Fire and Invasive Plants Special Feature

Resistance to Invasion and Resilience to Fire in Desert Shrublands of North America

Matthew L. Brooks[1] *and Jeanne C. Chambers*[2]

Authors are [1]*Research Botanist, US Geological Survey, Western Ecological Research Center, Yosemite Field Station, El Portal, CA 95318, USA; and* [2]*Research Ecologist, USDA Forest Service, Rocky Mountain Research Station, Reno, NV 89512, USA.*

Abstract

Settlement by Anglo-Americans in the desert shrublands of North America resulted in the introduction and subsequent invasion of multiple nonnative grass species. These invasions have altered presettlement fire regimes, resulted in conversion of native perennial shrublands to nonnative annual grasslands, and placed many native desert species at risk. Effective management of these ecosystems requires an understanding of their ecological resistance to invasion and resilience to fire. Resistance and resilience differ among the cold and hot desert shrublands of the Great Basin, Mojave, Sonoran, and Chihuahuan deserts in North America. These differences are largely determined by spatial and temporal patterns of productivity but also are affected by ecological memory, severity and frequency of disturbance, and feedbacks among invasive species and disturbance regimes. Strategies for preventing or managing invasive plant/fire regimes cycles in desert shrublands include: 1) conducting periodic resource assessments to evaluate the probability of establishment of an altered fire regime; 2) developing an understanding of ecological thresholds associate within invasion resistance and fire resilience that characterize transitions from desirable to undesirable fire regimes; and 3) prioritizing management activities based on resistance of areas to invasion and resilience to fire.

Resumen

Los asentamientos de Anglo-Americanos en los desiertos de matorrales de Norteamérica resultaron en la introducción y subsecuente invasión de varias especies de pastos no nativos. Estas invasiones, han alterado el régimen de fuego preestablecido, convirtiendo los matorrales de especies nativas en pastizales de gramíneas anuales inducidas y poniendo en riesgo varias especies desérticas nativas. El manejo efectivo de estos ecosistemas requiere de un entendimiento de la resistencia ecológica a la invasión y la resiliencia al fuego. La resistencia y resiliencia difieren entre los desiertos de matorral fríos y cálidos de Norteamérica tales como Great Basin, Mojave, Sonorense, y Chihuahuense. Estas diferencias son determinadas en gran medida por patrones espaciales y temporales de productividad pero también es afectado por la memoria ecológica, la severidad y frecuencia del disturbio y la retroalimentación entre las especies invasoras y el régimen de disturbio. Las estrategias para prevenir o manejar plantas invasoras/ciclos de régimen de fuego en los desiertos de matorral incluyen: 1) realizar evaluaciones periódicas de los recursos para evaluar la probabilidad de que se establezca un régimen de fuego alterado; 2) desarrollar un entendimiento de los umbrales ecológicos asociados entre la resistencia a la invasión y la resiliencia al fuego que caracteriza la transición entre regímenes de fuego deseables e indeseables; y 3) priorizar las actividades de manejo basadas en la resistencia de las áreas a la invasión y la resiliencia al fuego.

Key Words: Chihuahuan Desert, ecological resilience, ecological resistance, Great Basin Desert, Mojave Desert, Sonoran Desert

INTRODUCTION

Plant invasions and their interactions with fire regimes are recognized as threats to biodiversity and other natural resources worldwide (Brooks et al. 2004). In the desert regions of North America, invasive plants have altered fire regimes, which, in many cases, have resulted in large-scale conversions of native plant communities to invasive plant dominance (D'Antonio and Vitousek 1992; Brooks et al. 2004). These changes are affecting ecological processes including water cycles (Wilcox and Thurow 2006), nutrient dynamics (Evans et al. 2001), carbon budgets (Bradley et al. 2006), and regional albedos (Millennium Ecosystem Assessment 2005). Many of the native species associated with these desert ecosystems are at risk, and several are either listed or are being considered for listing under the Endangered Species Act (1973). Examples include the desert tortoise (*Gopherus agassizii*) and the sage grouse (*Centrocercus* spp.).

The concepts of ecological resistance and resilience are used increasingly to develop approaches for sustainable ecosystem management (Walker et al. 2004; Briske et al. 2008) and can provide useful insights into the factors influencing plant invasions and fire both within and among North American desert ecosystems. These concepts allow comparisons over a variety of spatial scales, and can be used to develop management approaches that are appropriate at scales ranging from landscapes (Walker et al. 2004) to ecological sites (Briske et al. 2008). In this paper, we discuss the concepts of resistance

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Correspondence: Matthew L. Brooks, US Geological Survey, Western Ecological Research Center, Yosemite Field Station, 5083 Foresta Road, El Portal, CA 95318, USA. Email: mlbrooks@usgs.gov

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and resilience in relation to plant invasions and fire in the deserts of North America with a specific focus on resistance to invasions and resilience to fire. We provide examples of how plant invasions have altered fire regimes from both cold and hot desert shrublands and present management strategies designed to prevent or mitigate these changes.

RESISTANCE TO PLANT INVASIONS AND RESILIENCE TO FIRE

We define ecological resistance to plant invasion as a function of the biotic and abiotic factors and ecological processes in an ecosystem that limit the establishment and population growth of an invading species (D'Antonio and Thomsen 2004). We define ecological resilience to fire as the amount of disturbance that an ecosystem can withstand before changes in processes and structures occur that are of sufficient magnitude to result in new alternative states (Holling 1973; Gunderson 2000). Thresholds define the limits of natural variability within ecosystems and are crossed when they do not return to the original state via natural processes after disturbance and instead transition to new alternative states that are adjusted to the altered processes (Laycock 1991; Whisenant 1999). When thresholds to invasion or fire are crossed, active restoration involving invasive species control, native plant revegetation, and in some cases direct fire management are required to return ecosystems to their original states.

The structure and function of desert systems and, consequently, resistance to invasion and resilience to fire differ based on variations in underlying abiotic characteristics, especially the amount and timing of precipitation. The deserts of North America contain four major regions that vary in both the annual amount and seasonal distribution of precipitation (Fig. 1). Regions that receive lower amounts of precipitation have relatively lower net primary productivity and biomass. Those that receive a higher percentage of their annual precipitation during winter are dominated by woody perennials, whereas those that receive most of their precipitation in summer are dominated by perennial grasses. The resilience of desert ecosystems to disturbances like fire typically increases along gradients of increasing available resources (water and nutrients) and annual net primary productivity (Chambers et al. 2007; Wisdom and Chambers 2009). Greater resources and a higher level of productivity by functionally diverse native plant communities increase the capacity of the native community to regenerate following disturbance and to effectively compete with invaders. Thus, the most productive desert ecosystems in the Great Basin and Chihuahuan deserts (Fig. 1) tend to be most resilient to fire and resistant to plant invasions.

The structure and function of desert systems are determined not only by the amount and seasonality of precipitation but also by their inherent variability (Noy-Meir 1973). Variability in precipitation tends to increase as total precipitation decreases and is highest for desert ecosystems that receive the least precipitation (Ehleringer 1985). When biomass of extant vegetation is low (such as in deserts), it has limited capacity for utilizing soil resource increases during episodic periods when precipitation is high (Davis and Pelsor 2001). The "fluctuating resource hypothesis" predicts that resistance to invasion decreases when

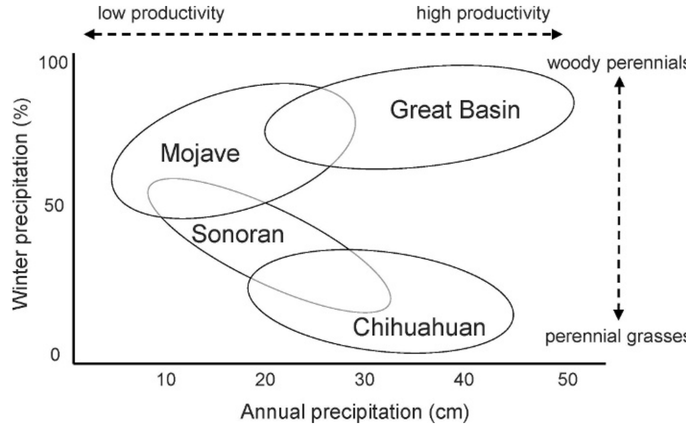

Figure 1. General precipitation patterns for the deserts of North America as they relate to average productivity and vegetation lifeform (adapted from MacMahon and Wagner 1985).

resource availability is higher than resource uptake, leaving resources for invading plants to utilize (Davis et al. 2000). Thus, ecosystems subject to pronounced fluctuations in resource supply may be more susceptible to invasion than systems with a more stable resource supply (Rejmanek 1989). The relationship between low precipitation and increased variability in precipitation is observed over elevation gradients within mountain ranges in the Great Basin cold desert and has been related to increased invasion potential at lower elevations (Chambers et al. 2007). An important caveat is that lower elevation hot desert areas with the most extreme environmental conditions may be relatively resistant to invasion because few nonnatives can establish and persist in these exceedingly harsh environments (Brooks 2009).

In desert areas with relatively low resistance to invasion, nonnative plants can severely compromise ecological resilience because of their effects on fuel characteristics, ignitability of landscapes, fire behavior, and, consequently, fire regimes (Brooks 2008). A fire regime is characterized by type (e.g., surface vs. crown fire), frequency (return interval), intensity (heat release), severity (effects on soils and/or vegetation), size, spatial complexity, and seasonality of fire within a given geographic area or vegetation type (Sugihara et al. 2006). "Presettlement" values are typically used as the baseline to determine if current fire regimes have been altered. Plant invasions that cause new fuel conditions and altered fire regimes can result in a self-perpetuating invasive plant/fire regime cycle (Fig. 2; Brooks et al. 2004). In addition, the invader may have direct negative effects on native vegetation through competition or other mechanisms that further promote the new fire regime. One of the most widely recognized examples of these types of changes is the grass/fire cycle in which invasive grasses invade native shrublands, increase fine fuels, and result in more frequent and larger fires than occurred prior to invasion (D'Antonio and Vitousek 1992). In the process, the landscape is converted from a native shrubland with a moderately long time between fires to nonnative grassland with very short periods of time between fires. It is also important to note that not all plant invasions increase the size, frequency, or intensity of fire. In some cases, invasive plants may expand into a landscape that has evolved with frequent fire, change fuel characteristics in ways that suppress burning, and alter historic fire regimes. Such is the case for native creosote bush that is expanding into hot desert

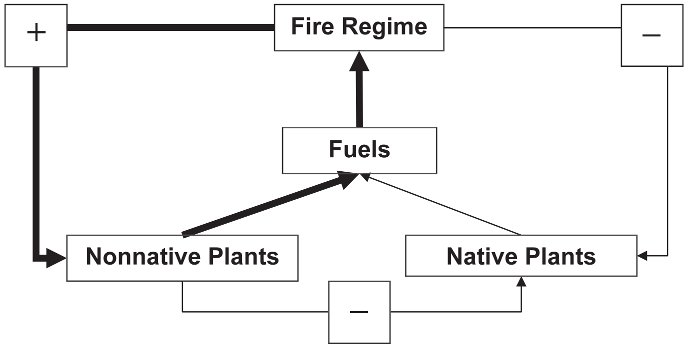

Figure 2. The invasive plant/fire regime cycle by which nonnative plants alter fire regimes through changes in fuel characteristics (reprinted with permission from Brooks 2008).

grasslands, changing the fuelbed to a more heterogenous distribution, impeding the spread of fire, and reducing fire frequency in the Chihuahuan Desert (Archer 1994; Archer et al. 1995).

Several interacting factors influence resistance to invasion and resilience to fire in desert ecosystems including ecological memory, severity and frequency of disturbance, and feedbacks among invasive species and disturbance regimes. Ecological memory consists of the legacies of information, materials, processes, and relationships that contribute to the continued functioning of an intact system and the recovery of that system following disturbance (Franklin and MacMahon 2000; Gunderson 2000; Peterson 2002; Bengtsson et al. 2003). A basic element of ecological memory is the capacity to support a given ecological site type as indicated by the climatic regime and soil characteristics. Factors that contribute to ecological memory include ecological condition as indicated by soil characteristics, the composition and abundance of residual native plants and animals, seed banks and seed sources, and the composition and abundance of invasive species. The severity and frequency of disturbance can alter the ecological memory of a site and, consequently, its capacity to support desirable alternative states and, in the worst case scenario, the historical ecological site type (Whisenant 1999; Briske et al. 2008). In the deserts of North America, inappropriate livestock grazing has significantly influenced ecological memory by reducing a major structural and functional component, specifically native perennial herbaceous species, and by serving as a dispersal agent for nonnative invaders (Milchunas et al. 1988; Van de Koppel et al. 2002). Loss of perennial herbaceous species decreases the resistance of desert ecosystems to invasion (Chambers et al. 2007) and resilience to disturbances like drought and wildfires (D'Antonio et al. 2009). Once established, invasive species can promote shorter fire return intervals and larger fire sizes than many deserts experienced historically. These changes can result in positive feedbacks for the invader and negative effects on native species, especially woody perennials (Fig. 2).

PRESETTLEMENT AND CURRENT FIRE REGIMES

The productivity and dominant life forms of the North American deserts affect fuels and fire behavior and, thus, the characteristics of both presettlement and current fire regimes. Desert ecosystems with relatively high productivity, like many middle to high elevation ecological types in cold desert shrublands, have relatively high fuel abundance and continuity, exhibited more frequent presettlement fires (Miller et al. 2011), and typically have many fire-tolerant species (Wright and Bailey 1982). Higher productivity coupled with the presence of fire-tolerant species result in greater resilience to fire. In contrast, in desert ecosystems with low productivity, including almost all hot desert shrubland ecological types and most lower elevation cold desert ecological types, fuel production and continuity are limited, presettlement fires were both infrequent and small (Humphrey 1974), and many of the species that characterize these ecological types evolved in the near-absence of fire and are fire intolerant (Wright and Bailey 1982; Brooks and Minnich 2006). Consequently, resilience to fire is typically low.

In the sections that follow, we describe presettlement and current fire regimes within cold and hot desert shrublands. We explain how invasive plants and land-use activities have altered fire regimes from presettlement conditions and discuss the implications of ecological resistance and resilience.

Cold Desert Shrublands

Cold desert shrublands dominated largely by woody plant communities typify the Great Basin desert of North America. Relative to other desert ecosystems, they are characterized by moderate to high productivity and relatively high precipitation that arrives primarily during the winter months (Fig. 1). However, cold desert shrubland types occur over elevation gradients that exhibit distinct differences in available resources and, consequently, in site productivity, vegetation composition, and fuel characteristics. Salt-desert shrublands are dominated by species in the Chenopodiaceae, occur typically on halomorphic soils, and are characterized by the lowest effective precipitation, productivity, and fuel loads (West 1983a). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*Artemisia tridentata vaseyana*), and mountain brush types occur at progressively higher elevations and are associated with increasing amounts of precipitation, productivity, and fuels (West and Young 2000). During presettlement times, salt-desert shrublands rarely if ever burned due to inherently low productivity and fuels (Brooks and Pyke 2001). Sagebrush dominated shrublands had highly variable fire return intervals ranging from decades to centuries (Frost 1998; Brown and Smith 2000; Baker 2006; Miller et al. 2011). At coarse regional scales, fire return intervals in sagebrush were determined by climate and its effects on fuel abundance and continuity. Consequently, fire frequency was higher both in sagebrush types with greater productivity and during periods of increased precipitation (West 1983b; Mensing et al. 2006). At fine scales within sagebrush types, fire return intervals in sagebrush shrublands likely were determined by topographic and soil effects on productivity and fuels and also were highly variable (Miller and Heyerdahl 2008).

Anglo-American settlement of cold desert shrublands beginning in the mid 1800s initiated a series of changes in vegetation composition and structure that interacted with other global change processes to alter fire regimes across the cold desert region. The first major change occurred when overgrazing by livestock led to a decrease in native perennial grasses and forbs and effectively reduced the abundance of fine fuels in shrublands (Knapp 1996; Miller and Eddleman 2001). Decreased competition from perennial herbaceous species in combination with ongoing climate change and favorable conditions for woody species establishment at the turn of the century resulted in increased abundance of shrubs (primarily *Artemisia* species) and trees including juniper (*Juniperus occidentalis*, *Juniperus osteosperma*) and pinyon pine (*Pinus monophylla*) (Miller et al. 2011). The initial effect of these changes in fuel structure was a reduction in fire frequency and size (Miller and Tausch 2001). The second major change occurred when annual grasses (*Bromus tectorum, Bromus madritensis ssp. rubens, Taeniatherum caput-medusa*) were introduced from Eurasia in the late 1800s and spread rapidly into low to mid-elevation shrublands with depleted understories (Knapp 1996). The annual grasses increased fine fuels, and the rate of fire spread in many shrubland communities and initiated grass/fire cycles characterized by shortened fire return intervals and larger, more contiguous fires. In recent decades, salt-desert shrublands began to burn for the first time in known history, and Wyoming sagebrush types began burning as frequently as every few years (Whisenant 1990; Brooks and Pyke 2001). The final change occurred as a result of expansion of juniper and pinyon pine trees into mid- to high elevation shrublands. Progressive infilling of the trees is increasing woody fuels and causing fires of greater size and intensity (Miller and Tausch 2001). The highly competitive trees also are resulting in depletion of species associated with sagebrush shrublands and reduced resilience to fire.

Resilience of cold desert shrublands to fire increases along gradients of increasing available resources and annual net primary productivity (Chambers et al. 2007; Wisdom and Chambers 2009). Resistance to annual grasses is associated with their ecological amplitude and is lowest for lower-elevation salt-desert shrub and Wyoming sagebrush types and highest for mountain big sagebrush and mountain brush types (Wisdom and Chambers 2009). In contrast, resistance to woodland expansion is lowest for mountain big sagebrush and mountain brush types (Miller and Eddleman 2001). Factors that result in depletion of native perennial herbaceous species like overgrazing by livestock and infilling of pinyon and juniper trees decrease resistance to invasion by annual grasses and resilience following fire. In sagebrush shrublands, the removal of perennial herbaceous species can increase cheatgrass biomass and seed production two- to threefold, whereas fire alone can result in a two- to sixfold increase in these variables (Chambers et al. 2007). However, in these same shrublands, the removal of herbaceous perennials coupled with fire can cause 10- to 30-fold increases in biomass and seed production of cheatgrass (Chambers et al. 2007).

Hot Desert Shrublands

Hot desert shrublands characterize most of the Mojave and Sonoran deserts of North America. Precipitation in these deserts is relatively low and occurs largely during the winter months (Fig. 1). Native vegetation types exhibit generally low productivity and fuel levels. However, similar to cold desert shrublands, elevation gradients and local edaphic conditions influence productivity and, thus, fuel loads and continuity (Brooks and Matchett 2006; Brooks and McPherson 2008). Low elevations are dominated by creosotebush (*Larrea tridentata*) scrub, while middle elevations generally are characterized by blackbrush (*Coleogyne ramosissima*) scrub (Brooks and Minnich 2006). Higher elevations are characterized by chaparral ecological types that are dominated by woody evergreen shrubs with dense crowns like buckbrush (*Ceonothus* spp.) and manzanita (*Arctostaphylos* spp.) or by cold desert types that are dominated by big sagebrush, juniper, and pinyon pine (Brooks and Minnich 2006).

In low elevation shrublands of the hot deserts, presettlement fires were infrequent. Fine fuels were derived primarily from winter annuals and were sparse except after very wet winters (Brown and Minnich 1986; Brooks and Esque 2002; Esque and Schwalbe 2002; Salo 2005; Brooks and Minnich 2006). In both the Mojave and western Sonoran deserts, invasion of nonnative annual grasses (*B. madritensis* subsp. *rubens* and *Schismus barbatus*) significantly increased fine fuel loads in creosotebush scrub (Rogers and Vint 1987; Brooks and Minnich 2006) and created conditions conducive to fire spread (Brooks 1999). Between 1955 and 1983, fire frequency increased in the Sonoran Desert (Schmid and Rogers 1988), and during the 1980s and early 1990s, fire frequency increased in the Mojave Desert (Brooks and Esque 2002; Brooks and Matchett 2006). High rainfall years result in significant increases in nonnative annual grass biomass (fine fuels) and can result in large fires (Rogers and Vint 1987; Schmid and Rogers 1988; Brooks and Matchett 2006; Brooks and Minnich 2006). In creosotebush scrub of the eastern Sonoran Desert, invasion of nonnative perennial grasses such as Lehmann lovegrass (*Eragrostis lehmanniana*), buffelgrass (*Pennisetum ciliare*), and purple fountaingrass (*Pennisetum setaceum*) have resulted in similar increases in fire frequency and size (Brooks and McPherson 2008).

In middle elevation shrublands characterized by blackbrush, presettlement fire return intervals appear to have been on the order of centuries (Webb et al. 1987). Low amounts of fine fuels in interspaces likely limited fire spread except during extreme fire weather conditions (high winds, low relative humidity, and low fuel moisture) when stand-replacing crown fires could occur. After settlement, extensive burning to remove blackbrush for range improvement coupled with livestock grazing contributed to invasion of nonnative brome grasses (*B. tectorum* and *B. madritensis* subsp. *rubens*) and red-stemmed filaree (*Erodium cicutarium*; Brooks and Matchett 2003; Brooks and McPherson 2008). The nonnative annual grasses and forbs increased fine fuels, and during high precipitation years greater production of these fine fuels is correlated with larger fires (Brooks and Matchett 2006). An increase in nonnative grass abundance after fire has the potential to promote recurrent fire and decrease resilience in blackbrush types.

In high elevation shrublands, woody fuels and fuel continuity are typically higher than in the middle elevation zone. Greater fuel loads and continuity coupled with more frequent lightning and steeper slopes that promote fire spread resulted in historical fire return intervals of 50 to 100+ yr, although local fire return intervals probably varied widely (Cable 1975; Brooks and Minnich 2006). In the Sonoran Desert, many lower elevation chaparral sites have been managed for livestock grazing since the 1880s (Pase and Brown 1994), and the use of fire to maintain grass dominance likely limited chaparral encroachment into lower elevation grasslands (Brooks and McPherson 2008). However, in areas where fire was not used as a management tool, removal of fine fuels by livestock grazing and fire suppression likely decreased fire frequency and resulted in chaparral expansion into these areas (Brooks and McPherson 2008). Higher elevation sites likely did not receive as much grazing pressure, but fire suppression, especially at the interface with ponderosa pine forests, may have resulted in tree expansion into shrublands. Nonnative annual grasses occur in high elevation shrublands and often increase in abundance immediately after fire. However, in most cases native woody vegetation quickly recovers, overtops, and suppresses annual grasses within the first decade unless some other disturbance factor is present such as recurrent fire or significant ungulate grazing (M. Brooks, personal observation, 2006).

Similar to cold desert shrublands, resilience of hot desert shrublands to fire tends to increase with elevation and productivity gradients. More mesic conditions at higher elevations result in greater vegetation production and, historically, these areas had more frequent fires. Many of the species that occur in higher elevation ecosystems evolved with more frequent fire and have higher tolerance to fire than those that occur at more arid lower elevations (Brooks and Minnich 2006). Higher elevation ecosystems also appear to be more resistant to dominance by annual grasses. This is largely a function of greater resilience to fire and a higher probability of recovery of these ecosystems to native species dominance following disturbance. Consequently, annual grass invasions have their greatest influence on fire regimes in low- to mid-elevation shrublands where they increase fuel continuity and repeated fires decrease the recovery potential of native species with low fire tolerances.

MANAGEMENT TOOLS TO PREVENT THE INVASIVE PLANT/FIRE REGIME CYCLE

A core objective for managing invasive plants and fire regimes in desert ecosystems is maintaining or increasing ecological resistance to plant invasions and resilience to fire prior to threshold crossings and the initiation of an invasive plant/fire regime cycle (D'Antonio and Chambers 2006; D'Antonio et al. 2009). Once a threshold has been crossed it is often ecologically and economically difficult, if not impossible, to return the system to its original state.

Managing for resistance to invasives and resilience to fire requires obtaining the necessary information for prioritizing restoration and other management activities and long-term monitoring data for adaptive management. In the sections below we describe three guiding principals that should be incorporated into management plans in order to prevent or minimize the invasive plant/fire regime cycle.

Conduct Resource Assessments and Periodic Monitoring

The first step is to assess the vegetation types and current ecological conditions, ideally the ecological types and their states and phases at landscape scales. This information should be obtained using consistent methods, and geographic information systems databases should be developed that are widely accessible (Chambers et al. 2009). This type of information provides the basis for determining priority management areas and appropriate management activities at scales that allow the preservation of ecosystems and conservation of species (Wisdom and Chambers 2009). It also provides the basis for monitoring the rate and magnitude of invasion, changes in fire return intervals, and effects of wildfire management activities on ecosystems and species.

Develop an Understanding of Ecological Resistance and Resilience

Managing for resistance to invasions and resilience to fire requires both developing an understanding of the abiotic and biotic factors that determine ecological resistance to invasives and resilience to fire and defining the ecological thresholds that exist in desert ecosystems. Both monitoring data and research and management experiments can be used to determine the abiotic and biotic conditions that influence resistance to invasion and resilience to fire and that result in threshold crossings. For example, the Joint Fire Science Program, Sagebrush Treatment Evaluation Project (www.sagestep.org) is using a collaborative research and management approach that spans the Great Basin Desert to define the ecological conditions (soils, vegetation composition, and structure) that influence resistance and resilience and that result in threshold crossings in sagebrush steppe ecosystems exhibiting annual grass invasion and pinyon and juniper tree expansion. Management treatments are applied over a gradient of ecological conditions (e.g., increasing tree cover, increasing annual grass cover, and decreasing herbaceous perennial cover) and the responses are quantified to determine the point at which ecological resilience is lost and a threshold is crossed to an alternative state. Once an appropriate set of metrics has been defined for evaluating resistance to invasives and resilience to disturbance, they can be incorporated into existing state and transition models (e.g., Briske et al. 2008). Providing for unanticipated states or phases will be necessary to accommodate changes due to climate change and alterations in land use.

Prioritize Management Activities Based on Resistance and Resilience

Determining priority management areas and appropriate management activities using an understanding of resistance to invasions and resilience to fire allows a strategic approach that can be used to address multiple objectives over larger scales. Using this approach, areas with a high priority for protection are those with inherently low invasion resistance and fire resilience, like many hot desert shrub communities and lower elevation cold desert shrub communities. Areas of high conservation value for threatened and endangered species, like the Snake River Birds of Prey Area in Idaho, also receive priority status for protection. Protection focuses on eliminating or reducing stressors such as repeated fire and inappropriate livestock grazing, controlling surface disturbances and invasion corridors like roads and trails, and increasing efforts to detect and eradicate invasive species.

Maintaining or increasing resistance to invasion and resilience to fire in areas that have declining ecological conditions or that are in the initial stages of invasion but that have not crossed ecological thresholds also receives high priority. Eliminating or reducing stressors and factors that increase invasion is still a primary focus. In addition, preventative vegetation management is used in areas that receive greater amounts of effective moisture, are characterized by inherently higher invasion resistance and fire resilience, and have a high probability of improved ecological conditions following treatment. Preventative management can be a viable approach in desert shrublands with reduced native herbaceous perennials and increased shrubs or trees (D'Antonio et al. 2009) and hot desert grasslands with encroaching shrub species (Drewa et al. 2001). Management objectives typically include increasing native perennial grass and forb dominance through competitive release from shrubs and trees, and reducing woody fuel loads to minimize the risk of high severity fires. Treatments are specific to the ecosystem and ecological conditions, but typically involve prescribed fire, mechanical shrub and tree thinnings, or herbicides. After wildfires, seeding with native species through the US Department of the Interior Bureau of Land Management, Emergency Stabilization and Rehabilitation program, and the US Department of Agriculture Forest Service Burn Area Emergency Response program may increase ecological resistance to invasives and resilience to fire in areas at risk of crossing an ecological threshold. Unfortunately, many areas where seedings successfully establish are on the high end of the regional productivity gradient, are naturally more resilient to fire, and do not need active management. In addition, seeding with introduced grasses in fire resilient areas that are capable of recovering on their own to native species can result in alternative stable states with altered ecological processes and reduced species diversity (Lesica and DeLuca 1996; Richards et al. 1998). Thus, decisions to apply postfire seeding treatments should be based on careful evaluation of a site's inherent resistance to invasion and resilience to fire in order to prevent unnecessary treatments and avoid undesirable effects.

Restoring or rehabilitating areas that have already crossed ecological thresholds to states that are dominated by invasive species is ecologically challenging and expensive and is of lower priority except in special situations. Lower priority status is assigned to these areas not because they are not valuable to society but because the magnitude of the problem relative to available human and financial resources indicates that greater benefit will be obtained by maintaining or increasing the invasive resistance and fire resilience of areas that have not yet crossed ecological thresholds. Areas that may be assigned priority status for restoration or rehabilitation include those that are located adjacent to intact vegetation communities that can serve as buffers or fire breaks, occur at the wildland–urban interface, represent endangered ecosystems, or provide critical habitat for threatened and endangered species. Restoration or rehabilitation of these areas typically involves integrated management strategies in which pretreatments are used to reduce the propagule pool or adult population of the invader followed by revegetation to establish the desired plant community (Brooks et al. 2004; D'Antonio and Chambers 2006; D'Antonio et al. 2009). The choice of seeded species depends on the management objective. Restoration of critical habitat or endangered ecosystems by definition requires diverse native species mixtures. In contrast, management objectives for wildland–urban interface areas and buffers or fire breaks may include high resistance to the invader and fuel characteristics that minimize the likelihood of fire (Brooks et al. 2004; Brooks 2009). In this case, it is appropriate to rehabilitate the area with native or introduced species that are highly competitive with invaders and have low flammability but that are not likely to become significant land management problems. Regardless of the objective, it is necessary to monitor the success of restoration and rehabilitation efforts and plan for the possibility of reseeding and repeated removal of the invader.

MANAGEMENT IMPLICATIONS

Land managers often have limited financial and human resources and are faced with managing a wide range of natural, recreational, and economic resources that can be negatively affected by multiple threats. The effectiveness of land management can be improved by using ecological concepts that transcend individual resources and threats, distill interacting factors into a subset of manageable parts, and can be applied at a variety of scales. The concepts of ecological resistance to invasion and resilience to fire exhibit these properties and can be used to manage the interrelated threats of plant invasions and altered fire regimes in the deserts of North America.

In this paper, we explain how resistance to invasion and resilience to fire differ both within and among the desert shrublands of North America. An understanding of the abiotic and biotic factors and the processes that determine invasion resistance and fire resilience in these desert shrublands provides critical information for management. Specifically, when and where plant invasions are most likely to occur, the ecological and environmental conditions that confer resistance to invasions and/or resilience to fire, and, conversely, the conditions that result in threshold crossings. This information can be used to:

- Prioritize land management activities at landscape scales in order to restore and maintain ecosystems and to meet conservation objectives (Wisdom and Chambers 2009).
- Develop ecological site descriptions based on ecological resilience that incorporate process-based indicators and describe triggers, feedback mechanisms, and restoration pathways (Briske et al. 2008).
- Develop invasive species management plans that are specific to the ecosystems of interest and that are based on abiotic and biotic factors and ecological processes that influence ecological resistance to plant invasions.
- Develop fire management plans that are specific to the ecosystems of interest and that are based on abiotic and biotic factors and ecological processes that influence ecological resilience to fire.

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