of scarce resources to manage risks across scales. We believe this approach is applicable to species conservation in other largely intact ecosystems with persistent, ecosystem-based threats.

Persistent threats to sagebrush ecosystems and impacts on sage-grouse

Euro-American arrival in sagebrush ecosystems in the mid-1800s initiated a series of changes in vegetation composition and structure that altered fire regimes and had negative consequences for sagebrush habitats. First, improper grazing (type and season of use that results in a phase at risk or departure from reference conditions) by livestock led to a decrease in native perennial grasses and forbs and effectively reduced abundance of fine fuels (Miller et al., 2011). Decreased competition from perennial herbaceous species, in combination with ongoing climate change and favorable conditions for woody species establishment at the turn of the 20th century, resulted in increased abundance of shrubs (primarily *Artemisia* species) and trees, including juniper (western juniper, *Juniperus occidentalis;* Utah juniper, *J. osteosperma*) and piñon pine (singleleaf piñon, *Pinus monophylla*), at mid to high elevations (Miller et al., 2011). The initial effect of these changes in fuel structure was a reduction in fire frequency and size.

Second, exotic annual grasses (e.g., cheatgrass, *Bromus tectorum;* medusahead, *Taeniatherum caput-medusa*) were introduced from Eurasia in the late 1800s and spread rapidly into relative warm and dry ecosystems at low to mid elevations with understories depleted by inappropriate livestock grazing (Pyke et al., 2016). These grasses increased the amount and continuity of fine fuels in many lower-elevation sagebrush habitats and initiated annual grass/fire cycles characterized by shortened fire return intervals and larger, more contiguous fires (Miller et al., 2013). Many warmer and drier sagebrush ecosystems at low to mid elevation have been converted to a new alternative state dominated by cheatgrass and other nonnative invasive annuals that is exceedingly difficult to restore (Germino et al., 2016). Cheatgrass and other invasive annuals now dominate at least 6% of the 650,000 km^2 central Great Basin (Balch et al., 2013) and have potential to spread across many of the remaining low to mid elevation sagebrush ecosystems in the sagebrush biome (Bradley et al., 2016).

Third, ongoing expansion of juniper and piñon pine trees into relatively cool and moist sagebrush types at mid to high elevations reduced the grass, forb, and shrub species associated with these types as a result of resource competition (Miller et al., 2011, 2013). Expansion and infilling of trees increased woody fuel loads, risk of high severity crown fires, and potential for conversion to an alternative state dominated by invasive annual grasses on relatively warm sites with depleted understories (Chambers et al., 2014b; Miller et al., 2014). Tree dominance also increased risk of soil loss and conversion to an eroded alternative state on erodible soils and steep slopes that may be largely irreversible (Chambers et al., 2014b; Miller et al., 2014). On the basis of tree-ring analyses at several Great Basin sites, it is estimated that the extent of piñon and/or juniper woodland increased twofold to sixfold since settlement and most of that area will exhibit canopy closure within the next 50 years (Miller et al., 2008).

Sage-grouse and other sagebrush-obligate species that require large and intact sagebrush landscapes without trees have been negatively impacted by these ongoing land cover changes (Schroeder et al., 2004). Regional analyses using remotely sensed data repeatedly confirm the importance of sagebrush-dominated landscapes as a key constraint on sage-grouse population persistence within a 5- to 30-km radius of leks or breeding sites (Aldridge et al., 2008; Wisdom et al., 2011; Knick et al., 2013). Landscapes with < 25% of the land area dominated by sagebrush cover have a low probability of sustaining lek activity. When sagebrush landscape cover exceeds 25%, the probability of maintaining active sage-grouse leks increases with increasing amounts of sagebrush landscape cover. With 50–85% of the landscape in sagebrush cover, the probability of sustaining sage-grouse leks increases further and then becomes relatively constant (Aldridge et al., 2008; Wisdom et al., 2011; Knick et al., 2013).

Progressive invasion of exotic annual grasses has reduced sage-grouse habitat quantity and quality. Most active leks have little annual grass cover (2.2%) within a 5-km radius (Knick et al., 2013), and lek use decreases as cover of invasive annual species increases at both the 5-km and 18-km scales (Johnson et al., 2011). Active leks that are not impacted by annual grasses can exhibit recruitment rates nearly twice as high as the population average and nearly six times greater than leks affected by annual grasses during years favorable for reproduction (Blomberg et al., 2012). At the scale of the nest site, female sage-grouse avoid nesting in areas with cheatgrass cover > 8% (Kirol et al., 2012).

Piñon and juniper expansion in sagebrush ecosystems at mid to upper elevations reduces sage-grouse habitat availability and suitability over large areas through decreases in sagebrush cover and perennial native grasses and forbs (Miller et al., 2013). Sage-grouse avoid or are negatively associated with low amounts of conifer cover during all life stages (i.e., nesting, brood-rearing, and wintering; Doherty et al., 2010a; Casazza et al., 2011), which is likely due to increased risk of predation by raptors and corvids that use trees as perches. The ability to maintain active leks is severely compromised when conifer canopy exceeds 4% in the immediate vicinity of the lek (Baruch-Mordo et al., 2013), and most active leks average less than 1% woodland cover at landscape scales (Knick et al., 2013).

Resilience and resistance of sagebrush ecosystems

An understanding of how spatial structure and variation in relevant landscape variables affects resilience to disturbance can help quantify resilience and determine effective management strategies at both regional and local scales (Allen et al., 2016). Spatial resilience is a subset of resilience theory that can be defined as the contribution of spatial components and attributes to the feedbacks that generate resilience in ecosystems and vice versa (based on Allen et al., 2016). This definition allows for operationalizing the spatial aspects of resilience in management and is consistent with the foundational aspects of resilience described by Nystrom and Folke (2001) and Cumming (2011). A key element of spatial resilience is that systematic heterogeneity within ecosystems, such as climate and soils, can create gradients in environmental and biotic variables and drive the spatial feedbacks and processes that maintain dynamic states of systems within distinct landscape units at a variety of scales (e.g., ecoregions, watersheds) (Norberg and Cumming, 2008; Allen et al., 2016).

Research in sagebrush ecosystems shows that resilience to stress and disturbance changes along environmental gradients in relation to climate and soils (Fig. 1A; Condon et al., 2011; Davies et al., 2012; Chambers et al., 2014a, 2014b). Systematic differences exist in total resources, resource availability, and net annual primary productivity along these gradients (West, 1983a, 1983b; Smith and Nowak, 1990) at both landscape and plant community scales (Chambers et al., 2014a). Higher precipitation and cooler temperatures, coupled with greater soil development and plant productivity at mid to high elevations, typically result in more favorable environmental conditions for plant growth and reproduction and thus higher resilience (see Fig. 1A). In contrast, reduced precipitation and high temperatures at low elevations typically result in lower resource availability for plant growth and lower resilience. More resilient ecosystems exhibit smaller changes following disturbance and recover more rapidly than less resilient ecosystems (Davies et al., 2012; Chambers et al., 2014b). These relationships are also observed at plant community scales where aspect, slope, and topographic position affect solar radiation, erosion processes, effective precipitation, soil development and, thus, vegetation composition and structure (Johnson and Miller, 2006; Condon et al., 2011).

A measure of spatial resilience is the spatial variability in both the system and disturbance under consideration over a given time period (i.e., resilience of what, to what, given the spatial characteristics and variability of each, over a given time period) (Carpenter et al., 2001; Allen et al., 2016). Differences in productivity, disturbance regimes, and adaptations to historical disturbances can equate to differences in spatial resilience to specific types of disturbances along environmental gradients (Davies et al., 2007). In sagebrush ecosystems, the historical role of fire, species adaptations to fire, and rate of recovery after fire differ along these gradients. Higher-elevation ecosystems with relatively high productivity, such as mountain big sagebrush and mountain brush ecological types, had more frequent presettlement fires due to high fuel abundance and continuity (see Fig. 1A; Baker, 2011; Miller et al., 2011, 2013). These types typically have more fire-tolerant species (Davies et al., 2012), are capable of recovering in a shorter period of time (Baker, 2011), and are at lower risk of transitioning to undesirable alternative states. In contrast, lower-elevation ecosystems with less productivity, such as Wyoming big sagebrush ecological types, tended to have smaller and less frequent fires due to limited fuel production and continuity (see Fig. 1A; West, 1983a; Baker, 2011; Miller et al., 2013). These types typically have fewer fire-tolerant species, require a longer period of time to recover, and are at greater risk of transitioning to alternative states (Brooks and Minnich, 2006; Baker, 2011; Miller et al., 2013; Chambers et al., 2014a, 2014b).

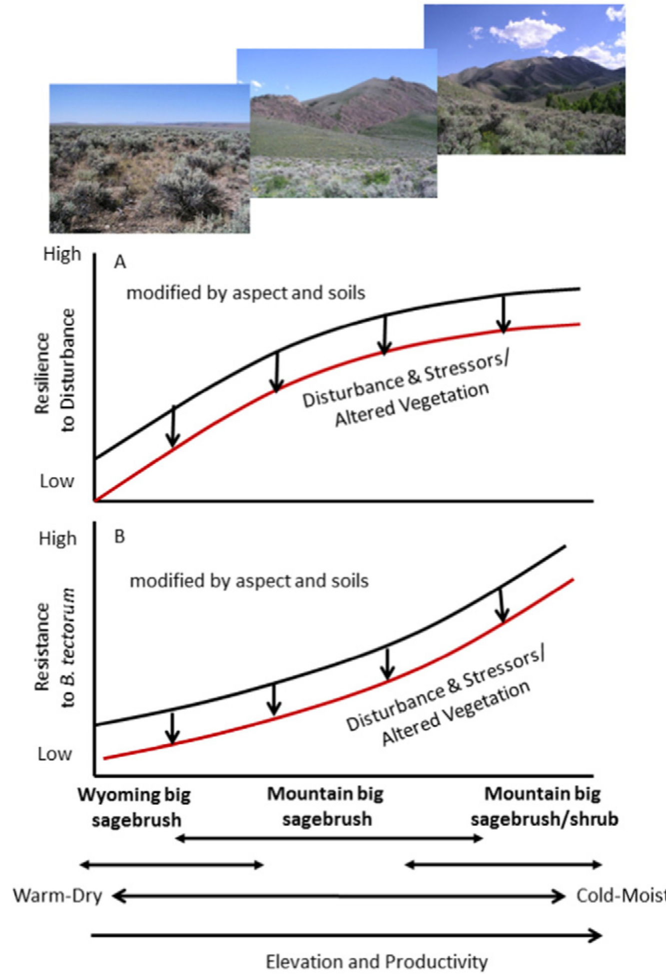


Figure 1. A, Resilience to disturbance and **B,** resistance to cheatgrass as modified by disturbance and stressors over a typical soil temperature and moisture gradient in sagebrush ecosystems of the western United States (adapted from Chambers et al., 2014a).

Resistance to invasion by annual grasses also depends on environmental factors and ecosystem attributes and is a function of 1) the invasive species' physiological and life history requirements for establishment, growth, and reproduction (i.e., fundamental niche) and 2) interactions with the native perennial plant community including interspecific competition and response to herbivores and pathogens (i.e., realized niche). In sagebrush ecosystems, resistance is strongly influenced by temperature and precipitation regimes (Fig. 1B; Chambers et al., 2007, 2014a, 2016). Germination, growth, and/or reproduction of cheatgrass is physiologically limited at low elevations by frequent, low-precipitation years, constrained at high elevations by low soil temperatures, and optimal at low to mid elevations under relatively moderate temperature and water availability (Chambers et al., 2007; Meyer et al. 2001). Slope, aspect, and soil characteristics modify soil temperature and water availability and determine expression of the fundamental niche of cheatgrass at landscape to plant community scales (Chambers et al., 2007; Condon et al., 2011; Reisner et al., 2013).

Occurrence and persistence of invasive annual grasses in sagebrush habitats are strongly influenced by interactions with the native perennial plant community. Cheatgrass, a facultative winter annual that can germinate from early fall through early spring, exhibits root elongation at low soil temperatures and has higher nutrient uptake and growth rates than most native species (Arredondo et al., 1998). Seedlings of native, perennial plant species are generally poor competitors with cheatgrass, but adults of native, perennial grasses and forbs, especially those with similar growth forms and phenology, can be highly effective competitors with the invasive annual (Chambers et al., 2007, 2016). Also, biological soil crusts, which are important components of plant communities in warmer and drier sagebrush ecosystems, can reduce germination or establishment of cheatgrass (Eckert et al., 1986). Disturbances or management actions that reduce abundance of native perennial grasses and forbs and biological soil crusts and increase distances between perennials are often associated with higher abundance of cheatgrass (Chambers et al., 2007; Reisner et al., 2013).

Type and magnitude of stress and disturbance strongly influence both resilience and resistance in sagebrush ecosystems (see Chambers et al., 2014a for a detailed review). Disturbances like inappropriate grazing of perennial plants by livestock and wild horses and more frequent or larger fires are typically outside of the historical range of variability (HRV), where the HRV is defined as the historical envelope of possible ecosystem conditions under the prevailing environmental conditions and disturbance regime(s) (based on Keane et al., 2009) (see Fig. 1). Such disturbances can trigger changes in abiotic processes and attributes like water and nutrient cycling and availability, as well as biotic processes and attributes such as vegetation productivity, structure, and composition (Chambers et al., 2014a) and cover of biological soil crusts (Reisner et al., 2013). Rising atmospheric CO_2 concentrations and climate change may be shifting fire regimes outside of the natural range of occurrence (i.e., longer wildfire seasons with more frequent and longer duration wildfires) (McKenzie et al., 2004) and increasing climate suitability for invasive annual grasses (Bradley, 2009; Bradley et al., 2016). Progressive losses in resilience and resistance can result in crossing of abiotic and/or biotic thresholds and an inability of many sagebrush ecosystems to recover without management intervention.

Operationalizing resilience and resistance concepts to manage sagebrush ecosystems

Conceptual applications of resilience to land management have received considerable attention recently (see reviews in Curtin and Parker, 2014; Pope et al., 2014; Allen et al., 2016; Angeler et al., 2016; Seidl et al., 2016; among others), yet real-world examples at large scales are lacking and putting theory into practice remains challenging (Angeler et al., 2016). Resilience management focuses on managing for systems that have the capacity to absorb, persist, and adapt to inevitable and unpredictable change (Curtin and Parker, 2014). Management actions are designed to 1) actively maintain or enhance ecological processes, functional characteristics, and feedbacks; 2) steer systems away from critical thresholds that would result in undesired states; and 3) increase the capacity of systems to cope with disturbance factors outside of the HRV (Pope et al., 2014). Implementation requires identifying indicators of ecosystem resilience for the system of interest and developing process-based objectives for the focal system that are linked to operational management strategies.

We suggest that indicators of changes in ecosystem resilience and resistance exist across the environmental gradients and ecological types that characterize sagebrush ecosystems and include landscape connectivity, functional plant communities, abundance of nonnative invasive annual grasses, fire regimes relative to the HRV, and ecosystem recovery to desired states after disturbance. Resilience management objectives incorporate multiple scales, and management strategies focus on maintaining and enhancing ecosystem processes, functional attributes, and feedbacks, as well as preventing the crossing of thresholds that decrease ecosystem functioning and services (Table 1; see Pope et al., 2014). For example, at large spatial scales, the extent and connectivity of intact sagebrush ecosystems are critical elements for maintaining the dispersal and reproductive processes of most plant and animal species; they enable these ecosystems and species to absorb the increasing footprint of human development and land use and adapt/migrate in response to climate change (e.g., Millar et al., 2007; Knick et al., 2011, 2013). Management activities include decreasing fragmentation through conservation easements, public land use plans and policies, and fire suppression where altered fire regimes increase risk of transitions to undesired alternative states (see Table 1). At relatively smaller spatial scales, restoring ecosystem processes and functionality following disturbances that remove vegetation is critical to stabilize hydrologic and geomorphic processes, promote desired successional processes, and lower risk of conversion to invasive annual grasses and altered fire regimes (Pyke, 2011). Management activities aimed at establishing functionally diverse species and ecotypes adapted to site conditions and to a warmer and drier climate where projections indicate longer-term climate change can increase capacity to absorb change (Finch et al., 2016); seeding or transplanting sagebrush following large and severe wildfires can increase recruitment rates and enhance landscape connectivity (see Table 1). Management objectives are often synergistic, and strategies designed to maintain or increase functionally diverse native perennial plant communities and decrease the probability of invasion of annual grasses, such as improved grazing management, can also reduce the risk of altered fire regimes, undesirable transitions, and decreased connectivity (see Table 1). Similarly, management aimed at reducing the severity and scale of wildfires outside of the HRV, such as conifer removal in expansion areas, can help maintain or increase the functional capacity of plant communities to resist invasive annual grasses and persist after the next wildfire (Chambers et al., 2014b; Roundy et al., 2014).

A key aspect of operationalizing resilience management is capacity to quantify the spatial components and attributes of landscapes and evaluate changes in these components and attributes over time in response to disturbance and management actions. Ecological site descriptions (ESDs) are part of a land classification system in which ecological sites (ESs) represent subdivisions of a landscape based on reoccurring soil, topographic, and/or climate properties known to influence vegetation composition and change (Caudle et al., 2013; USDA NRCS, 2015a; Williamson et al., 2016). Each ESD includes a state-and-transition model (STM) that describes the states, thresholds, and ecological conditions leading to alternative states in vegetation communities that are likely to occur following disturbances or management actions (Bestelmeyer et al., 2009, 2011). State-and-transition models provide a basis for linking spatial data to 1) the reference state and alternative states that exist for ecological sites and 2) the triggers (events, processes, and drivers) that result in transitions among states (Stringham et al., 2003; Briske et al., 2005, 2008; Bestelmeyer et al., 2009, 2011; Williamson et al., 2016). Together, ESs and STMs help managers evaluate the degree of departure, if any, from the reference state; determine when the reference or desirable state is no longer achievable; and adapt management. Developing an understanding of the spatial linkages among processes and feedbacks for adjoining ESs, such as changes in vegetation cover and hydrologic and geomorphic processes, can provide early warning indicators of the potential for state transitions (Bestelmeyer et al., 2011). Comparisons of the rate and magnitude of change among ESs in response to different triggers can provide an assessment of the relative risk of state transitions among areas and time periods (Williamson et al., 2016).

State-and-transition models that incorporate resilience and resistance concepts can be used to better evaluate change in landscape components and attributes in response to disturbance and management actions (Briske et al., 2008; Chambers et al., 2014a, 2014b). On the basis of recent research in sagebrush ecosystems, we developed a conceptual STM that illustrates the alternative vegetation states, transitions

Table 1
Indicators of resilience and resistance and management objectives and strategies for maintaining or enhancing ecological processes, functional characteristics, and feedbacks and avoiding critical thresholds that decrease ecosystem functioning and services. Objectives are synergistic, and in many cases strategies designed to meet one objective can help meet other objectives. A coordinated and integrated approach that includes nonnative invasive plant management, fire and fuels management, and range and wildlife management will be needed to achieve the objectives.

Indicator: Extent and connectivity of sagebrush ecosystems
Objective: Minimize fragmentation to maintain large landscape availability and connectivity for sage-grouse and other sagebrush dependent species (Wisdom et al., 2011; Aldridge et al., 2008; Aldridge et al., 2011; Knick et al., 2013; Donnelly et al., in press).
Strategies:
- Secure conservation easements to prevent conversion to tillage agriculture, housing developments, etc., and maintain existing connectivity
- Develop appropriate public land use plans and policies to protect sagebrush habitat and prevent fragmentation
- Manage conifer expansion to maintain connectivity among populations and facilitate seasonal movement
- Suppress fires in targeted areas where altered fire regimes (due to invasive annual grasses, conifer expansion, climate change, or their interactions) are resulting in fire sizes and severities outside of the historical range of variability (HRV), increasing landscape fragmentation, and impeding dispersal, establishment, and persistence of native plants and animals

Indicator: Functionally diverse plant communities
Objective: Maintain or restore key structural and functional groups including native perennial grasses, forbs, and shrubs and biological crusts to promote biogeochemical cycling and hydrologic and geomorphic processes, promote successional processes, and reduce invasion probabilities (Chambers et al., 2007, 2014b, 2016; Reisner et al., 2013, 2015; Roundy et al., 2014; Germino et al., 2016)
Strategies:
- Manage grazing to maintain soil and hydrologic functioning and capacity of native perennial herbaceous species, especially perennial grasses, to effectively compete with invasive plant species
- Reduce conifer expansion to prevent high-severity fires and maintain native perennial herbaceous species that can stabilize geomorphic and hydrologic processes and minimize invasions
- Restore disturbed areas with functionally diverse mixtures of native perennial herbaceous species and shrubs with capacity to persist and stabilize ecosystem processes under altered disturbance regimes and in a warming environment

Indicator: Introduction and spread of nonnative invasive plant species
Objective: Decrease the risk of nonnative invasive plant species introduction, establishment, and spread to reduce competition with native perennial species and prevent transitions to undesirable alternative states (Chambers et al., 2016; Pyke et al., 2016)
Strategies:
- Limit anthropogenic activities that facilitate invasion processes including surface disturbances, altered nutrient dynamics, and invasion corridors
- Use Early Detection and Rapid Response (EDRR) for emerging invasive species of concern to prevent invasion and spread (reference)
- Manage livestock grazing to promote native perennial grasses and forbs that compete effectively with invasive plants
- Actively manage invasive plant infestations using integrated management approaches such as chemical treatment of invasives and seeding of native perennials

Indicator: Wildfire regimes outside of the HRV
Objective: Reduce the risk of wildfires outside of the HRV to prevent large-scale landscape fragmentation and/or rapid ecosystem conversion to undesirable alternative states (Miller et al., 2013).
Strategies:
- Reduce fuel loads to 1) decrease fire size and severity and maintain landscape connectivity, 2) decrease competitive suppression of native perennial grasses and forbs by woody species, and thus 3) lower the longer-term risk of dominance by invasive annual grasses and other invaders
- Suppress fires in low to moderate resilience and resistance sagebrush-dominated areas to prevent conversion to invasive annual grass states and thus maintain ecosystem connectivity, ecological processes, and ecosystem services
- Suppress fires adjacent to or within recently restored ecosystems to promote recovery and increase capacity to absorb future change
- Use fuel breaks in carefully targeted locations along existing roads where they can aid fire-suppression efforts and have minimal effects on ecosystem processes (Maestas et al., 2016b).

Indicator: Ecosystem recovery toward desired states following disturbance
Objective: Restore and maintain ecosystem processes and functional attributes following disturbance that are consistent with current and projected environmental conditions and allow ecosystems to absorb change (Hobbs et al., 2009; Finch et al., 2016)
Strategies:
- Assess postdisturbance conditions and avoid seeding where sufficient native perennial herbaceous species exist to promote successional processes, stabilize hydrologic and geomorphic processes, and make conditions conducive to recruitment of sagebrush (Miller et al., 2013, 2015)
- Consider seeding or transplanting sagebrush species adapted to site conditions following large and severe wildfires that decrease recruitment probabilities to increase the rate of recovery and decrease fragmentation
- In areas with depleted native perennials, use species and ecotypes for seeding and outplanting that are adapted to site conditions and to a warmer and drier climate where projections indicate long-term climate change (Finch et al., 2016)
- Avoid seeding introduced forage species that outcompete natives (Lesica and Deluca, 1996; Davies et al., 2013).

among states, and thresholds for warm and dry (mesic/aridic soil temperature/precipitation regime) big sagebrush ecological types with low resilience and resistance relative to cool and moist (frigid/xeric soil temperature/precipitation regime) mountain big sagebrush ecological types with moderate to high resilience and resistance (Fig. 2; Davies et al., 2012; Miller et al., 2013; Chambers et al., 2014b). Soil temperature and moisture regimes are key determinants of sagebrush ecological types and are strongly related to ecosystem resilience and resistance (Chambers et al., 2007; Condon et al., 2011; Chambers et al., 2014b). In general, the highest potential resilience and resistance in sagebrush ecosystems occur with *cool* to *cold* (frigid to cryic) soil temperature regimes and relatively *moist* (xeric) soil moisture regimes characterized by mountain big sagebrush and mountain brush ecological types (see Fig. 1A and B and Fig. 2; Chambers et al., 2014a, 2014b). The lowest potential resilience and resistance occur with *warm* (mesic) soil temperatures and relatively *dry* (aridic) soil moisture regimes characterized by Wyoming big sagebrush ecological types (Fig. 1A and B and Fig. 2; Chambers et al., 2014a, 2014b). High soil moisture enhances productivity and recovery processes, resulting in greater resilience (Chambers et al., 2014b), while cold soil temperatures limit annual grass growth and reproduction, resulting in greater resistance to these species (Chambers et al., 2007). Disturbances, stressors, and management actions that increase resource availability decrease resistance to cheatgrass and other invasive species (Leffler and Ryel, 2012). In cool and moist sites with moderate to high resilience and resistance, various management strategies like proper grazing, Early Detection and Rapid Response management of invasive plant species (EDRR; USDI, 2016), and restoration of functionally diverse mixtures of native species can be used to maintain or increase ecosystem functioning (see Table 1). However, widespread invasion and increasing dominance of cheatgrass

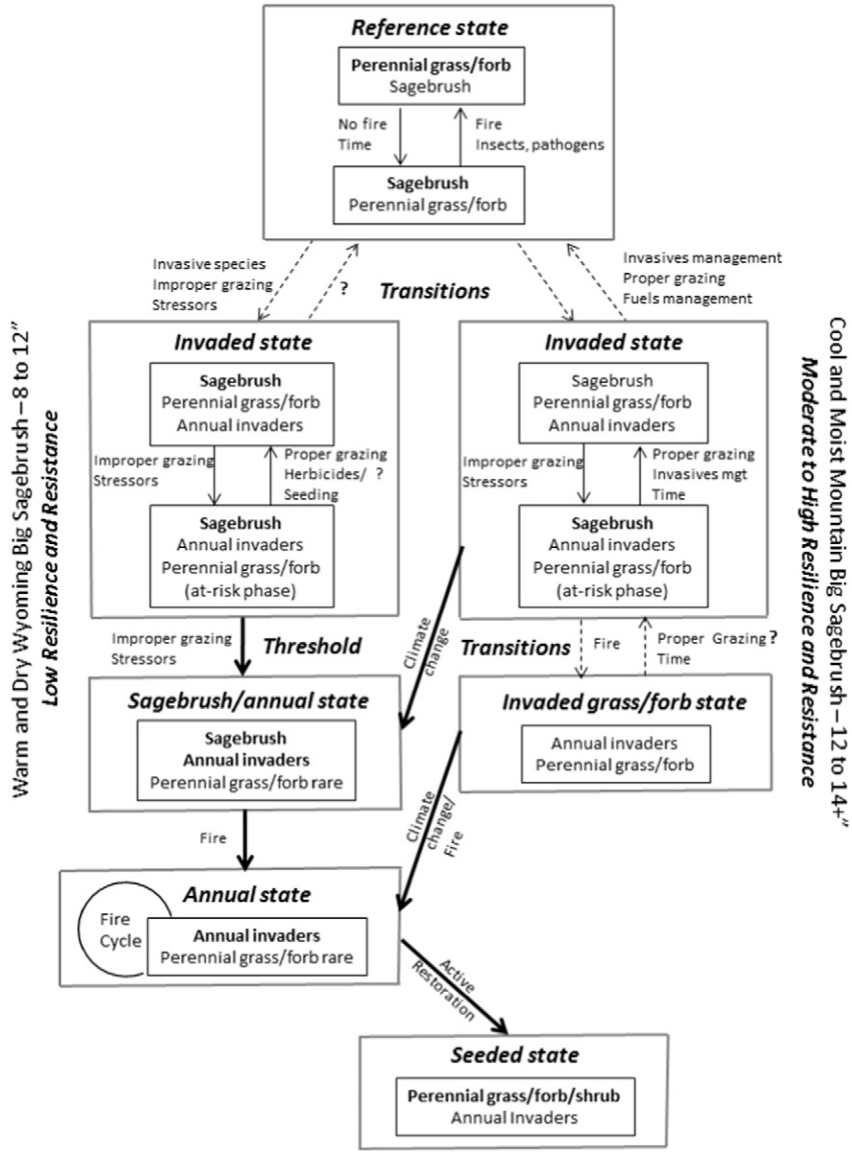


Figure 2. Generalized conceptual model showing the states, transitions, and thresholds for relatively warm and dry Wyoming big sagebrush ecosystems with low resilience and resistance to cheatgrass and cool and moist mountain big sagebrush ecosystems with moderately high resilience and resistance (adapted from Chambers et al., 2014a). **Reference state:** Vegetation dynamics are similar for both types. Perennial grass/forb increases due to disturbances that decrease sagebrush and sagebrush increases with time after disturbance**. Invaded state:** An invasive seed source, improper grazing, and/or stressors trigger a transition to an invaded state. Perennial grass/forb decreases and both sagebrush and invaders increase with improper grazing and stressors resulting in an at-risk phase in both types. Proper grazing, invasive species management, and fuels treatments may restore perennial grass and decrease invaders in relatively cool and moist Wyoming big sage and in mountain big sage types with adequate grass/forb, but return to the reference state is likely only for mountain big sage types. **Sagebrush/annual state:** In the Wyoming big sagebrush type, improper grazing and stressors trigger a threshold to sagebrush/annual dominance. **Annual state:** Fire, disturbances, or management treatments that remove sagebrush result in annual dominance. Perennial grass is rare, and repeated fire causes further degradation. **Seeded state:** Active restoration results in dominance of perennial grass/forb/shrub. Treatment effectiveness and return to the annual state are related to site conditions, post-treatment weather, and seeding mixture. **Invaded grass/forb state:** In the mountain big sagebrush type, fire results in a transition to annual invaders and perennial grass/forb. Proper grazing and time may result in return to the invaded state given adequate perennial grass/forb. Increases in climate suitability for cheatgrass and other annual invaders may shift vegetation dynamics of cooler and moister mountain big sagebrush ecosystems toward those of warmer and drier Wyoming big sagebrush ecosystems. Although not shown here, woodland expansion and infill in mountain big sagebrush sites with conifer potential can result in transition to woodland-dominated or eroded states leading to crossing of biotic and abiotic thresholds.

and other annual invaders in warmer and drier sites have altered vegetation dynamics, resulting in the crossing of thresholds that are difficult to reverse once the perennial herbaceous species required to promote recovery are depleted. As both resilience and resistance decrease on these sites, the degree of uncertainty increases and management options become increasingly limited. As the climate warms, climate suitability for big sagebrush species is projected to move upwards in elevation (Schlaepfer et al., 2012), potentially shifting vegetation dynamics of cooler and moister mountain big sagebrush ecosystems toward those of warmer and drier Wyoming big sagebrush ecosystems.

Monitoring of key ecological indicators of resilience and resistance coupled with large-scale research and management experiments to determine interactions among disturbance regimes, management actions, and capacity of ecosystems to adapt and absorb change can be used to identify thresholds and quantify departure from reference states (e.g., Pope et al., 2014; Seidl et al., 2016). Several monitoring strategies are being implemented by the agencies (e.g., Toevs et al., 2011) that can increase understanding of sagebrush ecosystem resilience and resistance and provide quantitative data to refine existing STMs. Depending on the objective, a realistic time frame for evaluating the effectiveness of management strategies is likely a few decades (i.e., 20 − 30 years, USFWS, 2015). However, there needs to be sufficient flexibility to adapt management if the system exhibits significant departure from the reference state or HRV.

Linking resilience and resistance concepts with sage-grouse

The scale, complexity, and dynamic nature of threats to sagebrush ecosystems and sage-grouse necessitate a strategic approach to conservation that can be used to prioritize management actions to increase ecosystem resilience and resistance to specific threats and efficiently allocate resources to minimize threats and improve sagebrush habitat conditions (Wisdom and Chambers, 2009; Pyke, 2011). At landscape scales, key biophysical characteristics can be used as indicators of potential ecosystem resilience and resistance and thus the likely response to disturbance and management treatments, while key habitat attributes can be used as indicators of potential sage-grouse habitat. Linking information on resilience and resistance with sage-grouse habitat provides the basis for a decision support process to prioritize management actions on the basis of risk assessment and likelihood of maintaining or increasing ecosystem and species capacity to adapt to change across scales.

Soil Temperature and Moisture Regimes as Surrogates for Ecosystem Resilience and Resistance

Resilience to stress and disturbance and resistance to invasive annual grasses reflect the biophysical conditions that an area is capable of supporting. Recent research shows that soil temperature and moisture regimes are key determinants of sagebrush ecological types and are strongly related to ecosystem resilience and resistance (Chambers et al., 2007, 2014b; Condon et al., 2011). Because of the strength of these relationships, we can use soil temperature and moisture regimes as measures of resilience and resistance at landscape scales to depict environmental gradients that range from cold/cool and moist to warm and dry (Fig. 3).

Soil temperature and moisture regimes are mapped as part of the National Cooperative Soil Survey (USDA NRCS, 2013) and thus can be used in large-scale analyses (Maestas et al., 2016a). These regimes are a key component of ESDs (Caudle et al., 2013; USDA NRCS, 2015a) and can be used to inform the development of STMs. As with most large-scale mapping products, there are limitations in using Soil Survey information including incongruities in soil regime classifications, especially along mapping boundaries, and variation in the level of survey detail available. Until improved products emerge, the Soil Survey still provides the most complete data set to advance understanding of ecosystem resilience and resistance. Projected changes in soil temperature and moisture regimes with global warming are currently being modeled for sagebrush ecosystems (John Bradford, USGS, Flagstaff, Arizona, personal communication, 2016), which will allow evaluations of how resilience and resistance are likely to change under different climate change scenarios. Site-level planning will benefit from local climate and soils data and ESDs.

Landscape Cover of Sagebrush as a Surrogate for Sage-grouse Habitat

Although there are many factors that determine habitat suitability for sage-grouse (Connelly et al., 2011; Doherty et al., in press), landscape cover of sagebrush is an important ecological minimum determining persistence of sage-grouse (Knick et al., 2013) and abundance of other sagebrush-obligate bird species (Donnelly et al., in press) that can be readily incorporated into large-scale assessments. Landscape cover of sagebrush is typically derived from remotely sensed land cover data such as LANDFIRE (USGS, 2013) using a moving window analysis (Knick et al., 2013). On the basis of findings of range-wide analyses of landscape cover around active leks (Aldridge et al., 2008; Wisdom et al., 2011; Knick et al., 2013), the relative probability of lek persistence can be estimated using percentage landscape sagebrush cover within each of three categories (low = < 25%, moderate = 25 − 65%, high = > 65%).

Sage-grouse Habitat Resilience and Resistance Matrix

Coupling the relative resilience and resistance of sagebrush ecosystems with proportion of sagebrush cover on the landscape provides a simplified decision support matrix that can help managers identify and prioritize management strategies (Table 2; Chambers et al., 2014c, in press). As resilience and resistance go from high to low, as indicated by rows in the matrix, timeframes required for sagebrush regeneration, as well as perennial grass and forb abundance, progressively limit capacity of a sagebrush ecosystem to recover after wildfire or other disturbances without management assistance (see Table 2). Risk of invasive annual grasses increases, and ability to successfully restore burned or otherwise disturbed areas decreases. As landscape cover of sagebrush goes from low to high within these same ecosystems, as indicated by columns in the matrix, capacity for sustaining populations of sage-grouse increases (see Table 2). Areas with less than 25% landscape cover of sagebrush are unlikely to provide adequate habitat for sage-grouse; areas with 25 − 65% landscape cover of sagebrush can provide habitat for sage-grouse but are at risk if sagebrush loss occurs. Areas with > 65% landscape cover of sagebrush provide a much higher likelihood of sage-grouse population persistence assuming other habitat requisites are met.

Overarching goals of the resilience and resistance decision matrix are to promote resilient sagebrush ecosystems, desired states, and well-connected sagebrush habitats at multiple spatial scales. This tool allows land managers to better depict and evaluate risks and decide where to focus specific management activities to promote successional trajectories that are consistent with achieving desired processes, species, and conditions (see Table 1; Chambers et al., 2014c). Management strategies can be linked directly to the cells in the matrix.

Areas with high landscape cover of sagebrush generally have high conservation value and are priorities for management designed to maintain and enhance ecosystem connectivity and functioning. Management strategies in and adjacent to these areas can include a diverse set of activities such as reducing anthropogenic disturbances, managing conifer expansion, or suppressing fires (see Table 1). Areas with lower resilience and resistance are slower to recover following fire and surface disturbances and are more susceptible to invasive plant species than areas with higher resilience and resistance. Consequently, these areas are at greater risk of long-term habitat loss and are among the highest priorities for fire suppression and implementing fuels reduction strategies (Chambers et al., 2014c, in press).

Areas with moderate landscape cover of sagebrush have lower habitat connectivity and may exhibit declining ecological conditions due to invasion of annual grasses, conifer expansion, and fires outside of the HRV. These areas are priorities for management designed to increase ecosystem functioning and prevent conversion to undesirable alternative states (Chambers et al., 2014a, 2014c). Management strategies may focus on managing for perennial native herbaceous species, decreasing the risk of nonnative species establishment and spread, and reducing the risk of wildfires outside of the HRV (see Table 1). The relative resilience and resistance of an area strongly influences its response to management activities and the risk of nonnative annual grass invasion. Areas with lower resilience and resistance may still be among the highest priorities for management, but they often require greater investment and repeated interventions to achieve management objectives.

Areas with low landscape cover of sagebrush are generally low priority for management interventions. It may still be possible to enhance

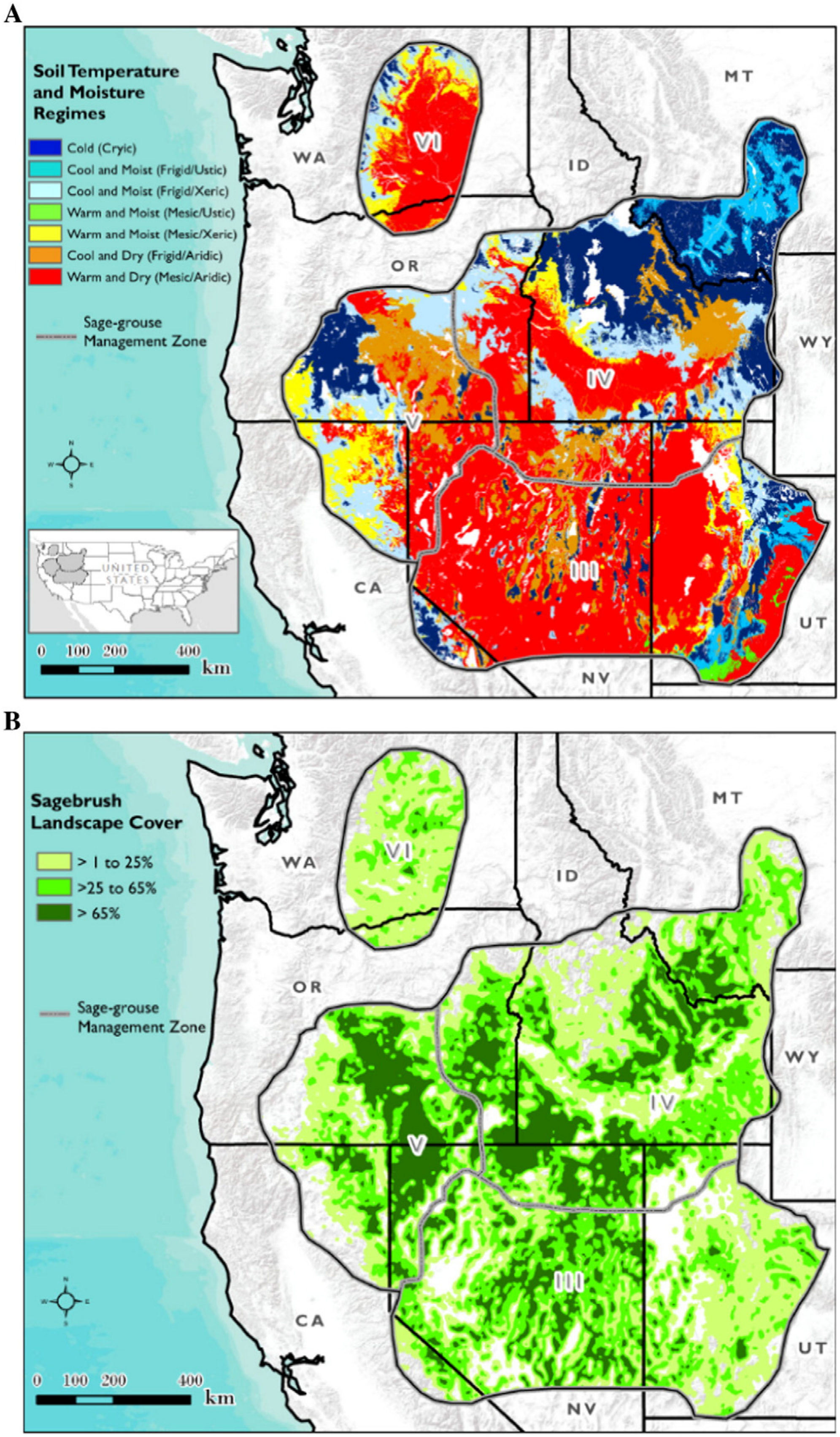
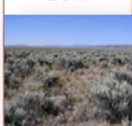


Figure 3. A, Soil temperature and moisture regimes (Maestas et al., 2016a) for sage-grouse management zones (MZs) III−VI (Stiver et al. 2006). **B,** Sagebrush landscape cover for MZs III−VI calculated as the proportion of sagebrush landscape cover relative to other land cover types within each of three classes in a 5-km (3.1-mi) radius surrounding each pixel (Knick et al., 2013; USGS, 2013).

Table 2
Decision support matrix linking ecosystem resilience and resistance with sage-grouse habitat for sagebrush ecosystems in the species' western range. Rows provide information on restoration/recovery potential of ecological types with relatively high, moderate, and low resilience and resistance (mountain big sagebrush/mountain brush, mountain big sagebrush, and Wyoming big sagebrush, respectively). Columns provide information on amount of time and types of intervention required to increase sagebrush cover and probability of sage-grouse persistence for large areas with low (< 25%), medium (25 — 65%), and high (> 65%) landscape cover (percentage area) of sagebrush.

Proportion of Landscape Dominated by Sagebrush

Resilience & Resistance of Sagebrush Ecosystem

	Low = < 25%	*Moderate = 25–65%*	*High = > 65%*
High 	**RESTORATION/RECOVERY POTENTIAL HIGH** *Native grasses and forbs often sufficient for recovery after disturbance* *Risk of annual invasive grasses becoming dominant is low* *Seeding/transplanting success typically high*		
	Longer timeframe for recovery may require moderate intervention	Some intervention to enhance connectivity and improve function	Minimal intervention; preventative management to maintain function
Moderate 	**RESTORATION/RECOVERY POTENTIAL VARIABLE** *Native grasses and forbs often adequate for recovery after disturbance* *Risk of annual invasive grasses becoming dominant is moderate* *Seeding/transplanting success depends on site characteristics*		
	Longer timeframe for recovery likely requires moderate-to-high intervention	Moderate intervention to minimize invasive risks, enhance connectivity, and improve function	Some intervention needed to minimize risk of invasion; preventative management to maintain function
Low 	**RESTORATION/RECOVERY POTENTIAL LOW** *Native grasses and forbs often inadequate for recovery after disturbance* *Risk of annual invasive grasses becoming dominant is high* *Seeding/transplanting may require multiple interventions*		
	Recovery unlikely without significant intervention over long timeframe	High intervention to minimize invasive risks, enhance connectivity, and improve function	Moderate-to-high amount of intervention to minimize risk of invasion and maintain and enhance function

ecosystem functioning and landscape connectivity, but careful assessment of the area will be required to determine if it has the potential for enhancement or supports important landscape components like brood-rearing habitat. If anthropogenic threats such as oil and gas development or cropland conversion are causing the reduction in sagebrush land cover, then increasing ecosystem functioning may not be feasible. However, if reduced land cover of sagebrush is due to persistent ecosystems threats, such as altered fire regimes or conifer expansion, it may be possible to strategically increase ecosystem functioning through appropriate management strategies. The degree of difficulty and time required increase as resilience and resistance decrease, and areas with relatively low resilience and resistance and low landscape cover of sagebrush may no longer have capacity to support sage-grouse or may be so altered that they are lower priority for allocation of limited conservation resources. Managers may decide to actively manage these areas but must recognize that substantial investment and repeated interventions may be required to achieve objectives. Careful assessment of the area of concern will always be necessary to determine the relevance of a particular strategy because sagebrush ecosystems occur over continuums of environmental conditions, such as soil temperature and moisture, and have differing land use histories and species composition (Pyke, 2011; Miller et al., 2014, 2015). Also, areas with low greater sage-grouse breeding habitat probabilities may support other resource values or at-risk species (Rowland et al., 2006) that could benefit from management strategies designed to improve habitat. Knowledge of the locations of other priority resources and at-risk species and their response to management treatments can help ensure that treatments are located and strategies are implemented in a manner that will also benefit these other resources and species.

Focal Areas for Management

Escalating numbers of at-risk species with large-scale persistent threats, amid ever limited budgets, requires a conservation triage approach that prioritizes resource allocation to maximize ecological return-on-investment (Wiens et al., 2012). Triage for addressing invasive species and wildfire threats to sagebrush ecosystems and sage-grouse builds on resilience, resistance, and species habitat information by explicitly incorporating additional information on known population concentration centers (Chambers et al., 2014c). Primary objectives are to maintain or increase large contiguous areas of sagebrush habitat that are resilient to disturbance and resistant to invasive annual grass conversion within the foreseeable future (i.e., 20 — 30 yr; USFWS, 2015).

Sage-grouse Priority Areas for Conservation (PACs) have been delineated using available habitat and population data to identify areas critical for conserving sage-grouse populations (USFWS, 2013) and can be used as a first filter in prioritizing management actions. Habitats outside of PACs are also important considerations where they provide genetic and habitat linkages and capture important seasonal habitats (USFWS, 2013). Further prioritization can be achieved by mapping high-abundance breeding areas. Sage-grouse breeding bird density areas can be modeled using lek counts to spatially depict the relative percentage of the known breeding population across large landscapes (Doherty et al., 2010b; Doherty et al., in press). Although breeding concentration centers do not encompass all seasonal habitat use areas, they provide a starting point for triage to address threats to breeding habitats supporting high numbers of birds.

Coupling breeding bird density areas with resilience and resistance as indicated by soil temperature and moisture regimes provides a key

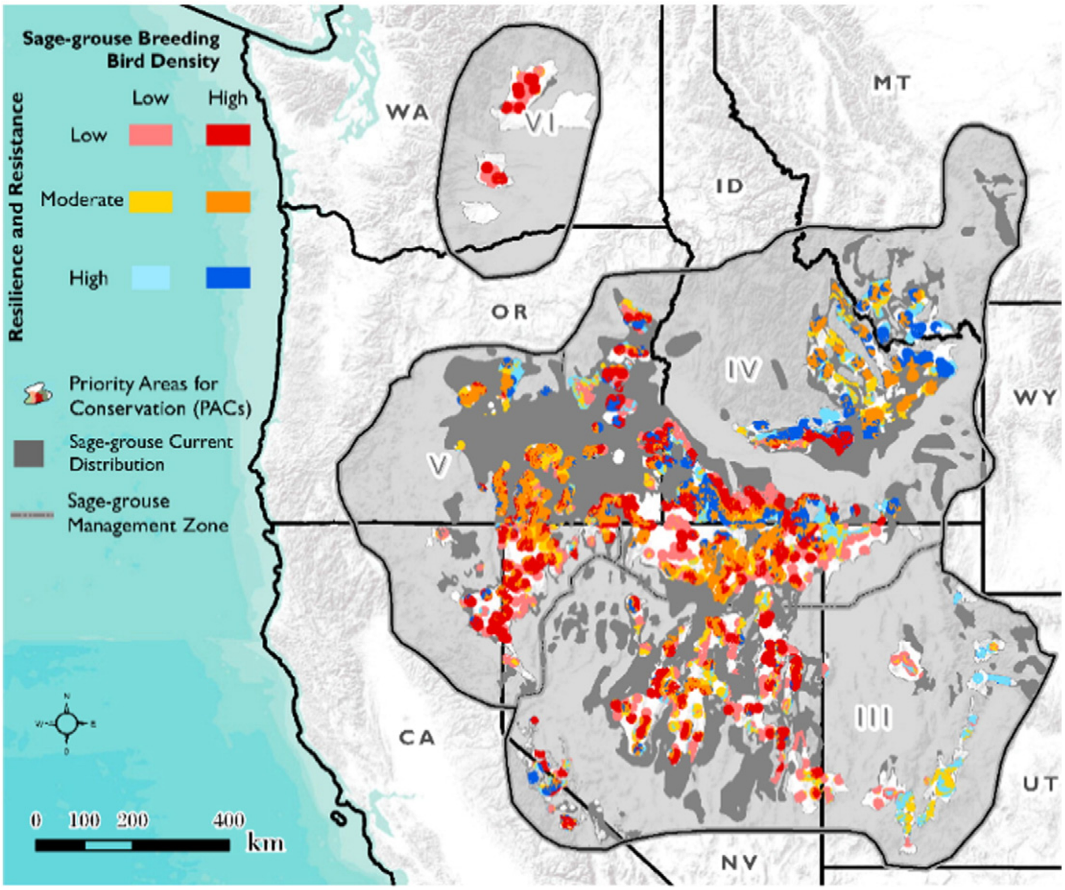


Figure 4. Sage-grouse breeding bird densities (BBDs; Doherty et al., 2010b) relative to resilience and resistance in priority areas for conservation (USFWS, 2013) for sage-grouse management zones III—VI (Stiver et al. 2006). High BBD = areas that contain 75% of known breeding bird populations; low BBD = areas that contain all remaining breeding bird populations. Resilience and resistance classes were derived from soil moisture and temperature regimes (Maestas et al., 2016a) and follow Chambers et al. (2014c).

layer that depicts landscapes with high bird concentrations that differ in the relative risk of being negatively affected by fire and invasive annual grasses at regional scales (Fig. 4). For prioritization purposes, areas supporting 75% of breeding birds can be categorized as relatively high density, while areas supporting the remaining 25% can be categorized as relatively low density (Chambers et al., 2014c). Similarly, warm and dry soils can be classified as having relatively low resilience to disturbance and resistance to invasive annual grasses, cool to cold and moist soils as having high resilience and resistance, and intermediate soil temperatures and moistures as having moderate resilience and resistance.

Additional data and layers can further inform the triage process. Evaluating resilience and resistance in conjunction with landscape cover of sagebrush and the distribution and magnitude of threats, such as invasive annual grass extent or conifer expansion areas, provides the necessary information to identify those locations on the landscape where management can be used to maintain or increase both landscape connectivity and ecosystem functioning. Similarly, fire probability maps and wildfire perimeter data can help identify areas that have developed or are at risk of developing altered fire regimes (Fig. 5). Evaluating each of these factors—resilience and resistance, landscape cover of sagebrush, and landscape cover of invasive annual grasses, conifer expansion, and/or fire risk—in combination with breeding concentration areas ensures that appropriate management actions are focused on areas that currently support viable populations, have the potential to increase habitat connectivity, or are close enough to breeding concentration areas that populations can recolonize reclaimed habitats (Fig. 6). Higher-resolution land cover data for sagebrush ecosystems, invasive annual grasses, and conifers, as well as more detailed data on sage-grouse populations and habitat use, can be used to further refine focal areas at local scales.

These data layers along with the sage-grouse habitat matrix (see Table 2) and management strategies provide a first step in prioritizing management activities such as wildland fire management, postfire rehabilitation, fuels management, and habitat restoration across large landscapes such as ecoregions or agency planning units (USDI BLM, 2014). Once potential priority areas are identified, land managers use higher-resolution spatial data along with local information and knowledge of other factors, such as seasonal sage-grouse habitat use and site conditions, to identify specific project areas. On the ground, general steps in the process involve assessing potential project areas to 1) identify the different ecological sites that occur across the area and determine their relative resilience to disturbance and resistance to invasive annual grasses, 2) evaluate the current successional states of the ecological sites and where possible their restoration pathways, and 3) select actions with the potential to increase ecosystem functioning and habitat connectivity (see Miller et al., 2014, 2015; Pyke et al., 2015a, 2015b for detailed descriptions of this process). Anticipating changes like climate warming and monitoring management outcomes can be used to adapt management over time.

Evaluating regional patterns

Large differences exist among sage-grouse management zones (MZs) in resilience and resistance of areas with sagebrush landscape cover that

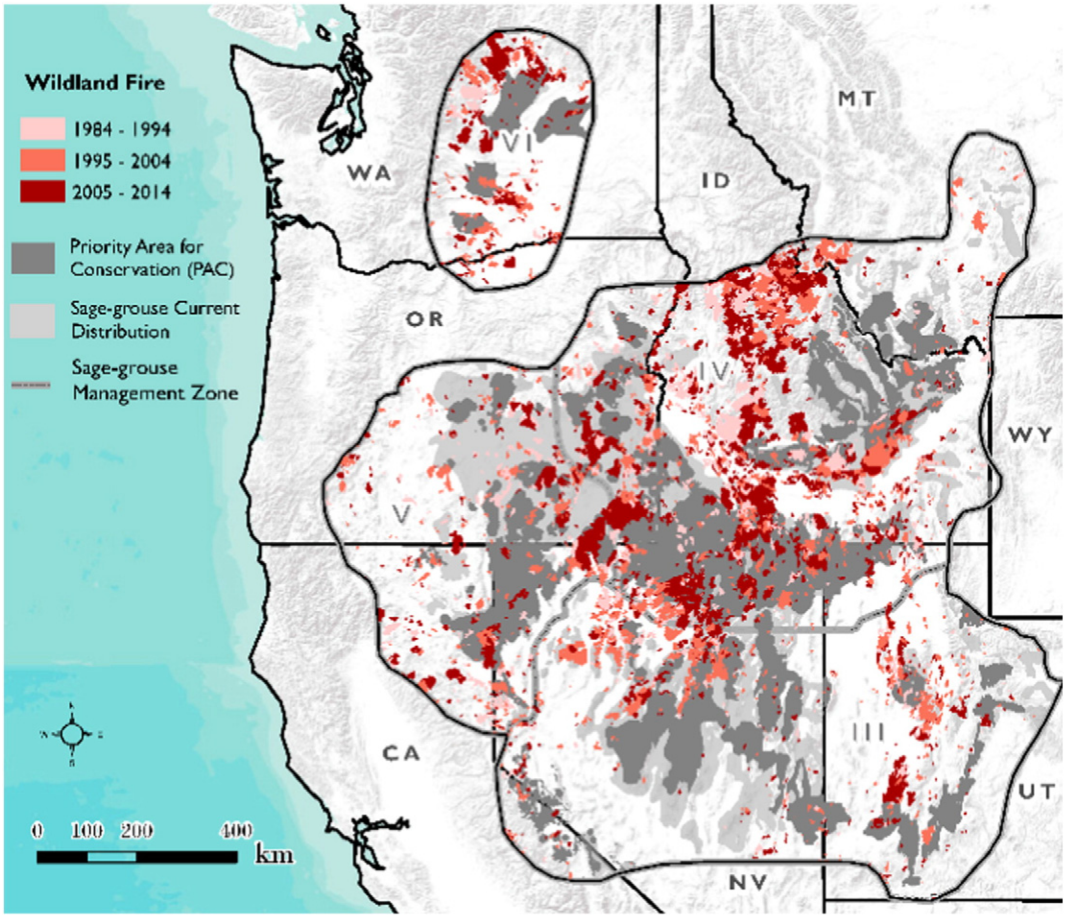


Figure 5. Fire perimeters from 1984 to 2014 (MTBS, 2015) within sage-grouse's current distribution and priority areas for conservation (USFWS, 2013) in management zones III—VI (Stiver et al. 2006).

is sufficient for sage-grouse populations to persist within PACs (Fig. 7A). MZs IV (Snake River Plains) and V (Northern Great Basin) have relatively large extents of sagebrush landscape cover > 65% in cool and moist areas with moderate to high resilience and resistance (37% and 35%, respectively); when sagebrush landscape cover > 25% in moderate to high resilience and resistance is considered, the areas increase (58% and 48%, respectively). In contrast, MZ III (Southern Great Basin) has relatively small extents of sagebrush landscape cover > 65% in cool and moist areas (7%) and MZ VI (Columbia Basin) has no areas in this category. When sagebrush landscape cover > 25% with moderate to high resilience and resistance is considered, values for MZ III increase (33%) but are the lowest (3%) for MZ VI.

Areas within PACs that have cool to cold soil temperature regimes, moist precipitation regimes, and moderate to high resilience and resistance are typically characterized by mountain big sagebrush, low sagebrush, or other mountain brush species. These areas have low risk of conversion to invasive annual grasses, are likely to recover in a reasonable amount of time following wildfires and other disturbances with minimal intervention (Miller et al., 2013), and are expected to be more resilient to climate change. They may still be at risk due to piñon and juniper expansion, and ecosystem functioning and habitat connectivity may be increased by removal of trees in expansion areas. Areas with warm to cool soil temperature regimes and moist precipitation regimes have moderate to moderately low resilience and resistance and are characterized largely by either Wyoming or mountain big sagebrush. Risk of conversion to annual grasses depends on site characteristics and is typically lower, but many of these areas are at risk of conversion to tree dominance (Miller et al., 2013). These areas require careful assessment after disturbances to determine the type of intervention, if any, and may benefit from tree removal.

All MZs have relatively large areas of sagebrush landscape cover > 25% in warm and dry areas with low resilience and resistance (see Fig. 7A; MZ IV = 30%; MZ V = 39%, MZ III = 46%; MZ VI = 34%). For MZ VI, a relatively high percentage of land area has < 25% sagebrush landscape cover. These warm and dry areas are typically characterized by Wyoming big sagebrush ecosystems with minor components of basin big sagebrush and are at greatest risk of conversion to annual grasses after wildfire. Repeated management intervention may be necessary to restore resilience and resistance in these areas (see Fig. 3; Miller et al., 2014; Chambers et al., 2014b).

Climate change and other human-induced factors, including more extreme fire weather, invasive annual grasses, and human-caused fire starts, are resulting in not only increases in fire area but also individual fires of unprecedented size (McKenzie et al., 2004; Brooks et al., 2015). Our analyses show that since 1984, 1 640 fires over 1 000 acres have burned within PACs, but just 17 of these fires accounted for 25% of the area burned.

A primary driver of change in sagebrush landscape cover is wildfire (see Fig. 5), and about 16% of the total area within PACs has burned one or more times in the past 30 years. Percentage fire area has been highest for MZs IV and V (21% and 20%, respectively), intermediate for MZ VI (14%), and lowest for MZ III (7%) (Fig. 7B). In all MZs a relatively high

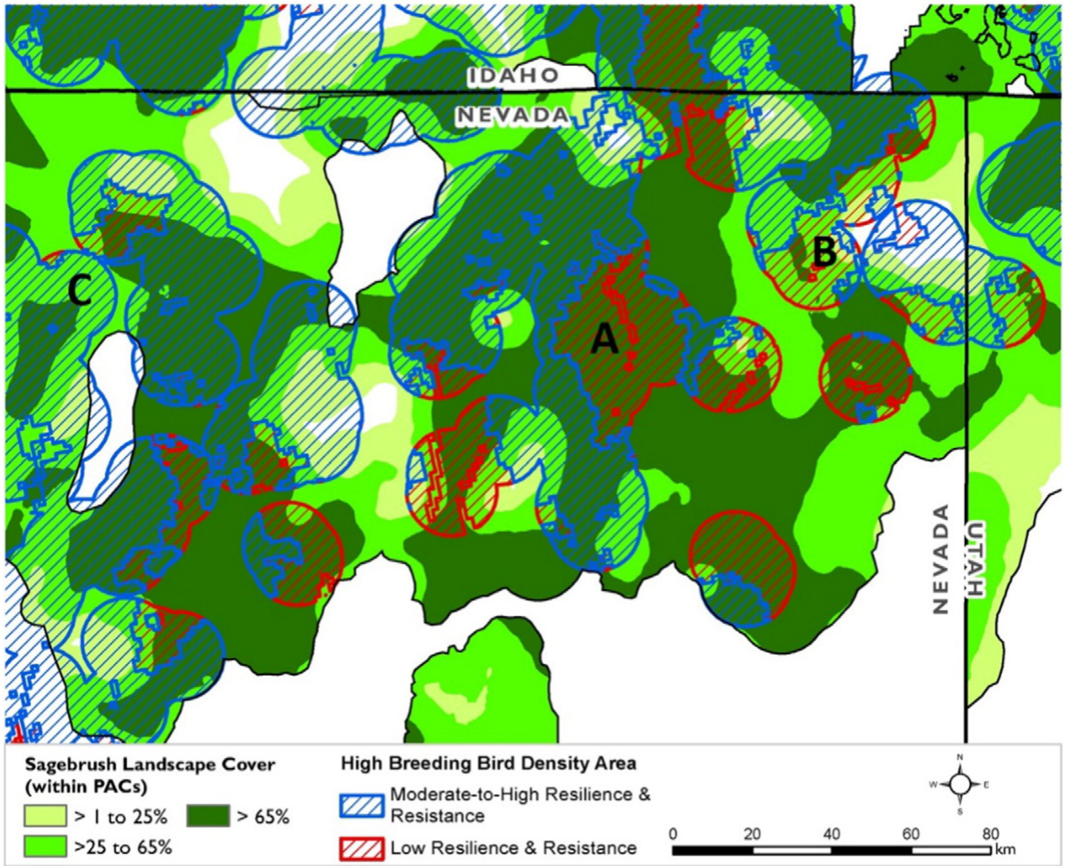


Figure 6. Sagebrush landscape cover intersected with areas of high sage-grouse breeding bird densities and moderate/high or low resilience and resistance for the northeast corner of Nevada. Combining this information with other local data and knowledge of threats helps land managers quickly identify and prioritize potential focal areas and management strategies, such as **A,** prepositioning of firefighting resources and proactive fuels management, **B,** multiyear postfire rehabilitation and invasive species control, and **C,** reduction of fuels due to conifer expansion. Sagebrush landscape cover was calculated as the proportion of sagebrush landscape cover within each of three classes as in Figure 2B. Sage-grouse breeding bird densities relative to resilience and resistance were calculated as in Figure 3.

percentage of total fire area (≥ 35%) has been in the low-resilience and low-resistance categories. Also, percentage of fire area within each resilience and resistance category has been highly similar to total area of sagebrush landscape cover within each category (< 5% difference) for all but MZ VI (see Fig. 7B; Tables A1 and A2). Historically, areas with low resilience and resistance typified by Wyoming big sagebrush burned less frequently than higher resilience and resistance areas characterized by mountain big sagebrush and mountain brush due to lower productivity and thus lower fuel loads (Miller et al., 2013). Our analyses indicate that these low-resilience and low-resistance areas appear to be burning at least as frequently as the higher-resilience and higher-resistance areas.

Policy and management applications

Our framework provides a transparent, ecologically defensible approach for making policy and management decisions to increase ecosystem resilience and resistance and reduce persistent threats at multiple scales. US federal land management and natural resource agencies are using this risk-based framework for prioritizing sage-grouse conservation resources at national and regional scales and for developing more ecologically effective wildland fire operations, postfire rehabilitation, fuels management, and habitat restoration strategies (USDI BLM, 2014; USDI, 2015; USDA NRCS, 2015a). Specifically, agencies used the framework to develop the Fire and Invasives Assessment Tool (FIAT)—a spatially explicit decision process that now informs strategic management actions designed to address the effects of invasive annual grasses, conifer expansion, and wildfires outside of the HRV and maintain or enhance ecosystem processes and functioning in sagebrush ecosystems and sage-grouse habitat (USDI BLM, 2014). For example, intact sagebrush landscapes supporting high breeding sage-grouse density with relatively low resilience and resistance have become priorities for 1) prepositioning firefighting resources to prevent ecosystem conversion to invasive annual grasses, 2) implementing fuel management treatments to decrease fire severity and extent and limit negative consequences of future wildfires, and 3) postfire rehabilitation and habitat improvement to restore native ecosystem structure and function (USDI BLM, 2014). Similarly, sagebrush habitats with moderate to high sagebrush land cover, higher resilience and resistance, and viable populations of birds are high priority for managing conifer expansion areas to prevent large-scale ecosystem fragmentation and/or rapid ecosystem conversion to undesirable alternative states (Miller et al., 2013).

Postfire rehabilitation programs and policies have also been improved to allow for prompt and sustained investment to reestablish desired vegetation, especially in priority habitats with low resilience and resistance where multiple interventions may be needed (USDI, 2015). A new national seed strategy for restoration and rehabilitation will help to ensure that the necessary native seed sources and quantities are available for rehabilitation and restoration activities (Native Plant Alliance, 2015). Incorporating our risk-based approach into agency land use planning helped decision makers provide the scientific

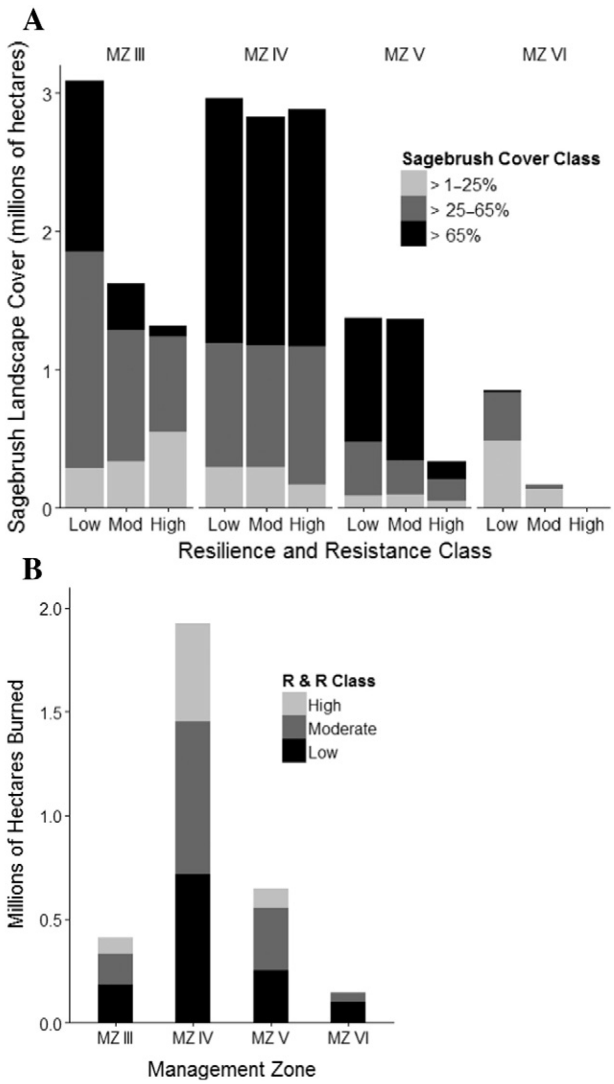


Figure 7. A, Sagebrush landscape cover within low, moderate, and high resilience and resistance classes for sage-grouse priority areas for conservation (PACs, USFWS, 2013) in management zones III—VI (Stiver et al. 2006). Resilience and resistance classes were derived from soil moisture and temperature regimes (Maestas et al., 2016a) and follow Chambers et al. (2014c). Sagebrush landscape cover was calculated as the proportion of sagebrush landscape cover within each of three classes in a 5-km (3.1-mi) radius surrounding each pixel relative to other land cover types (Knick et al., 2013; USGS, 2013). **B,** Total land area burned from 1984 to 2014 within PACs in MZs III—VI by resilience and resistance (R & R) class. Land area burned was obtained from fire perimeter data (MTBS, 2015). Resilience and resistance classes were derived from soil moisture and temperature regimes (Maestas et al., 2016a) and follow Chambers et al., (2014c).

rationale to affect policy change and funding levels, thereby equipping local land managers with resources needed to be more successful. However, agency leaders remain challenged with ensuring that adequate flexibility and funding are provided to local managers to respond to the dynamic nature of these problems and often narrow windows of opportunity to affect change.

Practitioners are also incorporating resilience science into project-level planning with the help of new field guides and tools (Miller et al., 2014, 2015; Pyke et al., 2015a, 2015b). At local land management scales, our framework provides ecosystem and species-specific context for evaluating potential project areas and anticipating project-scale vegetation responses to disturbance and planned land treatments. Spatially depicting the sage-grouse habitat resilience and resistance matrix in a geographic information system served as a key visual aid for FIAT interagency teams to rapidly identify potential project areas and select appropriate management strategies (USDI BLM, 2014). Field tools assist land managers in assessing risks based on resilience and resistance concepts and designing management prescriptions to promote desired successional trajectories and increase ecosystem functioning using information from Ecological Site Descriptions and on-site inventories of soil properties, current or potential vegetation, and wildfire or treatment severity (Miller et al., 2014, 2015; Pyke et al., 2015a, 2015b; USDA NRCS, 2015b). Importantly, resilience science at the project scale helps focus management and monitoring discussions on key variables influencing the capacity to maintain basic ecological function without crossing thresholds to undesired states. For example, maintaining or improving perennial native grass abundance becomes an overarching goal for all management decisions because of its disproportionate role in maintaining sagebrush ecosystem resilience and resistance (Chambers et al., 2007, 2014a, 2014b; Reisner et al., 2013, 2015).

Practical application of our risk-based approach helped to address persistent threats to sage-grouse and sagebrush ecosystems in the western portion of the species range (USDI BLM, 2014) and played a crucial role in range-wide efforts to preclude the need for federal species protections (USFWS, 2015). The approach has recently been applied to the eastern portion of the sage-grouse range (i.e., Northwestern Glaciated Plains, Northwestern Great Plains, Wyoming Basins, Colorado Plateau, Middle and Southern Rockies, US EPA, 2016) (Chambers et al., in press) and has been updated to incorporate newly developed information on sage-grouse breeding habitat probabilities (Doherty et al., in press). Operationalizing resilience and resistance concepts in the context of sage-grouse conservation has provided, for the first time, a nuanced examination of wildfire and invasive annual grass threats, a common basis for communicating relative risks, and a strategic path forward to minimize impacts over time. This new applied framework allowed federal regulators considering protections for sage-grouse under the ESA to more effectively assess the likelihood of species and habitat persistence, gain confidence that threats can be ameliorated over time using an ecologically based approach, and ultimately determine that the species no longer warranted regulatory protection (USFWS, 2015).

Implications

We successfully operationalized resilience and resistance concepts in a risk-based framework to help managers reduce persistent threats to a species of high concern in one of the largest terrestrial ecosystems in North America. By linking our understanding of sagebrush ecosystem resilience to disturbance and resistance to invasive annual grasses to sage-grouse distribution and habitat requirements, we provided a means for decision makers to strategically allocate resources and triage complex problems. This approach offers an innovative decision support system to address the needs of at-risk species in the context of dynamic and adaptive ecosystems. We believe this approach is applicable to species conservation in other largely intact ecosystems with persistent, ecosystem-based threats such as invasive species and altered disturbance regimes.

Acknowledgments

We thank the Western Association of Fish and Wildlife Agencies, Fire and Invasive Working Group, especially Kenneth E. Mayer, Steven Campbell, Shawn Espinosa, Douglas W. Havlina, and Steven T. Knick for assistance in developing this approach. Jeffrey L. Beck and Christian A. Hagen provided manuscript review. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government.

Appendix A

Table A.1
The amount and relative proportion (%) of hectares within each sagebrush landscape cover and resilience and resistance class within the occupied range of sage-grouse and within priority areas for conservation (PACs) by management zone (MZ) and across all MZs.

	MZ III		MZ IV		MZ V		MZ VI		Total	
	ha	%	ha	%	ha	%	ha	%	ha	%
Occupied Range										
Low R&R										
1-25%	986 285	16%	822 682	15%	174 692	7%	268 195	70%	2 251 853	15%
26-65%	3 186 818	51%	1 910 371	36%	902 342	34%	97 097	25%	6 096 628	41%
> 66%	2 015 088	32%	2 274 593	42%	1 527 449	57%			5 817 129	40%
Total	6 282 162	61%	5 361 216	37%	2 666 089	39%	381 778	81%	14 691 245	46%
Moderate R&R										
1-25%	427 068	19%	580 983	14%	192 291	6%	66 836	82%	1 267 177	13%
26-65%	1 334 514	61%	1 570 306	38%	753 055	24%	9 785	12%	3 667 661	39%
> 66%	416 391	19%	1 849 462	45%	2 070 969	67%		0%	4 336 822	46%
Total	2 190 999	21%	4 136 514	29%	3 095 549	45%	81 707	17%	9 504 769	30%
High R&R										
1-25%	581 694	39%	694 318	15%	268 735	30%	1 486	95%	1 546 232	22%
26-65%	828 101	55%	2 105 789	45%	402 560	46%	82	5%	3 336 531	48%
> 66%	88 082	6%	1 726 804	37%	179 251	20%		0%	1 994 137	28%
Total	1 502 872	15%	4 631 784	32%	882 731	13%	1 572	0%	7 018 959	22%
Grand Total	10 257 273		14 461 918		6 915 323		473 748		32 108 262	
PACs										
Low R&R										
1-25%	283 757	9%	295 996	10%	88 731	6%	490 108	56%	1 158 592	14%
26-65%	1 565 117	51%	897 624	29%	387 142	27%	347 732	40%	3 197 615	38%
> 66%	1 240 310	40%	1 774 202	57%	898 009	63%	14 677	2%	3 927 198	46%
Total	3 090 375	50%	3 088 762	34%	1 420 656	43%	876 286	82%	8 476 079	43%
Moderate R&R										
1-25%	338 171	21%	294 680	10%	100 811	7%	136 800	79%	870 462	14%
26-65%	948 293	58%	882 436	30%	246 359	17%	30 666	18%	2 107 754	34%
> 66%	336 729	21%	1 653 660	56%	1 021 117	71%	383	0%	3 011 889	49%
Total	1 623 632	26%	2 938 121	32%	1 442 323	44%	173 039	16%	6 177 114	31%
High R&R										
1-25%	552 955	42%	165 620	6%	45 975	13%	1 755	70%	766 304	17%
26-65%	685 815	52%	1 002 851	34%	161 406	44%	763	30%	1 850 835	40%
> 66%	82 638	6%	1 715 446	59%	127 843	35%			1 925 927	42%
Total	1 324 246	21%	2 930 033	32%	364 253	11%	2 522	0%	4 621 054	24%
Grand Total	6 165 010		9 135 215		3 269 208		1 074 894		19 644 326	

Table A.2
Total number and relative proportion (%) of hectares that have burned one or more times from 1984 through 2014 within the occupied range of sage-grouse and within priority areas for conservation (PACs) by resilience and resistance (R&R) class for each management zone (MZ) and across all MZs.

	MZ III		MZ IV		MZ V		MZ VI		Total	
	ha	%	ha	%	ha	%	ha	%	ha	%
Occupied Range										
Low R&R	602 983	58	1 582 439	48	401 501	37	41 489	63	2 628 412	48
Moderate R&R	346 637	33	1 037 201	31	487 441	45	23 349	35	1 894 628	34
High R&R	90 527	9	690 019	21	175 014	16	895	1	956 454	17
Total fire area	1 044 856		3 333 083		1 076 515		65 969		5 520 424	
Total fire area in MZ (%)		10		23		16		14		
PACs										
Low R&R	185 497	45	714 234	37	254 021	39	99 867	67	1 253 619	40
Moderate R&R	147 009	36	736 169	38	299 286	46	46 676	31	1 229 139	39
High R&R	76 263	19	476 657	25	94 490	15	999	1	648 409	21
Total fire area	410 099		1 937 160		650 059		149 570		3 146 888	
Total fire area in PACs (%)		7		21		20		14		

References

Abatzoglou, J.T., Kolden, C.A., 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. Rangeland Ecology & Management 64, 471–478.

Aldridge, C.L., Hanser, S.E., Nielsen, S.E., Leu, M., Cade, B.S., Saher, D.J., Knick, S.T., 2011. Chapter 6: Detectability adjusted count models of songbird abundance. In: Hanser, S.E., Leu, M., Knick, S.T., Aldridge, C.L. (Eds.), Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, KS, USA, pp. 141–220.

Aldridge, C.L., Nielsen, S.E., Beyer, H.L., Boyce, M.S., Connelly, J.W., Knick, S.T., Schroeder, M.A., 2008. Range-wide patterns of greater sage-grouse persistence. Diversity Distribution 14, 983–994.

Allen, C.R., Angeler, D.G., Cumming, G.S., Folke, C., Twidwell, D., Uden, D.R., 2016. Quantifying spatial resilience. Journal of Applied Ecology 53, 625–635.

Angeler, D.G., Craig, R., Allen, C.R., 2016. Quantifying resilience. Journal of Applied Ecology 53, 617–624.

Arredondo, J.T., Jones, T.A., Johnson, D.A., 1998. Seedling growth of Intermountain perennial and weedy annual grasses. Journal of Range Management 51, 584–589.

Baker, W.H., 2011. Pre–Euro-American and recent fire in sagebrush ecosystems. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse—ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA, USA, pp. 185–201.

Balch, J.K., Bradley, B.A., D'Antonio, C.M., Mez-Dans, J., 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology 19, 173–183.

Baruch-Mordo, S., Evans, J.S., Severson, J.P., Naugle, D.E., Maestas, J.D., Kiesecker, J.M., Falkowski, M.J., Hagen, C.A., Reese, K.P., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biology Conservation 167, 233–241.

Bestelmeyer, B.T., Tugel, A.J., Peacock, G.L.J., Robinett, D.G., Shaver, P.L., Brown, J.R., Herrick, J.E., Sanchez, H., Havstad, K.M., 2009. State-and transition models for heterogeneous landscapes: a strategy for development and application. Rangeland Ecology & Management 62, 1–15.

Bestelmeyer, B.T., Goolsby, D.P., Archer, S.R., 2011. Spatial perspectives in state-and-transition models: a missing link to land management? Journal of Applied Ecology 2011, 746–757.

Blomberg, E.J., Sedinger, J.S., Atamian, M.T., Nonne, D.V., 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3, 55.

Boyd, C.S., Johnson, D.D., Kerby, J.D., Svejcar, T.J., Davies, K.W., 2014. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? Rangeland Ecology & Management 67, 358–368.

Bradley, B.A., 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology 15, 196–208.

Bradley, B.A., Curtis, C.A., Chambers, J.C., 2016. *Bromus* response to climate and projected changes with climate change. In: Germino, M.J., Chambers, J.C., Brown, C.S. (Eds.), Exotic brome-grasses in arid and semi-arid ecosystems of the Western US: causes, consequences and management implications. Springer, New York, NY, USA, pp. 257–274.

Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2005. State-and-transition models, thresholds, rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecology Management 58, 1–10.

Briske, D.D., Bestelmeyer, B.T., Stringham, T.K., Shaver, P.L., 2008. Recommendations for development of resilience-based state-and-transition models. Rangeland Ecology & Management 61, 359–367.

Brooks, M.L., Minnich, R.A., 2006. Southeastern deserts bioregion. In: Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), Fire in California's ecosystems. University of California Press, Berkeley, CA, USA, pp. 391–414.

Brooks, M.L., Matchett, J.R., Shinneman, D.J., Coates, P.S., 2015. Fire patterns in the range of greater sage-grouse, 1984–2013—Implications for conservation and management. Open-File Report 2015-1167. US Geological Survey. (66 p. Available at:) http://dx.doi.org/10.3133/ofr20151167 Accessed 13 June 2016.

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

Casazza, M.L., Coates, P.S., Overton, C.T., 2011. Linking habitat selection and brood success in greater sage-grouse. In: Sandercock, B.K., Martin, K., Segelbacher, G. (Eds.), Ecology, conservation, and management of grouse. Studies in Avian Biology 39. University of California Press, Berkeley, CA, USA, pp. 151–167.

Caudle, D., DiBenedetto, J., Karl, M., Sanchez, H., Talbot, C., 2013. Interagency ecological site handbook for rangelands. Available at: http://jornada.nmsu.edu/sites/jornada.nmsu.edu/files/InteragencyEcolSiteHandbook.pdf Accessed 24 April 2016.

Chambers, J.C., Pellant, M., 2008. Climate change impacts on Northwestern and Intermountain US rangelands. Rangelands 30, 29–33.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77, 117–145.

Chambers, J.C., Bradley, B.A., Brown, C.A., D'Antonio, C., Germino, M.J., Hardegree, S.P., Grace, J.B., Miller, R.F., Pyke, D.A., 2014a. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in the cold desert shrublands of western North America. Ecosystems 17, 360–375.

Chambers, J.C., Miller, R.F., Board, D.I., Grace, J.B., Pyke, D.A., Roundy, B.A., Schupp, E.W., Tausch, R.J., 2014b. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangeland Ecology & Management 67, 440–454.

Chambers, J.C., Pyke, D.A., Maestas, J.D., Pellant, M., Boyd, C.S., Campbell, S.B., Espinosa, S., Havlina, D.W., Mayer, K.E., Wuenschel, A., 2014c. Using resistance and resilience concepts to reduce impacts of annual grasses and altered fire regimes on the sagebrush ecosystem and sage-grouse—a strategic multi-scale approach. Gen. Tech. Rep. RMRS-GTR-326. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

Chambers, J.C., Germino, M.J., Belnap, J., Brown, C.S., Schupp, E.W., Clair, S.B.S., 2016. Plant community resistance to invasion by *Bromus* species—the role of community attributes, *Bromus* interactions with plant communities and *Bromus* traits. In: Germino, M.J., Chambers, J.C., Brown, C.S. (Eds.), Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, New York, NY, USA, pp. 275–306.

Chambers, J. C., J. L. Beck, S. Campbell, J. Carlson, T. J. Christiansen, K. J. Clause, J. B. Dinkins, K. E. Doherty, K. A. Griffin, D. W. Havlina, K. F. Henke, J. D. Hennig, L. L. Kurth, J. D. Maestas, M. Manning, K. E. Mayer, B. A. Mealor, C. McCarthy, M. A. Perea, D. A. Pyke [in press]. Using resilience and resistance concepts to manage threats to sagebrush ecosystems, Gunnison sage-grouse, and greater sage-grouse in their eastern range: a strategic multi-scale approach. Gen. Tech. Rep. RMRS-GTR-000. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Condon, L., Weisberg, P.L., Chambers, J.C., 2011. Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. International Journal of Wildland Fire 20, 1–8.

Connelly, J.W., Rinkes, E.T., Braun, C.E., 2011. Characteristics of Greater Sage-Grouse habitats: a landscape species at micro- and macroscales. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology. University of California Press, Berkeley, CA, USA, pp. 69–83.

Cumming, G.S., 2011. Spatial resilience: integrating landscape ecology, resilience, and sustainability. Landscape Ecology 26, 899–909.

Curtin, C.G., Parker, J.P., 2014. Foundations of resilience thinking. Conservation Biology 4, 912–923.

D'Antonio, C.M., Thomsen, M., 2004. Ecological resistance in theory and practice. Weed Technology 18, 1572–1577.

Davies, K.F., Harrison, S., Safford, H.D., Viers, J.H., 2007. Productivity alters the scale dependence of the diversity-invasibility relationship. Ecology 88, 1940–1947.

Davies, G.M., Bakker, J.D., Dettweiler-Robinson, E., Dunwiddie, P.W., Hall, S.A., Downs, J., Evans, J., 2012. Trajectories of change in sagebrush-steppe vegetation communities in relation to multiple wildfires. Ecological Applications 22, 1562–1577.

Davies, K.W., Boyd, C.S., Nafus, A.M., 2013. Restoring the sagebrush component in crested wheatgrass–dominated communities. Rangeland Ecology & Management 66, 472–478.

Doherty, K. E, J. S. Evans, P. S. Coates, L. Juliusson, and F. C. Fedy [in press]. Importance of regional variation in conservation planning: a range-wide example of the Greater Sage-grouse. Ecosphere.

Doherty, K.E., Naugle, D.E., Walker, B.L., 2010a. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74, 1544–1553.

Doherty, K.E., Tack, J.D., Evans, J.S., Naugle, D.E., 2010b. Mapping breeding densities of greater sage-grouse: a tool for range-wide conservation planning. BLM completion report: Agreement # L10PG00911.

Donnelly, J. P., J. D. Tack, K. E. Doherty, D. E. Naugle, B. W. Allred, and V. J. Dreitz [in press]. Extending conifer removal and landscape protection strategies from sage-grouse to songbirds, a range-wide assessment. Rangeland Ecology & Management.

Eckert, R.E., Peterson, F.F., Meurisse, M.S., Stephens, J.L., 1986. Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. Journal of Range Management 39, 414–420.

Finch, D.M., Pendleton, R.L., Reeves, M.C., Ott, J.E., Kilkenny, F.F., Butler, J.L., Ott, J.P., Pinto, J.R., Ford, P.L., Runyon, J.B., Rumble, M.A., Kitchen, S.G., 2016. In: Vose, J.M., Clark, J.S., Luce, C.H., Patel-Weynard, T. (Eds.), Effects of drought on forests and rangelands in the United States: a comprehensive science synthesis. Gen. Tech. Rep. WO-93b. US Department of Agriculture, Forest Service, Washington Office, Washington, DC, pp. 155–194.

Folke, C., Carpenter, S., Walker, B., Scheffer, M, Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology and Systematics 35, 557–581.

Germino, M.J., Belnap, J., Stark, J.M., Allen, E.B., Rau, B.M., 2016. Ecosystem impacts exotic annual invaders. In: Germino, M.J., Chambers, J.C., Brown, C.S. (Eds.), Exotic brome-grasses in arid and semiarid ecosystems of the Western US: causes, consequences and management implications. Springer, New York, NY, USA, pp. 61–98.

Goble, D.D., Wiens, J.A., Scott, J.M., Male, T.D., Hall, JA, 2012. Conservation-reliant species. Bioscience 62, 869–873.

Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution 24, 599–605.

Holling, C.S., 1973. Resilience and stability in ecological systems. Annual Review of Ecology and Systematics 4, 1–23.

Johnson, D.D., Miller, R.F., 2006. Structure and development of expanding western juniper woodlands as influenced by two topographic variables. Forest Ecology Management 229, 7–15.

Johnson, D.H., Holloran, M.J., Connelly, J.W., Hanser, S.E., Amundson, C.L., Knick, S.T., 2011. Influence of environmental and anthropogenic features on greater sage-grouse populations. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse—ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA, USA, pp. 407–450.

Keane, R.E., Hessburg, P.F., Landres, P.B., Swanson, F.J., 2009. The use of historical range and variability (HRV) in landscape management. Forest Ecology Management 258, 1025–1037.

Kirol, C.P., Beck, J.L., Dinkins, J.B., Conover, M.R., 2012. Microhabitat selection for nesting and brood rearing by the greater sage-grouse in xeric big sagebrush. The Condor 114, 75–89.

Knick, S.T., Hanser, S.E., Miller, R.F., Pyke, M.J., Wisdom, M.J., Finn, S.P., Rinkes, T.E., Henny, C.J., 2011. Ecological influence and pathways of land use in sagebrush. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse—ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA, USA, pp. 203–251.

Knick, S.T., Hanser, S.E., Preston, K.L., 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, U.S.A. Ecology and Evolution 3, 1539–1551.

Leffler, A.J., Ryel, R.J., 2012. Resource pool dynamics: conditions that regulate species interactions and dominance. In: Monaco, T.A., Sheley, R.L. (Eds.), Invasive plant ecology and management. Linking processes to practice. CAB International, Cambridge, MA, USA, pp. 57–78.

Lesica, P., Deluca, T.H., 1996. Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. Journal of Soil and Water Conservation 51, 408–409.

Maestas, J.D., Campbell, S.B., Chambers, J.C., Pellant, M., Miller, R.F., 2016a. Tapping soil survey information for rapid assessment of sagebrush ecosystem resilience and resistance. Rangelands 38 (3), 120–128.

Maestas, J.D., Pellant, M., Okeson, L., Tilley, D., Havlina, D., Cracroft, T., Brazee, B., Williams, M., Messmer, D., 2016b. Fuel breaks to reduce large wildfire impacts in sagebrush ecosystems. Boise, ID, USA: Plant Materials Technical Note No. 66. USDA-NRCS.

McKenzie, D., Gedalof, Z., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire, and conservation. Conservation Biology 18, 890–902.

Meyer, S.E., Garvin, S.C., Beckstead, J., 2001. Factors mediating cheatgrass invasion of intact salt desert shrubland. In: McArthur, DE, Fairbanks, DJ, (Comps.) Shrubland ecosystem genetics and biodiversity: proceedings. Proc. RMRS-P-21. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp. 224–232.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecology Applications 17, 2145–2151.

Miller, R.F., Tausch, R.J., McArthur, E.D., Johnson, D.D., Sanderson, S.C., 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the Intermountain West. Res. Pap. RMRS-RP-69. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J., Hild, A.L., 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse—ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA, USA, pp. 145–185.

Miller, R.F., Chambers, J.C., Pyke, D.A., Pierson, F.B., Williams, C.J., 2013. A review of fire effects on vegetation and soils in the Great Basin Region: response and ecological site characteristics. Gen. Tech. Rep. RMRS-GTR-308. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

Miller, R.F., Chambers, J.C., Pellant, M., 2014. A field guide to selecting the most appropriate treatments in sagebrush and pinyon-juniper ecosystems in the Great Basin: evaluating resilience to disturbance and resistance to invasive annual grasses and predicting vegetation response. Gen. Tech. Rep. RMRS-GTR-322. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

Miller, R.F., Chambers, J.C., Pellant, M., 2015. A field guide for rapid assessment of post-wildfire recovery potential in sagebrush and piñon -juniper ecosystems in the Great Basin: evaluating resilience to disturbance and resistance to invasive annual grasses and predicting vegetation response. Gen. Tech. Rep. RMRS-GTR-338. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

MTBS, 2015. Monitoring trends in burn severity. http://www.mtbs.gov.

Norberg, J., Cumming, G.S. (Eds.), 2008. Complexity theory for a sustainable future. Columbia University Press, New York, NY, USA, p. 312.

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

Plant Conservation Alliance, 2015. National Seed Strategy for Rehabilitation and Restoration. 2015−2020. Available at: www.blm.gov/seedstrategy Accessed 23 April 2016.

Pope, K.L., Allen, C.R., Angeler, D.G., 2014. Fishing for resilience. Transactions of the American Fisheries Society 143, 467–478.

Pyke, D.A., 2011. Restoring and rehabilitating sagebrush habitats. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA, USA, pp. 531–548.

Pyke, D.A., Chambers, J.C., Pellant, M., Knick, S.T., Miller, R.F., Beck, J.L., Doescher, P.S., Schupp, E.W., Roundy, B.A., Brunson, M., McIver, J.D., 2015a. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat—Part 1. Concepts for understanding and applying restoration. US Geological Survey Circular 1416.

Pyke, DA., Knick, S.T., Chambers, J.C., Pellant, M., Miller, R.F., Beck, J.L., Doescher, P.S., Schupp, E.W., Roundy, B.A., Brunson, M., McIver, J.D., 2015b. Restoration handbook for sagebrush steppe ecosystems with special emphasis on greater sage-grouse habitat—Part 2. Landscape level restoration decisions. US Geological Survey Circular 1418.

Pyke, D.A., Chambers, J.C., Beck, J.L., Brooks, M.L., Mealor, B.A., 2016. Land uses, fire and invasion: exotic annual Bromus and human dimensions. In: Germino, M.J., Chambers, J.C., Brown, C.S. (Eds.), Exotic brome-grasses in arid and semiarid ecosystems of the Western US: causes, consequences and management implications. Springer, New York, NY, USA, pp. 307–337.

Reisner, M.D., Grace, J.B., Pyke, D.A., Doescher, P.S., 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. Journal of Applied Ecology 50, 1039–1049.

Reisner, M.D., Doescher, P.S., Pyke, D.A., 2015. Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America's semi-arid *Artemisia tridentata wyomingensis* ecosystems. Journal of Vegetation Science http://dx.doi.org/10.1111/jvs.12327.

Roundy, B.A., Young, K., Cline, N., Hulet, A., Miller, R.R., Tausch, R.J., Chambers, J.C., Rau, B., 2014. Piñon-juniper reduction increases soil water availability of the resource growth pool. Rangeland Ecology & Management 67, 495–505.

Rowland, M.M., Wisdom, MJ., Suring, L.H., Meinke, C.W., 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biology Conservation 129, 323–335.

Schlaepfer, D.R., Lauenroth, W.K., Bradford, J.B., 2012. Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush. Ecography 35, 374–384.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braim, C.E., 2004. Distribution of sage-grouse in North America. Condor 106, 33–76.

Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conservation Letters 3, 91–97.

Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hick, J.A., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. Journal of Applied Ecology 53, 120–129.

Smith, S.D., Nowak, R.S., 1990. Ecophysiology of plants in the Intermountain lowlands. In: Osmond, C.B., Pitelka, L.F., Hidy, G.M. (Eds.), Plant biology of the basin and range. Springer-Verlag, Berlin, pp. 179–242.

Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., et al., 2014. Temperate and boreal forest mega-fires: characteristics and challenges. Frontiers in Ecology and the Environment 12, 115–122.

Stiver, S.J., Apa, A.D., Bohne, J.R., Bunnell, S.D., Deibert, P.A., Gardner, S.C., Hilliard, M.A., McCarthy, C.W., Schroeder, M.A., 2006. Greater Sage-grouse Comprehensive Conservation Strategy. Unpublished report on file at, Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Stringham, T.K., Krueger, W.C., Shaver, P.L., 2003. State and transition modeling: an ecological process approach. Journal of Range Management 56, 106–113.

Suring, L.H., Rowland, M.M., Wisdom, M.J., 2005. Identifying species of conservation concern. In: Wisdom, M.J., Rowland, M.M., Suring, L.H. (Eds.), Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, KS, USA, pp. 150–162.

Toevs, G.R., Karl, J.W., Taylor, J.J., Spurrier, C.S., Karl, M., Bobo, M.R., Herrick, J.E., 2011. Consistent indicators and methods and a scalable sample design to meet assessment, inventory, and monitoring information needs across scales. Rangelands 33, 14–20.

US Department of Agriculture, Natural Resources Conservation Service [USDA NRCS], 2013o. National Cooperative Soil Survey. Available at: http://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/partnership/ncss/ (Accessed 25 June 2016).

US Department of Agriculture, Natural Resources Conservation Service [USDA NRCS], 2015o. Sage Grouse Initiative. Wildlife Conservation through Sustainable Ranching. Available at: http://www.sagegrouseinitiative.com (Accessed 9 January 2016).

US Department of Agriculture, Natural Resources Conservation Service [USDA NRCS], 2015o. Ecological Site Descriptions. Available at: http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/ecoscience/desc/ (Accessed 9 January 2016).

US Department of Interior [USDI], 2015. Secretarial Order Number 3336, Rangeland Fire Prevention, Management, and Restoration. Available at: http://www.forestsandrangelands.gov/rangeland/documents/SecretarialOrder3336.pdf (Accessed 9 January 2016).

US Department of Interior, Bureau of Land Management [USDI BLM], 2014l. Greater sage-grouse wildfire, invasive annual grasses, and conifer expansion assessment. Available at: http://www.blm.gov/style/medialib/blm/wo/Communications_Directorate/public_affairs/sagegrouse_planning/documents.Par.15341.File.dat/GRSG%20Wildfire,%20Invasives,%20and%20Conifer%20Assessment_June2014_final%20copy.pdf (Accessed 24 December 2015).

US Department of the Interior [USDI], 2016. Safeguarding America's lands and waters from invasive species: a national framework for early detection and rapid response, Washington DC. (55 pp. Available at: https://www.doi.gov/sites/doi.gov/files/National%20EDRR%20Framework.pdf. Accessed 17 July 2016).

US Environmental Protection Agency [USEPA], 2016. Level III and IV Ecoregions of the Continental United States. Available at: https://archive.epa.gov/wed/ecoregions/web/html/level_iii_iv-2.html (Accessed 24 April 2016).

US Fish and Wildlife Service [USFWS], 2013. Greater sage-grouse *(Centrocercus urophasianus)* conservation objectives: final report. US Fish and Wildlife Service, Denver, CO, USA (91 p).

US Fish and Wildlife Service [USFWS], 2015. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the greater sage-grouse *(Centrocercus urophasianus)* as an endangered or threatened species; proposed rule. Federal Register 80, 59858–59942 Available at: http://www.gpo.gov/fdsys/pkg/FR-2015-10-02/pdf/2015-24292.pdf (Accessed 9 January 2016).

US Geological Survey [USGS], 2013. LANDFIRE 1.2.0 Existing vegetation type layer. Updated 3/13/2013. US Department of the Interior, Geological Survey, Washington, DC (Available at: http://landfire.cr.usgs.gov/viewer/. Accessed 9 January 2016).

United States Government, 2002. Endangered Species Act of 1973, as amended by Congress. https://www.epw.senate.gov/esa73.pdf (Accessed 21 Sept 2016).

West, N.E., 1983a. Intermountain salt-desert shrubland. In: West, N.E. (Ed.), Temperate deserts and semi-deserts. Elsevier Publishing Company, Amsterdam, The Netherlands, pp. 375–378.

West, N.E., 1983b. Great Basin-Colorado Plateau sagebrush semi-desert. In: West, N.E. (Ed.), Temperate deserts and semi-deserts. Elsevier Publishing Company, Amsterdam, The Netherlands, pp. 331–350.

Wiens, J.A., Goble, D.D., Scott, J.M., 2012. Time to accept conservation triage. Nature 488, 281.

Williamson, J.C., Bestelmeyer, B.T., McClaranb, M.P., Robinett, D., Briske, D.D., Wu, X., Fernández-Giménez, M.E., 2016. Can ecological land classification increase the utility of vegetation monitoring data? Ecology Indicators 69, 657–666.

Wisdom, M.J., Chambers, JC., 2009. A landscape approach for ecologically-based management of Great Basin shrublands. Restoration Ecology 17, 740–749.

Wisdom, M.J., Meinke, C.W., Knick, S.T., Schroeder, M.A., 2011. Factors associated with extirpation of sage-grouse. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA, USA, pp. 451–474.