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Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities

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Review

Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities

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ABSTRACT

Vegetation change and anthropogenic development are altering ecosystems and decreasing biodiversity. Successful management of ecosystems threatened by multiple stressors requires development of ecosystem conservation plans rather than single species plans. We selected the big sagebrush (*Artemisia tridentata* Nutt.) ecosystem to demonstrate this approach. The area occupied by the sagebrush ecosystem is declining and becoming increasingly fragmented at an alarming rate because of conifer encroachment, exotic annual grass invasion, and anthropogenic development. This is causing range-wide declines and localized extirpations of sagebrush associated fauna and flora. To develop an ecosystem conservation plan, a synthesis of existing knowledge is needed to prioritize and direct management and research. Based on the synthesis, we concluded that efforts to restore higher elevation conifer-encroached, sagebrush communities were frequently successful, while restoration of exotic annual grass-invaded, lower elevation, sagebrush communities often failed. Overcoming exotic annual grass invasion is challenging and needs additional research to improve the probability of restoration and identify areas where success would be more probable. Management of fire regimes will be paramount to conserving sagebrush communities, as infrequent fires facilitate conifer encroachment and too frequent fires promote exotic annual grasses. Anthropogenic development needs to be mitigated and reduced to protect sagebrush communities and this probably includes more conservation easements and other incentives to landowners to not develop their properties. Threats to the sustainability of sagebrush ecosystem are daunting, but a coordinated ecosystem conservation plan that focuses on applying successful practices and research to overcome limitations to conservation is most likely to yield success.

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1. Current situation

Conservation efforts have traditionally focused on individual species and have been exceedingly expensive for limited successes (Vitousek et al., 1997a; Tear et al., 1995). Single species conservation plans are often a reactive response that provides protection for species that are at risk of extinction if new management is not implemented to halt or reverse their decline (Simberloff, 1998). More comprehensive conservation efforts that focus on entire ecosystems will be more effective and benefit more species (Vitousek et al., 1997a; Lester et al., 2010). Multiple conservation objectives can be achieved by focusing on ecosystem conservation as opposed to single species conservation. Ecosystem conservation efforts would be proactive and subsequently decrease the risk of needing individual species conservation plans to prevent their demise. However, ecosystem conservation requires identifying the major stressors degrading the ecosystem and developing strategies to overcome or mediate those factors. The sagebrush (*Artemisia*) ecosystem is a prime example of an area where many conservation objectives could be simultaneously achieved by developing a comprehensive ecosystem conservation plan.

The sagebrush ecosystem is one of the most imperiled in the United States (Noss et al., 1995). More than 350 sagebrush-associated plants and animals have been identified as species of conservation concern (Suring et al., 2005a,b; Wisdom et al., 2005). The continued loss of the sagebrush ecosystem is increasing the risk of local extirpation or even regional loss of sagebrush obligate and facultative species and is interrupting the economic sustainability of livestock operations that rely on sagebrush plant communities for forage. The sagebrush ecosystem at one time occupied over 62 million hectares in the western United States and southwestern Canada (Küchler, 1970; McArthur and Plummer, 1978; Miller et al., 1994; Tisdale et al., 1969; West and Young, 2000). Despite its large geographical distribution, the sagebrush ecosystem is being lost at an alarming rate and only occupies about 56% of its historic range and is highly fragmented (Schroeder et al., 2004; Knick et al., 2003). This ecosystem is being converted to conifer woodlands, exotic annual grass and introduced grass communities, and croplands, and is being degraded and fragmented by anthropogenic development.

The objectives of this paper are to (1) highlight existing problems relative to maintaining and restoring the ecological integrity of the big sagebrush ecosystem, (2) provide specific solutions (where possible) to overcoming the aforementioned problems, (3) identify critical areas of research to support these efforts, and (4) provide an example of an approach that could be applied to conserve other ecosystems. This will provide the information needed to prioritize and direct research and management to halt and subsequently reverse the decline in the area occupied by the sagebrush ecosystem. The strategies proposed to restore and conserve the big sagebrush ecosystem in North America should provide direction to assist in developing conservation plans for other ecosystems around the world. These include other *Artemisia* ecosystems threatened by desertification, overharvesting of shrubs for fuel, and improper grazing (Han et al., 2008; Sasaki et al., 2008; Bedunah et al., 2010; Louhaichi and Tastad, 2010), as well as, many other ecosystems facing multiple stressors (Samson et al., 2004; Bond and Parr, 2010; Lester et al., 2010; Lindenmayer and Hunter, 2010).

2. Impacts of the stressors

An interesting conservation conundrum exists for the sagebrush ecosystem, because the fire regime alterations underlying the undesirable shifts in vegetation can be either a decrease or an increase in fire frequency. At higher elevations, exemplified by mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* (Rydb.) Beetle) plant communities, the lack of periodic fire has allowed conifer encroachment (Fig. 1) (Miller and Rose, 1999; Miller et al., 2000). While at the lower elevations, commonly Wyoming big sagebrush (*A. tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) communities and at times basin big sagebrush (*A. tridentata* Nutt. ssp. *tridentata*) communities, frequent fires have promoted exotic annual grass dominance (Knapp, 1996; Chambers et al., 2007). Similar issues have been seen in the tropics where increases in fire frequency have eliminated tropical forests at the same time decreases in fire frequency have allowed tree encroachment in savannas and grasslands (Bond and Parr, 2010). Though exotic annual grass invasion and conifer encroachment mostly occur in different sagebrush plant community types, conifer encroachment and exotic annual grass invasion appear to be overlapping more commonly than they have in the past (Fig. 2). When sagebrush communities are at risk of or are both annual grass-invaded and conifer-encroached, conservation efforts are most limited by the annual grass invasion and therefore, recommendations for management addressing the annual grass issue are most relevant.

Fig. 1. Sagebrush plant community encroached by conifers in Idaho (left) and invaded by exotic annual grass in Oregon (right). Photos courtesy of Kirk Davies.

Fig. 2. Sagebrush plant community in Oregon invaded by exotic annual grass and encroached by junipers. Photo courtesy of Kirk Davies.

Conifer woodlands have expanded from historically fire-safe sites into more productive sagebrush communities (Miller and Wigand, 1994; Gruell, 1999; Miller and Rose, 1999; Miller and Tausch, 2001; Miller et al., 2005; Weisberg et al., 2007; Romme et al., 2009) and the tree density has increased in historically open savannah like stands (Nichol, 1937; Johnson and Miller, 2008). Juniper (*Juniperus osteosperma* [Torr.] Little, *Juniperus occidentalis* Hook., *Juniperus scopulorum* Sarg.) and piñon (*Pinus monophylla* Torr. & Frén, *Pinus edulis* Engelm.) woodlands occupy approximately 19 million ha in the Intermountain West. As much as 90% of the current area of these woodlands was sagebrush plant communities prior to the European American settlement (Tausch et al., 1981; Johnson and Miller, 2006; Miller et al., 2008). Increasing tree cover in sagebrush communities eliminates sagebrush and can significantly decrease the herbaceous understory (Blackburn and Tueller, 1970; Miller et al., 2000; Bates et al., 2005; Suring et al., 2005a,b; Chambers et al., 2007). Conifer encroachment is detrimental to sagebrush obligate wildlife because of the loss of sagebrush, fragmentation of sagebrush habitats, potential decreases in herbaceous forage, and increased predation (Connelly et al., 2000; Miller et al., 2005). Decreased herbaceous understory production and cover with conifer encroachment (Blackburn and Tueller, 1970; Barney and Frischknecht, 1974; Miller et al., 2000; Suring et al., 2005a,b; Chambers et al., 2007) also reduces livestock carrying capacity and accelerates soil erosion (Davenport et al., 1998; Bates et al., 2005; Pierson et al., 2007).

Exotic annual grasses have invaded many lower elevation sagebrush communities and are expanding into higher elevation communities. Exotic annual grass invasion is especially devastating to sagebrush communities because it increases fire frequency (Brooks et al., 2004; Pellant et al., 2004; Davies and Svejcar, 2008; Davies, in press). Increased fire frequency prevents reestablishment of sagebrush and is detrimental to most other native perennial plants, leading to near monocultures of exotic annual grasses. Plant community diversity and native plants abundance decline exponentially with increasing densities of exotic annual grass (Davies, in press). Exotic annual grass invasions are changing sagebrush landscapes to a new state dominated by exotic annual grasslands and high fire frequencies (Knick and Rotenberry, 1997). Pellant and Hall (1994) estimate that 5.7 million ha of publicly-owned lands in the Intermountain West were infested with the exotic annual grasses, medusahead (*Taeniatherum caput-medusae* (L.) Nevski), cheatgrass (*Bromus tectorum* L.), or both; however, they concluded that the area at risk of invasion by these two grasses is at least 25 million hectares. Much of the area at risk and already converted to exotic annual grasslands would otherwise be sagebrush communities. This estimate is probably conservative given the recent expansion of exotic annual grasses into more productive plant communities that were thought to be resistant to annual grass invasion and because Pellant and Hall (1994) only evaluated public lands. Meinke et al. (2009) estimated a moderate to high probability of cheatgrass dominance on 28 million ha in the Intermountain West in Idaho, Oregon, Nevada, Utah, and Washington. A large portion of this area is or was dominated by sagebrush. Based on these estimates it is evident that exotic annual grasses have caused large declines in the area occupied by the sagebrush ecosystem and threaten substantial additional reductions. The exotic annual grass problem is likely to become more severe due to increasing atmospheric CO_2 levels, which can increase exotic annual grass productivity and fuel loads and, thereby, may increase fire frequency and intensity (Ziska et al., 2005).

Livestock grazing is nearly ubiquitous across the sagebrush ecosystem. However, its impact on sagebrush communities varies considerably by management. Heavy, repeated use without rest or at least growing season deferment negatively impacts the herbaceous component of sagebrush plant communities and can facilitate exotic annual grass invasion of lower elevation sites (Daubenmire, 1970; Mack, 1981; Knapp, 1996) and, by decreasing fire frequency in higher elevation sites, the encroachment of conifers (Miller et al., 1994, 2005). Improperly managed livestock grazing negatively impacts sagebrush plant communities; however, its most significant impacts are the effects of its interaction with other factors to cause changes in vegetation. In contrast to heavy grazing, moderate levels of grazing with periods of rest and/or growing season deferment do not negatively impact sagebrush plant communities (West et al., 1984; Courtois et al., 2004; Manier and Hobbs, 2006). Properly managed livestock grazing can also decrease risk, size, and severity of wildfires (Diamond et al., 2009; Davies et al., 2010a) and thereby decrease the risk of post-fire exotic annual grass invasion (Davies et al., 2009). Though appropriately managed grazing is critical to protecting the sagebrush ecosystem, livestock grazing per se is not a stressor threatening the sustainability of the ecosystem. Thus, cessation of livestock grazing will not conserve the sagebrush ecosystem.

Energy extraction and exploration and other development have also fragmented and degraded sagebrush communities (Braun et al., 2002; Bergquist et al., 2007; Lyon and Anderson, 2003; Naugle et al., 2011). Fragmentation can be very high in sagebrush landscapes developed for energy extraction. For instance, every 1 km^2 was bounded by a road and bisected by a powerline in portions of the Powder River Basin of northeastern Wyoming where ranching, energy development, and tillage agriculture occurred (Naugle et al., 2011). Infrastructure associated with energy development including earthen dams, pipelines, roads, and well pads serve as vectors for the introduction of invasive plants within sagebrush-dominated systems, leading to further degradation of fragmented landscapes (Bergquist et al., 2007). Roads are particularly noted for their ability to encourage invasion of exotic weeds in semiarid rangelands (Gelbard and Belnap, 2003). Sagebrush wildlife including mule deer (*Odocoileus hemionus*) (Sawyer et al., 2006, 2009), sage-grouse (*Centrocercus urophasianus*) (Doherty et al., 2008; Walker et al., 2007; Naugle et al., 2011), and song birds (Ingelfinger and Anderson, 2004) avoid energy development infrastructure, leading to indirect habitat loss in areas near energy development. The area occupied by sagebrush has also been reduced and fragmented by cultivation. The portion of the sagebrush ecosystem converted to cropland and introduced grassland is unknown, but can be locally substantial. For example, areas with deep loamy soils that once supported big sagebrush communities are now largely cultivated (Winward, 1980; Vander Haegen et al., 2000). Large expanses of sagebrush plant communities have also been divided into smaller parcels (e.g., ranchettes) as human populations have increased in western states. Dividing large parcels of largely undeveloped wild and agricultural lands into large lot residencies is termed ex-urban development and is the fastest growing form of land use across the United States (Brown et al., 2005).

Ex-urban growth decreases native plant and animal diversity, increases exotics (including non-native predators), and restricts the use of ecosystem management options such as fire to prevent conifer encroachment (Knight et al., 1995; Maestas et al., 2003; Hansen et al., 2005). Increases in human populations have been demonstrated to increase fire frequency in Mediterranean-climate ecosystems (Syphard et al., 2009), thus ex-urban development of sagebrush plant communities will also elevate the risk of frequent fires promoting exotic annual grass invasion and dominance.

The loss of sagebrush communities is a concern in part because these plant communities provide critical habitat for sagebrush obligate and facultative wildlife species. Sagebrush obligate wildlife species populations are of increasing concern. Long-term monitoring of sage-grouse populations has documented a steady decline across their range since the 1960s (Connelly and Braun, 1997; Connelly et al., 2004). Aldridge et al. (2008) suggested that the loss of sagebrush habitat was a critical factor in the extirpation of local sage-grouse populations. Areas of reduced sagebrush and elevated herbaceous cover may provide seasonal habitat benefits, but only when they are a small portion of an otherwise sagebrush-dominated landscape (Dahlgren et al., 2006). Winter diets of sage-grouse consist almost exclusively of sagebrush leaves (Patterson, 1952; Wallestead et al., 1975). Similarly, pygmy rabbits (*Brachylagus idahoensis*) consume large quantities of sagebrush (Green and Flinders, 1980; Shipley et al., 2006). Facultative wildlife species may also depend on sagebrush for a large component of their diets. Mule deer, elk (*Cervus elaphus*), and pronghorn (*Antilocapra Americana*) seasonal diets may also contain large amounts of sagebrush (Mason, 1952; MacCracken and Hansen, 1981; Austin and Urness, 1983).

High quality forage production in sagebrush communities is decreased with exotic annual grass invasion (Hironaka, 1961; Davies and Svejcar, 2008; Davies, in press) and conifer encroachment (Tausch and Tueller, 1990; Miller et al., 2000; Bates et al., 2005, 2011), which could significantly reduce the economic stability of many rural communities. The loss of forage also increases the risk of conversion of additional sagebrush communities to introduced grasslands and irrigated croplands as livestock producers strive to offset the loss in production. The loss of productive native rangelands may compel some livestock producers to consider selling their property for ex-urban development to offset loss of income.

To conserve sagebrush plant communities land managers and policy makers need to: (1) prevent undesirable vegetation shifts from occurring, (2) restore communities invaded by exotic annual grass or encroached by conifers, and (3) reduce and mitigate anthropogenic development. Conserving the sagebrush ecosystem will protect sagebrush obligate and facultative wildlife species, provide sustainable livestock production, maintain ecosystem function, and decrease the risk of catastrophic wildfires.

3. Preventing undesirable vegetation shifts

3.1. Preventing exotic annual grass invasion

Restoring plant communities after they have been invaded by exotic plants is expensive and often fails (Vitousek et al., 1997b; D'Antonio et al., 2001). In addition, seed sources for many native plant species displaced by exotic plant invasion are not available or are exceedingly expensive to obtain for restoration (Davies and Svejcar, 2008). Thus, where possible, there should be efforts to prevent exotic annual grass invasion into intact sagebrush communities to preclude the need for restoration (Radosevich et al., 1997; Byers et al., 2002). The importance of prevention is heightened by the spatial scale of current invasive annual grass problem. With contemporary technology, active management of a problem of this spatial magnitude would require inordinate amounts of capital input and levels of logistical resources that are likely infeasible. Clearly, prevention must play an important role in maintaining the integrity of sagebrush plant communities at risk of conversion to exotic annual grass communities. Preventing exotic plant invasion can be accomplished by focusing on increasing or maintaining the invasion resistance of native plant communities and reducing the propagule pressure of exotic annual grasses (Simberloff, 2003; Davies and Sheley, 2007; Davies et al., 2010b).

The invasion resistance of sagebrush plant communities to exotic annual grasses is largely driven by perennial grasses. Perennial grasses are one of the most important consumers of soil resources in sagebrush plant communities (James et al., 2008) and therefore, the ability of exotic annual grasses to invade native plant communities is inversely correlated to perennial grass density (Davies, 2008; Davies et al., 2010b). However, other functional groups are also important to the use of a site's resources and thereby decreasing invasibility (Davies et al., 2007a; James et al., 2008; Prevéy et al., 2010).

Management actions have significant influence on the invasion resistance of sagebrush plant communities. Overuse by domestic livestock reduces the ability of lower elevation sagebrush plant communities to resist annual grass invasion (Daubenmire, 1970; Mack, 1981; Knapp, 1996). However, Svejcar and Tausch (1991) and Davies et al. (2006) also found exotic annual grasses in sagebrush communities that had not been grazed by livestock. Complete grazing exclusion can also promote exotic annual grass invasion in some situations. Davies et al. (2009) determined that long-term grazing exclusion followed by fire resulted in exotic annual grass invasion, while fire following moderate levels of grazing did not promote invasion. Moderate levels of livestock grazing made the perennial herbaceous component of the sagebrush plant communities more tolerant of fire (Davies et al., 2009), perhaps due to a reduction in crown litter which can decrease fire severity in the vicinity of growing points on perennial bunchgrasses (Davies et al., 2010a).

Severe disturbances should be minimized because they may eliminate native plants and greatly increase the resources available to invasive plants (Sheley et al., 1999; Clark, 2003; Davies et al., 2009). For example, severe fires or other disturbances in sagebrush plant communities are often followed by exotic annual grass invasion (Stewart and Hull, 1949; Evans and Young, 1985; Young and Allen, 1997). However, eliminating all disturbances is not advised. Low severity disturbances are less likely to promote invasion and may actually increase the biotic resistance of the plant community to invasion over the long-term (Davies et al., 2008, 2009). For example, low severity burning of Wyoming big sagebrush plant communities did not result in exotic annual grass invasion (Davies et al., 2007b), even with moderate levels of livestock use (Bates et al., 2009). Low severity disturbances may also increase the ability of sagebrush communities to tolerate potentially more severe disturbances (Davies et al., 2009). Increases in perennial grasses following disturbances that remove woody vegetation are critical to preventing exotic annual grass invasions (Bates et al., 2005; Davies et al., 2009).

Wildfires present a critical risk in conversion of invasion-prone sagebrush communities to exotic annual grasslands (Chambers et al., 2007). Moderate levels of livestock grazing play a vital role in reducing the risk and severity of wildfires by decreasing fine fuel loads and continuity (Davies et al., 2010a). Strategic grazing and other fuel management techniques could be used to interrupt otherwise continuous high fine fuel loads and provide opportunities to suppress catastrophic wildfires or otherwise limit the spread of such fire events. Diamond et al. (2009) demonstrated that strategically grazing exotic annual grass dominated plant communities could reduce fuel loads and continuity enough to

prevent a flame front from carrying across the treated areas even under peak fire conditions. Targeted grazing may be a critical tool for breaking the exotic annual grass-fire cycle by decreasing the probability of fire disturbance (Diamond et al., 2009).

3.2. Preventing conifer encroachment

Restoring infrequent fires in mountain big sagebrush is critical to preventing the continued expansion of conifer woodlands. Similar needs for restoring fire disturbance regimes to prevent woody plant encroachment exists around the world (Samson et al., 2004; Bond and Parr, 2010; Wiens and Bachelet, 2010). Prescribed fires are more efficient than mechanical treatments across large landscapes because they are less costly to apply and control tree seedlings that would be missed with mechanical treatments. Mechanical treatments of conifers also result in an accumulation of dry, combustible fuels on a site that pose a significant wildfire risk (Miller et al., 2005; Bates and Svejcar, 2009).

Restoring periodic fires to sagebrush landscapes threatened by woodland encroachment is challenging because fire is frequently viewed negatively by the public, can be difficult to control, may promote annual grass dominance, and poses some risk to property and life. Furthermore, with the decline in sagebrush and sagebrush obligate wildlife, it may seem counter-productive to burn existing sagebrush plant communities, because fire removes sagebrush from the plant community. However, to successfully maintain the sagebrush ecosystem over time, periodic fires will probably be necessary to curtail conifer encroachment. The key will be to maintain a balance of productive sagebrush plant communities for sagebrush obligate wildlife species, while burning acreages sufficient to halt the continued expansion of woodlands. It is critical that reintroduction of fire be limited to sagebrush communities threatened by conifer encroachment and not applied to Wyoming big sagebrush communities without woodland development and at risk of exotic annual grass invasion. While fire is an important tool to reduce conifer encroachment, at lower elevations it can increase the risk of exotic annual grass invasion (Chambers et al., 2007) and degrade the quality of habitat for sagebrush obligate wildlife (Beck et al., 2009; Rhodes et al., 2010). Furthermore, it may take 25–100 years for Wyoming big sagebrush to recover following burning (Baker, 2011).

Planning for landscape-level burns will be especially challenging, given the impacts on a wide variety of ecosystem services. Implementing large scale prescribed burning projects may require rotationally burning segments of a landscape to control encroaching conifers, but simultaneously providing adequate habitat to maintain sagebrush obligate wildlife populations. These projects would be deployed over decades to allow for recovery of sagebrush in prior burned areas to limit the total reduction of sagebrush dominated acreage at any one point in time.

4. Restoration

4.1. Restoring exotic annual grass-invaded communities

Successful restoration of Wyoming big sagebrush communities invaded by annual grasses is a difficult process (Rafferty and Young, 2002; Eiswerth et al., 2009) complicated by multiple factors including: (1) the complex nature of the problem, (2) deficiencies in knowledge of contextual ecology and restoration technologies, and (3) the large spatial scale of the problem. Restoring annual-grass infested sagebrush communities is a complex problem in which environmental variability defines windows of management opportunity in space and time (Thompson et al., 2001; Boyd and Svejcar, 2009). Wyoming big sagebrush plant communities are drier and hotter than mountain big sagebrush plant communities (West et al., 1978; Winward and Tisdale, 1977; Winward, 1980), thus there may not be as many years (i.e., windows of opportunity) where successful establishment of native vegetation will occur. This problem is even greater where competition from exotic annuals makes success even less likely. The central challenges for restoration in complex ecological environments are to determine the properties that define *existing* windows and/or determine how to create *new* windows of opportunity.

This process is made more difficult by acute deficiencies in our knowledge of the ecological context surrounding the problem. First, our knowledge of the seedling ecology of most native plants is limited with many basic questions unanswered. For example, whereas research indicates that maintenance of perennial grasses is critical to minimizing annual grass invasion (e.g., Davies, 2008), the life history stage(s) (i.e., germination, emergence, or establishment) most limiting to seeded perennial grass species or environmental conditions that are most favorable to success at any of these stages remains unknown. Secondly, we must be able to link plot scale knowledge of mechanisms controlling seedling ecology to the scale at which the problem actually occurs (i.e., the landscape). This will involve, among other things, a dramatic increase in knowledge of variability in environmental conditions over space and time.

While established, adult perennial grasses can compete effectively with invasive annual species (Chambers et al., 2007), the same is not true at the seedling stage; slower growing perennial grass seedlings will be outcompeted by faster growing annual grass seedlings (Young and Mangold, 2008). There are a number of herbicides that can be used to non-selectively kill annual grasses (e.g., glyphosate) or selectively reduce their emergence (e.g., imazapic). However, even if exotic annual grasses are successfully controlled, seeded native perennial bunchgrasses often fail to establish and exotics rapidly reinvade (Young, 1992; Monaco et al., 2005; Rafferty and Young, 2002). To date, there are no cost-efficient techniques to control large acreages invaded by exotic annual grass (Stohlgren and Schnase, 2006).

4.2. Restoring conifer-encroached communities

Compared to exotic grass-dominated sites, successful restoration is more likely in conifer-encroached sagebrush plant communities. Conifers encroaching into mountain big sagebrush plant communities are effectively controlled with mechanical and prescribed fire treatments (Barney and Frischknecht, 1974; Tausch and Tueller, 1977; Everett and Ward, 1984; Skousen et al., 1989; Bates et al., 2000; Rau et al., 2008). The greatest threat to successful restoration of conifer-encroached sagebrush plant communities is post-control exotic plant invasion, especially by invasive annual grasses (Evans and Young, 1985; Young et al., 1985; Baughman et al., 2010). Fortunately, however, many conifer-encroached sagebrush plant communities are at minimal risk of exotic annual grass invasion and steps can be taken to reduce the risk of invasion in susceptible communities, such as winter and spring burning (Bates and Svejcar, 2009).

It is important to recognize woodland development phases when managing conifer encroachment (Miller et al., 2005). Phase I woodlands are dominated by sagebrush and herbaceous species with few trees present. In Phase II, trees co-dominate with sagebrush and herbaceous vegetation. In Phase III, trees dominate vegetation, sagebrush is largely eliminated, and the herbaceous layer is reduced. Cutting one-quarter to one-third of the trees is required in some Phase II and most Phase III woodlands to increase surface fuels to carry prescribed fire through woodlands in early to mid-fall (Miller et al., 2005; Bates et al., 2006, 2011). Spring burning requires higher precutting levels, between 33% and 75% of the stand,

to carry prescribed fire through the woodlands (Bates et al., 2006). Seasonality of prescribed burning can influence the effectiveness of encroaching woodland control and the response of understory vegetation (Bates et al., 2006). Fall burning compared to spring burning can eliminate more trees, but can also result in large decreases in understory vegetation and potentially increase the risk of exotic annual grass invasion (Bates et al., 2006). Spring burning will probably need follow-up management to control trees that survived the burn (Bates et al., 2006). Similarly, mechanically treated woodlands may also need follow-up treatments because tree seedlings and seed often survive and may rapidly reoccupy sites (Tausch and Tueller, 1977; Skousen et al., 1989; Bates et al., 2005). Exotic annual grasses may initially increase in some woodland control treatments, but if sufficient perennial herbaceous vegetation remains, the exotic annual grasses eventually become an insignificant component of the plant community (Bates et al., 2005; Bates and Svejcar, 2009). On sites without adequate understory, favorable response to woodland control requires revegetation (Sheley and Bates, 2008). However, 2–3 perennial grasses/m^2 appear to be sufficient to permit natural recovery after conifer control (Bates et al., 2005; Bates and Svejcar, 2009). Sagebrush and other shrubs often recover after conifer control (Barney and Frischknecht, 1974; Tausch and Tueller, 1977; Skousen et al., 1989), but the rate of recovery can be slow when shrub densities are low prior to woodland control (Bates et al., 2005). Thus, there may be some benefit to post-control sagebrush seeding in woodlands with little sagebrush remaining. Seeded sagebrush can rapidly establish and grow at sites that have been prescribed burned to control encroaching conifers (Davies, unpublished data).

In critical sagebrush wildlife habitat where encroaching conifers are sub- or co-dominant with sagebrush (Phases I and II) cutting conifers without subsequent broadcast prescribed fire post-cutting would be the most prudent treatment option. This would remove the immediate threat of habitat loss to conifer encroachment, while maintaining sagebrush in the plant community. This treatment could also be used to increase the amount of functional sagebrush habitat, so adjacent landscapes could be treated with prescribed fire without significantly reducing the local habitat available to sagebrush obligate and facultative wildlife. However, this treatment is expensive and requires more frequent re-application than prescribed burning to control encroaching conifers (Miller et al., 2005). Thus, this treatment should be limited to habitat that if lost would cause irreversible declines in sagebrush associated wildlife.

Though exotic annual grasses can be a threat after conifer control, these treatments are useful to restore sagebrush plant communities and protect sagebrush wildlife habitat. Priority should be given to areas with minimal risk of exotic annual grass invasion post-treatment and efforts should be made to reduce negative impacts of conifer control on residual desirable vegetation. In treatment areas with minimal understory (pre or post-conifer control), reseeding may be necessary to expedite recovery and reduce the risk of exotic annual grass invasion (Sheley and Bates, 2008). At present, restoration of sagebrush plant communities encroached by piñon and juniper is limited by inadequate resources to apply control treatments across enough landscapes to have meaningful reductions in the area encroached by conifers. Thus, restoring sagebrush plant communities encroached by conifers will require greater resource allocation than is currently applied. Restoration of a fire cycle that will prevent conifer encroachment, but allow sagebrush dominated plant communities to develop is critically needed for long-term success.

4.3. Native versus introduced perennial bunchgrasses

Practitioners in low elevation sagebrush communities (e.g., the Wyoming big sagebrush alliance) often use non-native bunchgrasses in revegetation efforts due to low establishment and limited availability and high cost of native perennial bunchgrass seed (Asay et al., 2001; Epanchin-Niell et al., 2009). In addition, some non-native perennial grasses may remain green longer than natives during the summer period, helping to reduce the incidence of wildfires (Pellant, 1990). Non-native bunchgrasses most frequently used in revegetation efforts are crested wheatgrasses (*Agropyron cristatum* (L.) Gaertn. and *A. desertorum* (Fisch. Ex Link) Schult.) and, at times, Siberian wheatgrass (*A. fragile* (Roth) P. Candargy) (Holechek, 1981). Crested wheatgrass was originally seeded in the sagebrush biome to increase livestock forage and to displace halogeton (*Halogeton glomeratus* (M. Bieb.) C.A. Mey), a plant poisonous to sheep (Miller, 1956; Frischknecht, 1968).

Crested wheatgrass is highly competitive with native perennial bunchgrasses of sagebrush communities and may limit diversity of native species (Hull and Klomp, 1967; Asay et al., 2001). Marlette and Anderson (1986) suggested that stability of crested wheatgrass stands over time may be associated with their ability to dominate the soil seed pool and that diversification of plant communities dominated by this species will involve removal of both mature plants and propagules. At present, the feasibility of restoring non-native *Agropyron* plant communities to their full complement of native species diversity has not been rigorously evaluated. Limited research suggests that success in re-introducing native vegetation following control of crested wheatgrass may vary strongly based on environmental conditions as well as restoration technique (Bakker et al., 2003; Hulet et al., 2010; Fansler and Mangold, 2011). Because of this variability, the most effective restoration treatment regime will likely be dependent on conditions in time and space, making adaptive management necessary (Henderson and Naeth, 2005).

From the standpoint of wildlife diversity, crested wheatgrass has been reported to provide a forage resource for mammalian wildlife (Urness et al., 1983; Ganskopp et al., 1993), but provides limited habitat resources for shrub-associated avifauna (Reynolds and Trost, 1981; McAdoo et al., 1989) and caused decreased densities of small mammal and reptilian species (Reynolds and Trost, 1980). Crested wheatgrass stands do not provide habitat for sagebrush obligate wildlife species until sagebrush reestablishes (Reynolds and Trost, 1981; McAdoo et al., 1989). It will also be important to facilitate perennial forb establishment in crested wheatgrass stands to increase their value as habitat for sagebrush wildlife. In grassland ecosystems, non-native perennial grasses, including crested wheatgrass, may not strongly impact avian abundance and reproduction as long as structural conditions are similar to native habitats (Davis and Duncan, 1999; Kennedy et al., 2009).

Much of the work addressing the influence of crested wheatgrass on ecological processes has taken place in the Great Plains ecoregion (Smoliak et al., 1967; Dormaar et al., 1978; Trlica and Biondini, 1990; Dormaar et al., 1995; Henderson and Naeth, 2005) and thus, probably is not relevant to the sagebrush ecosystem. In sagebrush plant communities, Chen and Stark (2000) found little difference in C and N cycling associated with presence of crested wheatgrass. Similarly, Chambers et al. (2007) reported that low elevation crested wheatgrass sites had similar soil water and nitrate availability compared to low elevation sites dominated by native perennial vegetation. Overall, current research contains little evidence to suggest substantive changes in ecological processes when native perennial bunchgrass is replaced with crested wheatgrass in sagebrush plant communities.

Ultimately, decisions regarding the practical aspects (as opposed to sociologic concerns) of using non-native perennial bunchgrasses in the revegetation context will be influenced strongly by ecological site. On higher elevation mountain big sagebrush sites, use of native species may be more practical given increased resource availability and rates of revegetation success,

and diminished threat of annual grass invasion (Dahlgren et al., 1997; Chambers et al., 2007; Leger et al., 2009). On lower elevation Wyoming big sagebrush sites, where revegetation success is relatively low and the threat of annual grass invasion is high, use of non-native bunchgrass species, such as crested wheatgrass, may represent a prudent interim revegetation alternative from an ecological standpoint (Asay et al., 2001). The benefits of using crested wheatgrass in lower elevation revegetation must be weighed against the potential for inhibition of native plant diversity. While restoration of crested wheatgrass communities to native plant dominance remains problematic (Hulet et al., 2010; Fansler and Mangold, 2011), maintenance of soil resources and ecological processes associated with introduced perennial plant communities suggests that this transition would be much easier than restoring native vegetation on annual grass-dominated sites (Cox and Anderson, 2004; Ewel and Putz, 2004). Establishing some form of perennial grass is key to preventing invasion by exotic annual grass species (Eiswerth and Shonkwiler, 2006; Davies, 2008) and associated degradation of ecosystem function. On Wyoming big sagebrush ecological sites, establishment of crested wheatgrass is substantially higher than native species (Robertson et al., 1966; Hull, 1974; Boyd and Davies, 2010). If exotic annual grasses invade a plant community, they increase the risk that adjacent plant communities will burn frequently and subsequently be invaded (D'Antonio and Vitousek, 1992). Exotic annual grass invasion also decreases soil organic matter, disrupts nutrient cycling, decreases soil water availability, reduces energy capture, increases susceptibility to soil erosion, decreases biodiversity, and promotes frequent fire disturbances (Melgoza et al., 1990; Whisenant, 1990; D'Antonio, 2000; Davies and Svejcar, 2008; Davies, in press). These alterations to site characteristics greatly decrease the likelihood of successful restoration (D'Antonio and Meyerson, 2002). Thus, crested wheatgrass, in certain situations, may be an important species to preventing the expansion of exotic annual grasses (Waldron et al., 2005; Davies et al., 2010b) and conserving important site characteristics.

Although sagebrush seldom establishes in exotic annual grass communities, it often reestablishes in crested wheatgrass stands (Frischknecht and Bleak, 1957; McAdoo et al., 1989). Once established, sagebrush can coexist and persist with crested wheatgrass because of large niche differentiation (Gunnell et al., 2010). Sagebrush-crested wheatgrass communities provide better wildlife habitat for sagebrush obligate and facultative wildlife (McAdoo et al., 1989) and are more desirable than exotic annual grass-dominated plant communities.

5. Anthropogenic development

Anthropogenic development is a global threat to ecosystems, including the sagebrush ecosystem. Energy extraction and exploration and other development have fragmented and degraded sagebrush plant communities, often to the detriment of sagebrush obligate and facultative wildlife species (Braun et al., 2002; Lyon and Anderson, 2003; Naugle et al., 2011). This threat has increased in recent years with the demand for energy and the push for more wind energy development. As the United States increases its domestic energy production to decrease its dependence on foreign sources, impacts will continue to increase (Doherty et al., 2010). At the same time, ex-urban development is also increasing. Ex-urban development is the fastest growing land use in the United States (Brown et al., 2005) and expanding in the western United States at three times that of the rest of the country (Cromartie and Wardwell, 1999).

Because development is a societal issue, as long as the desire for energy and ex-urban residences exceeds the desire to conserve sagebrush plant communities and associated fauna, sagebrush communities will be lost. However, there are options to decrease these types of developments, strategically protect vital areas, and mitigate impacts. Application of the mitigation hierarchy of avoid, minimize, restore, or offset will reduce the impacts of development. Conservation can be improved by using a landscape vision with the mitigation hierarchy, especially where offsets are used, to minimize the impact of development (Kiesecker et al., 2010; Doherty et al., 2010). Offsets are implemented to address the remaining environmental damage after efforts have implemented to avoid or reduce impacts with the goal of achieving a net neutral or positive environmental outcome (Kiesecker et al., 2009, 2010). Strategic placement of offsets can protect high value conservation areas and ensure enough continuous sagebrush habitat to meet wildlife needs. Conservation easements to land trusts, open-space tax initiatives, and watershed- and community-based conservation efforts can also provide the means to protect sagebrush plant communities from development. There are also options for zoning, condemnation, and tax regulations to control development; that, though legal, are increasingly unpopular (Knight, 1999). Although zoning and planning offer pathways to conserve rural lands, they have proven to be relatively ineffective (Brunson and Huntsinger, 2008).

One approach to preventing development of sagebrush plant communities is to keep ranching operations, especially ranching families, on their ranches. Though some have argued that ranching does not conserve native plant communities (Fleischner, 1994; Noss, 1994; Jones, 2000), functioning livestock ranches provide better wildlife habitat and have less exotic species than ex-urban development lands, and, at times, preserves (Knight et al., 1995; Maestas et al., 2003), and can maintain many ecological processes that would otherwise be lost (Brunson and Huntsinger, 2008). Well-managed livestock grazing either has limited impact (West et al., 1984; Rickard, 1985; Courtois et al., 2004; Manier and Hobbs, 2006) or beneficial effects including decreased risk of conversion to exotic annual grass communities (Davies et al., 2009, 2010a). If ranches are not maintained or profitable, they will be sold and most likely developed (Wilkins et al., 2003). Conservation easements are effective tools to provide incentives for ranching operations to continue ranching and not develop their properties. In sagebrush ecosystems experiencing high development pressure, properties with easements had greater evidence of wildlife use and were less fragmented by roads than properties without easements (Pocewicz et al., 2011). Conservation easements that deed development rights in perpetuity to a land trust have the potential to minimize the negative consequences of issues associated with tax and inheritance liabilities by limiting the value of the property for purposes other than agriculture or conservation. Additionally, easements that retire development rights will, by definition, prevent ex-urban development of the property. Reduced inheritance taxes and other tax break incentives can decrease the cost of maintaining privately owned ranches (Sheridan, 2007; Brunson and Huntsinger, 2008) and help preempt the need to sub-divide properties for financial reasons. Decreasing monetary reasons for private landowners to sell their properties for development, either through conservation easements, tax breaks, or other options, is critical to successfully protecting remaining sagebrush communities.

6. Research needs

The most pressing research questions related to conserving sagebrush communities revolve around restoration of exotic annual grass-invaded areas. Research is needed to develop either long-term control of exotic annual grasses and/or permanently reduce their competitive ability. Efforts to use high concentrations of

indigenous soil bacterium (Kennedy et al., 1991, 2001) and fungi (Meyer et al., 2008) that are pathogens to some exotic annual grasses could prove quite valuable in reducing the abundance of annual grasses in the restoration environment. Because exotic annual grasses are so widespread at this point, some form of biological control is very appealing. Other biological control measures should continue to be investigated, but to date none have demonstrated much promise at providing a long-term solution to annual grass invasion and dominance in sagebrush communities.

Even with successful control of exotic annual grasses, restoration is constrained by a lack of knowledge pertaining to seedling establishment ecology and the variability (in time and space) of opportunities to successfully restore these plant communities. This knowledge would enhance restoration success by defining existing opportunities for restoration, developing techniques to create new restoration opportunities, and maximizing success when opportunities arise. Efforts to define existing windows of opportunity will benefit greatly from working within process-based ecological frameworks that identify primary causes of succession and provide direction and structure in uncertain ecological environments (Boyd and Svejcar, 2009). Identifying factors that drive restoration success will increase the utility of research findings over a broader spatial and temporal horizon.

Ultimately, if existing windows of restoration opportunity can be defined, linking remotely-sensed recognition of these windows to seeding technologies (e.g., seed drills) has the potential to maximize seeding success while minimizing logistical and capital restoration expenditures. It is conceivable that we may one day be able to use precision agriculture-like technologies in rangeland seeding that adjust seed rate and other factors in accordance with variability in environmental conditions (Berry et al., 2003). In general, there have not been major advances in the tools and technologies used to implement restoration strategies within the rangeland context. For example, each year managers spend tens of millions of dollars seeding vegetation on western rangelands, predominately with aerial or drill seeding technologies (Knutson et al., 2009). The practice of aerial seeding has changed little since its inception and rangeland seed drills are a rudimentary outgrowth of early 20th Century row crop agriculture. James and Svejcar (2010) demonstrated that drill seeding is not consistently an effective method to revegetate rangelands. To fully realize on-the-ground benefits of our growing knowledge of seedling ecology there must be concomitant improvement in seeding tools and technologies.

While it may be tempting to mimic pre-European settlement conditions in an effort to bolster restoration success, practitioners should be cautious when inferring present-day restoration strategies based on the historical ecology of existing plant species. Historical disturbance regimes and climate patterns that shaped the environment in which perennial species evolved may or may not relate strongly to current disturbance regimes (Whisenant, 1990) and environmental conditions (Tausch et al., 1993; Ziska et al., 2005), particularly in Wyoming big sagebrush communities at risk of exotic annual grass invasion (Davies et al., 2009). Creating new opportunities for restoring sagebrush plant communities will involve modifying the seeding and/or seedling environment to create conditions suitable for germination, emergence and survival; regardless of whether these conditions bear resemblance to the pre-European environment. One advantage to creating new opportunities is that existing opportunities may occur only sporadically in space and time (Boyd and Svejcar, 2009). Such efforts would benefit from, but are not necessarily contingent upon a comprehensive understanding of seedling ecology of native plants. An example of this approach could be the use of seed coating technologies (e.g. Madsen et al., 2010) to delay germination until soil water levels will adequately promote emergence and growth of germinated seeds. Alternatively, creating new management options may be linked to more clearly defining existing windows. For example, Boyd and Davies (2010) found that post-fire seeding success of perennial grasses was several orders of magnitude higher in microsites that were previously under sagebrush canopies as opposed to interspaces between canopies. If the mechanisms driving such differential seeding success can be identified, it may be possible to incorporate those processes into existing technologies to amend the seeding environment; effectively creating new opportunities for successful restoration. Global changes in atmospheric chemistry, climatic patterns, and species distributions may require that past restoration practices be re-evaluated on a broad scale.

While perennial bunchgrasses have been the focus of much of the revegetation effort in sagebrush communities, restoring the full diversity of sagebrush plant community structure and species is important. For example, restoring sagebrush is critical to providing many of the services needed by sagebrush obligate wildlife species. As with perennial grasses, success of sagebrush restoration on annual grass-prone sites has been dubious and varies strongly over time and space (Lysne and Pellant, 2004). Active restoration of sagebrush is often necessary because large burns reduce or eliminate propagule production (Ziegenhagen and Miller, 2009) and less than half of the seeds in the soil seed pool remain viable after 2 years (Wijayratne and Pyke, 2009). Sagebrush seeds are also only dispersed relatively short distances (Young and Evans, 1989), thus considerable time would be required for seeds to reach the interior of large burns. On-going efforts with transplanted nursery or wild sagebrush (e.g., Monsen et al., 2004) are encouraging, but these techniques are labor intensive and costly. The economic feasibility of transplant efforts could be increased substantially by determining where to create strategically located sagebrush islands that could serve as future propagule sources for a larger area (Reever-Morghan and Sheley, 2005; Ziegenhagen and Miller, 2009).

Because of the difficulty and cost of restoring sagebrush plant communities, research investigating how management, disturbances, and climate interact to influence the invasibility of sagebrush communities is critical. For example, Davies et al. (2009) demonstrated that management prior to fire had substantial influence on post-fire exotic annual grass invasion, even though prior to burning few vegetation differences were detected. In addition, research needs to scale-up plot research to the land management scale, because research plots are commonly less than a quarter of a hectare, whereas management actions are frequently applied at scales of thousands to tens of thousands of hectares.

Though the majority of research gaps relate to restoring annual grass invaded sagebrush plant communities, there are a few research needs related to conifer control treatments. Additional research is needed to expedite sagebrush plant community recovery post-treatment and determine the longevity of different woodland control treatments across varying stand development and site characteristics. Such research would also be valuable to allocating resources and planning retreatment needs to maintain restored sagebrush communities.

Mitigation could also be improved by determining where and how anthropogenic development should be implemented to have the least impact. Critical to successfully conserving the sagebrush ecosystem will be determining where offset should be applied to achieve the best conservation results. Improving low-impact energy development is needed to allow the United States to meet its domestic energy production needs, while conserving sagebrush and other native ecosystems.

7. Conclusions

We suggest that any comprehensive effort to maintain or restore an ecosystem must involve the following steps: (1) identifica-

tion of primary stressors and risks to the ecosystem, (2) application of conservation practices which are known to be successful, (3) targeting research efforts on stressors which cannot currently be resolved with management practices, and (4) periodic evaluation of stressors, management opportunities and research needs. It is not unusual to see management efforts expended in areas where success is low and unpredictable, and research spread across many different areas. We suggest that targeting management to practices which are usually successful and focusing research on areas where success is limited will be the most efficient approach from an overall conservation standpoint.

The sagebrush ecosystem and the species dependent upon it are threatened by a wide variety of "natural" and anthropogenic disturbance processes. Other ecosystems throughout the world are faced with similar situations where multiple stressors are simultaneously threatening their sustainability (Samson et al., 2004; Lester et al., 2010; Lindenmayer and Hunter, 2010). Thus, development and implementation of comprehensive ecosystem conservation plans are critical. Research and active management are needed to decrease the impacts of multiple stressors and restore already degraded plant communities. Additionally, limiting anthropogenic development and mitigating its impacts will be critical factors to reducing the degradation of ecosystems. This will require strategic application of the mitigation hierarchy at the ecosystem level and increased use of conservation easements and other incentives to keep private landowners, predominately livestock ranchers in the sagebrush ecosystem, from selling or leasing properties for development.

The general success of restoring mountain big sagebrush plant communities by controlling encroaching conifers and frequent failure of efforts to restore Wyoming big sagebrush plant communities invaded by exotic annual grasses suggest that: (1) future research will be crucial in restoring annual grass-invaded sagebrush plant communities and (2) management should focus on preventing the spread of exotic annual grasses and controlling conifer encroachment. Research could make significant headway in restoring sagebrush plant communities invaded by exotic annual grasses by delineating communities by their probability of successful restoration. Thus, efforts could first focus on sites with the greatest probability of being restored. Identifying the mechanisms that cause restoration success and failure is critical to developing successful restoration techniques and technologies.

Fire is a controversial issue in sagebrush plant communities because of exotic annual grasses and the decline of the sagebrush ecosystem. Fire disturbance needs to be minimized in the drier Wyoming big sagebrush communities and be reintroduced in mountain big sagebrush communities. Priority should be placed on restoring infrequent fires to sagebrush plant communities that are in the early phases of woodland development, especially in areas where fire will still occur without additional treatment. Once this has been accomplished, efforts can be directed at restoring sagebrush plant communities that are in late phases of conifer encroachment. A longer-term view of restoration is needed, where short-term loss of sagebrush dominance to reduce early conifer encroachment is acceptable and practiced where it will not result in a devastating decline in habitat for sagebrush-associated wildlife. Management in areas at risk of exotic annual grass invasion should focus on preventing the continued spread of exotic annual grasses and limiting disturbances, particularly fire, which removes sagebrush from the plant community. This may include seeding introduced perennial grass after wildfires within areas that are already invaded or around the perimeter of existing exotic annual grass infestations. Maintaining the status quo is not adequate, successful conservation of the sagebrush ecosystem will require addressing exotic annual grass invasions, encroaching conifers, and anthropogenic development issues. The threats to the sagebrush ecosystem are significant, but with sufficient resources and time, the outlined strategy can, in the opinion of the authors, be successful. Similar ecosystem conservation plans can be developed for other areas by identifying major stressors, determining and applying conservation practices that are often successful, and identifying where research is needed to overcome conservation limitations.

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