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Fungal Facilitation in Rangelands: Do Arbuscular Mycorrhizal Fungi Mediate Resilience and Resistance in Sagebrush Steppe?☆

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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) may exert profound influences on ecosystem resilience and invasion resistance in rangelands. Maintenance of plant community structure through ecological feedback mechanisms such as facilitation of nutrient cycling and uptake by host plants, physical and chemical contributions to soil structural stability, and mediation of plant competition suggest AMF may be important facilitators in stressful arid environments. Plant-AMF interactions could influence succession by increasing native plant community resilience to drought, grazing, and fire and resistance to exotic plant invasion. However, invasive exotic plants may benefit from associations with, as well as alter, native AMF communities. Furthermore, questions remain on the role of AMF in stressful environments, specifically the mycorrhizal dependency of sagebrush (*Artemisia* spp.) steppe plant species. Here, we review scientific literature relevant to AMF in rangelands, with specific focus on impacts of land management, disturbance, and invasion on AMF communities in sagebrush steppe. We highlight the nature of AMF ecology as it relates to rangelands and discuss the methods used to measure mycorrhizal responsiveness. Our review found compelling evidence that AMF mediation of resilience to disturbance and resistance to invasion varies with plant and fungal community composition, including plant mycorrhizal host status, plant functional guild, and physiological adaptations to disturbance in both plants and fungi. We conclude by outlining a framework to advance knowledge of AMF in rangeland invasion ecology. Understanding the role of AMF in semiarid sagebrush steppe ecosystems will likely require multiple study approaches due to the highly variable nature of plant-AMF interactions, the complex mechanisms of resilience conference, and the unknown thresholds for responses to environmental stressors. This may require shifting away from the plant biomass paradigm of assessing mycorrhizal benefits in order to obtain a more holistic view of plant dependency on AMF, or lack thereof, in sagebrush steppe and other semiarid ecosystems.

Introduction

Arbuscular mycorrhizal fungi (AMF) are root endophytes that can directly influence host plant establishment and survival by increasing uptake of mineral nutrients, primarily phosphorus (Smith and Read, 2008), and increasing water uptake and water use efficiency (Augé, 2001). Arbuscular mycorrhizal fungi, the primary organisms within the subphylum Glomeromycotina (Spatafora et al., 2016), evolved at least 400 million yr ago, possibly earlier (Hedges and Kumar, 2009), and appear to have helped early land plants colonize the terrestrial environment (Smith and Read, 2008). Present-day AMF are obligate biotrophs and rely on obtaining reduced carbon (sugars and fatty acids) from host plants in order to complete their life cycles (Smith and Read, 2008). There are two physiologically distinct components of the fungal partner in mycorrhizas. The external (extraradical) hyphae, or soil hyphae phase, absorbs phosphorus and other nutrients (e.g., nitrogen and potassium) from soil, essentially increasing absorptive root surface area of host plants into soil micropores (Smith and Read, 2008). Internal root colonizing hyphae form exchange sites (arbuscules and arbusculate coils) within cortical cells, wherein nutrients are exchanged for host plant photosynthates (Smith and Read, 2008). Arbuscular mycorrhizal fungi have been implicated as drivers of plant community composition (van der Heijden et al., 1998; Hartnett and Wilson, 1999), as well as contributors to ecosystem functionality

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(Rillig, 2004; Johnson and Gehring, 2007), and are considered to be one of the organisms responsible for observed plant-soil-feedback effects (Klironomos, 2002; Garcia-Parisi and Omacini, 2017).

Rangeland plants may benefit from AMF through increased nutrient uptake (Smith et al., 2011) and water use efficiency (Augé, 2001; Bolandnazar et al., 2007; Pena-Becerril et al., 2016), especially considering these benefits are greater in conditions of moderate nutrient and water stress versus nutrient rich (Johnson et al., 1997) or amply watered conditions (Worchel et al., 2013). Rangeland soils are not only typically low in nutrients and moisture content but also prone to erosion, especially in areas affected by vegetation loss due to drought, fire (Shakesby, 2011), and grazing (with associated soil disturbance) (Trimble and Mendel, 1995; Carbajal-Moron et al., 2017). AMF contribute to soil structural stability through increased soil aggregate formation, which affects water availability, erodibility, carbon cycling, and microbial habitats within aggregates (Rillig and Mummey, 2006). Furthermore, while invasive plant species' responsiveness to AMF varies (Reinhart et al., 2017; Bunn et al., 2015), AMF-mediated plant competition and negative effects of AMF on nonmycorrhizal species (plants which lack the ability to exchange nutrients with AMF) (Reynolds et al., 2006; Vogelsang and Bever, 2009) may increase resistance to invasion in some instances, especially when perennial plants are competing with annuals (Lin et al., 2015).

Relationships between AMF and their host plants have been of scientific interest in rangelands since at least the late 1970s (e.g., Fitter, 1977; Reeves et al., 1979), with the majority of research focusing on identification of mycorrhizal plant species (see Wicklow-Howard, 1994) and AMF influence on competition between native and exotic plants (see Goodwin, 1992). Although early work laid the foundation for considering AMF as mediators of resiliency, it is only over the past decade that technological advancements and decreased costs of genetic sequencing (Lindahl et al., 2013; Kohout et al., 2014) have revealed potential threats to AMF-mediated resilience (i.e., disturbance and invasion), which shift mycorrhizal community structure in the soil (e.g., Busby et al., 2013; Lekberg et al., 2013). Recent reviews implicate soil biota as the focal point of the invasive plant paradigm and have included AMF as a component (e.g., Wolfe and Klironomos, 2005; Reinhart and Callaway, 2006; Pringle et al., 2009). Smith et al. (2010) conceptualized the potential for greater significance of AMF in stressful (i.e., arid) environments. A recent review of soil biota in rangelands (Caesar and Caesar-TonThat, 2010) focused on the possible influence of pathogens and basidiomycetes (which is justifiable) rather than the importance of AMF but acknowledged the need for more research on the impacts of soil biota, generally, in rangelands. Therefore, while there have been reviews of the role of AMF and other soil biota in plant invasion ecology, there remains a need to synthesize contemporary AMF research specific to rangelands, especially sagebrush steppe, which is currently facing considerable conservation risks. We do so here by reviewing AMF ecology in rangelands, with a focus on sagebrush steppe. We begin by examining the role of AMF in mediating ecosystem resilience (Fig. 1). Next, we review AMF disturbance ecology, including the effects of fire and grazing on AMF community structure and function (Fig. 2). We examine the, as of yet, equivocal evidence of relationships between AMF and the sagebrush steppe keystone plant species big sagebrush and bluebunch wheatgrass. Finally, we explore the role of AMF in the invasion ecology of common invasive plant species of sagebrush steppe and conclude with a framework that guides research, assessment, and management actions concerning the role of AMF in rangeland ecosystems threatened by plant invasion.

Resilience and Resistance in Sagebrush Steppe

The semiarid rangelands of the Intermountain West, United States, predominated by sagebrush steppe ecosystems, are experiencing rapid landscape-scale shifts in plant community composition due to historic and prevailing land use practices and increased frequency and intensity of natural disturbances, which allow for the invasion and persistence of exotic plants (Brooks et al., 2004). Invasive annual grasses such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski) are replacing big sagebrush (*Artemisia tridentata* spp. Nutt.) and historically fire-resilient bunchgrass steppe communities with monocultures of spatially contiguous fine fuels (Brooks et al., 2004). The resulting grass-fire cycle (D'Antonio and Vitousek, 1992) promotes the persistence and spread

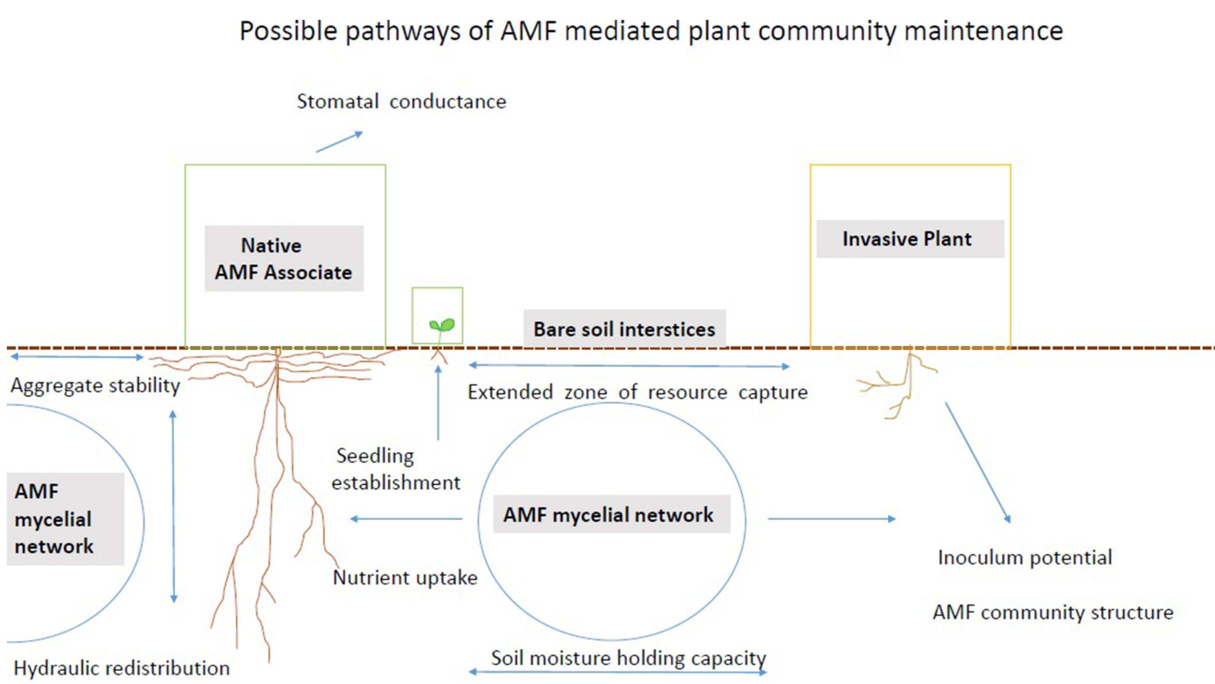

Figure 1. Conceptual diagram illustrating the role of arbuscular mycorrhizal fungi in maintaining a disturbance resilient sage steppe community. Community maintenance is mediated through alleviation of environmental stresses in plant hosts, enhancing seedling establishment through common mycelial networks, maintaining soil structural/functional stability, and maintaining bare soil interstices through enhanced competitive effects of plant hosts and decreased plant performance in nonmycorrhizal invaders. The potential for an invasive plant to negatively affect arbuscular mycorrhizal fungi community structure and inoculum potential is also shown.

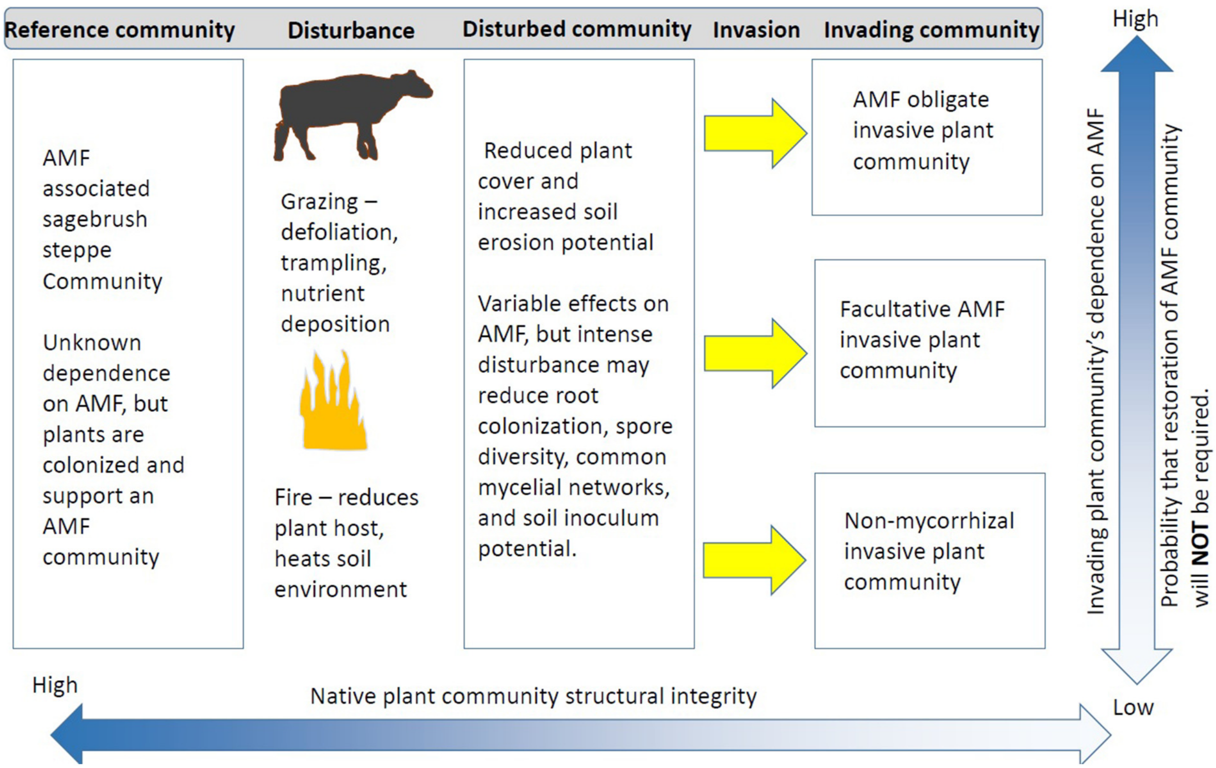

Figure 2. Conceptual diagram illustrating the potential for arbuscular mycorrhizal fungi (AMF) to influence invasion success and restoration outcomes after disturbance-mediated invasion of exotic plant species of varying mycorrhizal status. Plant communities on the left side of the diagram use subtle AMF-mediated negative feedback loops, while plant communities on the right side of the diagram either use AMF-mediated positive feedback loops or create their own positive feedback loops through other methods of soil conditioning and alteration of fire regimes.

of disturbance-associated annual grass species while decreasing the quality of habitat for wildlife such as sage-grouse (Pyke, 2011). Development and persistence of these annual grass—dominated invasions have driven researchers to identify the causative agents that foster maintenance of native plant communities in order to define management strategies to promote resilience to disturbance and resistance to invasion (Bestelmeyer and Briske, 2012; Chambers et al., 2017). The extent to which a native plant community can maintain ecological function and/or return to its previously established composition following a disturbance is a measurement of that community's resilience (Holling, 1973). In arid systems (< 600 mm of annual precipitation) such as sagebrush steppe, where primary productivity, and hence postdisturbance plant reestablishment, is limited by water (Austin et al., 2004), local resilience may be mediated (in part) topographically or biologically by mesoclimates or microclimates that provide greater moisture availability, such as sites located on steep north-facing slopes (in the northern hemisphere) or beneath shrub canopies (Chambers et al., 2014a, b; Germino et al., 2016). Biological mediation of resilient microsites in sagebrush steppe aligns with the stress gradient hypothesis and increased role of facilitation (i.e., fitness supporting symbiosis) in arid systems (Brooker and Callaghan, 1998; Michalet et al., 2006). Facilitation occurs when the benefits of establishment beneath the canopy of a larger plant outweigh the costs of competition for soil resources and reductions in light availability. Keystone plant species such as big sagebrush and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Á. Löve) are common perennial nurse plants that mediate seedling establishment in sagebrush steppe (Jackson and Caldwell, 1993; Reisner et al., 2015). Possible benefits incurred from growing beneath a nurse plant include reductions in evaporative stress through shading, reduced herbivory, access to soil moisture through hydraulic redistribution, and exposure to high densities of beneficial soil biota (Holmgren et al., 1997). In summary, the benefits incurred from AMF potentially occur along a stress gradient curve (Wahl and Spiegelberger, 2016) and include amelioration of nutrient and drought stress, but they are also an important component of a broader theory of biologically facilitated stress amelioration (Revillini et al., 2016), which occurs along a similar gradient (Michalet et al., 2006). Considering the importance of stress amelioration and facilitation in maintaining plant communities in arid systems, AMF may function as belowground facilitators of stress avoidance to some species in sagebrush steppe ecosystems, thus contributing to native plant community resilience and resistance to invasion. However, questions remain as to the benefits of and dependency on AMF by sagebrush steppe plant species and the ecosystem at large, which necessitate understanding the role of AMF in invasion and disturbance ecology, and the environmental conditions (i.e., stressors and stress levels) in which AMF dependency is most likely to be expressed.

Stress Amelioration

In general, drought stress can be ameliorated by associations with AMF through multiple indirect mechanisms, such as AMF altered plant root morphology (Miller et al., 1997), regulation of stomatal conductance (Augé, 2001), and possibly via altered expression of aquaporins, which regulate cross-membrane transfers (Ouziad et al., 2006; Uehlein et al., 2007). Increased phosphorus availability can indirectly increase water use efficiency as well (Singh and Sale, 1991; Payne et al., 1992; and see Waraich et al., 2011). Direct effects of increased water uptake through hyphal cytoplasm and along the exterior of extraradical hyphae have also been proposed to increase drought tolerance in AMF plants (Allen, 2007; Wu et al., 2013). Although the direct transfer of water along or inside AMF hyphae has not been shown to significantly impact the host's overall water budget, research in this area is limited.

Water availability is an important aspect of ecosystem resilience, especially in low-production systems such as sagebrush steppe (Chambers et al., 2014, 2014); however, the contribution of AMF to increased water availability in arid systems is uncertain. In more mesic grasses, AMF are likely to improve growth more in drier soils than in wetter soils when compared with nonmycorrhizal plants (Worchel et al., 2013). It has been suggested that when soil water potential reaches −1.5 MPa, soil water will be restricted to micropores accessible only to plants via mycorrhizal soil hyphae (Allen, 2007). However, if soils are too dry, then soil phosphorus may be inaccessible, even to AMF, and AMF communities may exhibit lower diversity and abundance compared with less stressed systems (Millar and Bennett, 2016). Plant functional traits evolved to deal with extreme drought environments, such as high root-to-shoot ratios, or fine root structure (Comstock and Ehleringer, 1992) may then negate the dependence on AMF to ameliorate drought stress in some systems (Lugo et al., 2015). Root stele tissue circumference, a morphologic trait associated with increased water uptake, may increase in C4 grasses associated with AMF, while in some C3 grasses, including the sagebrush steppe species *Elymus cinereus* (Scribn and Merr) Á. Löve, this root feature may be reduced (Miller et al., 1997). Plants using the C4 photosynthetic pathway are generally considered to incur greater mycorrhizal benefits than C3 plants in the field (Hoeksema, 2010); however, while C4 species respond more positively to AMF in soils with phosphorous deficiencies, C3 plants, at least those adapted to mesic environments, may respond more positively to AMF under (at least artificially induced) drought conditions (Worchel et al., 2013; Augé et al., 2015).

Soil Functional and Structural Stability

Amelioration of drought-induced stress by AMF is related to not only colonization of plant roots but also hyphal colonization of the soil (Augé, 2004). One way AMF may alter available soil moisture is through increased soil aggregation, physically, via hyphal enmeshment (Rillig et al., 2010). Hyphal enmeshment and the creation of water stable soil aggregates also reduce soil erosion potential (Mardhiah et al., 2016) and are expected to increase infiltration rates. Soil aggregate formation may also be mediated chemically via contributions of the glycoprotein glomalin (Rillig and Mummey, 2006). Although current extraction methods do not distinguish between the various sources of glomalin-related soil proteins (Hurisso et al., 2018), glomalin is found in spore walls and the walls of extraradical hyphae of AMF (Driver et al., 2005), and glomalin-related soil proteins have been positively correlated with increased carbon and nitrogen sequestration (Wilson et al., 2009). Carbon inputs via AMF hyphal decomposition (Rillig and Mummey, 2006) and reduced decomposition of lignin (Leifheit et al., 2015) also contribute to increased soil carbon pools. As sagebrush steppe systems have the potential to act as carbon sinks (Svejcar et al., 2008), researchers should consider assessing the contribution (Rillig and Mummey, 2006; Wilson et al., 2009; Leifheit et al., 2015) of different AMF communities to carbon sequestration in these systems.

Although AMF contribute to soil aggregate stability and organic matter content, it is uncertain whether these contributions have a significant impact on soil functional stability. Chaudhary et al. (2009) demonstrated that soils in southern Utah shrublands contained hyphal densities (0.27–7.80 m/cm^3) much lower than those found in a similar study conducted in tall grass prairie (16.9–45.4 m/cm^3); however, relative contributions to subsurface soil stability were similar. Plant cover was the most significant indicator of subsurface soil stability, while biological soil crusts were correlated with high soil surface stability, followed by plant cover and AMF. Surprisingly, organic matter content was not a significant contributor to soil stability (Chaudhary et al., 2009). Relative contributions of plants and AMF to soil stability were again measured in a pot experiment by Hallett et al. (2009). Although AMF did contribute to soil stability, the contribution was greatly outweighed by the effect of, and mechanisms associated with, plant presence. While the impact of AMF on soil aggregation at the site level likely varies depending on plant root and fungal hyphal traits (Rillig et al., 2015), soil aggregation and altered soil hydraulic properties, such as increased soil water holding capacity (Rillig, 2004), appear to play a significant role in maintaining resilient plant communities in arid systems (Briske et al., 2006; Miller et al., 2013).

Arbuscular Mycorrhizal Fungi —Mediated Plant Competition

Arbuscular mycorrhizal fungi may also contribute to native plant community maintenance by enhancing native plant competitive effects against invaders (i.e., increasing resistance to invasion), particularly when the invader is nonmycorrhizal. While nonmycorrhizal plants may represent only a fraction of the global population of vascular plant species (~15%), facultative and nonmycorrhizal plants are common in rangelands as disturbance-dependent invasive annuals, ruderal forbs, and halophytes such as cheatgrass, *Sisymbrium* mustard species, and members of the Chenopodiaceae family (Brundrett, 2009). The growth of nonmycorrhizal plants is often negatively affected by neighboring AMF host plants (Allen et al., 1989; Lambers and Teste, 2013; Veiga et al., 2013). The mechanism for observed deleterious effects on nonmycorrhizal species in the presence of AMF has only been speculated as a cost of defense without the benefit of nutrient exchange (Daisog et al., 2012; Veiga et al., 2013). However, plant identity and an increased capacity of AMF hosts to outcompete nonmycorrhizal plants for nutrients in the presence of AMF contributes to the observed negative effects (Rinaudo et al., 2010). In a meta-analysis on the AMF-mediated plant competition studies, Lin et al. (2015) found plant life history traits to have a significant effect on the outcome of competition with perennial species outcompeting annual species to a greater extent in the presence of AMF. Large, established plants colonized by AMF (e.g., bunchgrasses) may suppress nearby seedling growth of both mycorrhizal and nonmycorrhizal species (Janoušková et al., 2011), presumably due to a reduction in soil nutrients and moisture resulting from AMF hyphal exploration. Extended distances of resource acquisition may be a mechanism for the creation of invasion-resistant bare soil patches surrounding large plants, which would assist in the maintenance of landscape heterogeneity and reduced fuel continuity.

AMF likely play a role in plant competition in all instances where at least one of the competitors is either an obligate or facultative host; however, the extent to which AMF actually alter the outcome of plant competition is in many cases unknown. The instances in which AMF are more likely to facilitate native plant community maintenance are, intuitively, when nonmycorrhizal plants are invading a community dominated by obligate or facultative AMF hosts (see Fig. 1) or when facultative AMF host plants are invading a community dominated by obligate AMF hosts. In rangelands, this can be exemplified by ruderal plant invaders, such as Russian thistle (*Salsola tragus* L.) and tumble mustard (*Sisymbrium altissimum* L.), which are nonmycorrhizal hosts (Brundrett, 2009) and typically establish in disturbed sites where competition with AMF host plants is limited. Facultative host plant invaders such as the exotic annual cheatgrass are also disturbance associated but are less likely to be negatively affected by AMF colonization (Allen, 1984) because they derive some benefit and appear to establish in bare patches between AMF-associated natives. Contrastingly, when the invading plant is an obligate AMF host, an intact AMF community/network is less likely to contribute to native plant community resilience since the invading species may benefit more from the AMF network/community. In fact, obligate AMF host plant invaders may use intact common mycelial networks (CMNs) in order to distribute allelopathic exudates throughout the system (Achatz and Rillig, 2014). Plant competition and AMF-mediated effects could also be subject to adaptation of plant species over time. Waller et al. (2016) examined the influence of AMF on competition between the exotic forb *Centaurea solstitialis* L. and the native bunchgrass *Nassella pulchra* (Hitchc.) Barkworth. Arbuscular mycorrhizal fungi reduced competitiveness of *C. solstitialis* plant genotypes selected from their native range when grown with *N. pulchra*, but this negative effect was less pronounced in *C. solstitialis* genotypes that were selected from their invaded range (i.e., North America). Therefore, as exotic invasive species become more adapted to their invaded communities, the ability for the native community to resist that invasion may decrease.

Arbuscular Mycorrhizal Fungi Disturbance Ecology

Although AMF can influence plant competition between exotic and native species, invasion is often preceded by disturbances such as fire or grazing, which may alter AMF functionality before invasion. Different species of AMF have varying tolerance to abiotic stressors such as drought, extreme temperatures, and salinity (Lenoir et al., 2016). Some AMF species, such as those found in the family Glomeraceae, appear to be ruderal (Chagnon et al., 2013); however, they tend to tolerate some types of disturbances more than others (van der Heyde et al., 2017). Fungal community composition is at least partly driven by plant community composition (see Hartmann et al., 2009), and some species of AMF appear to associate with a broader range of host plants than others (Chagnon et al., 2013; Koziol and Bever, 2016). Therefore, AMF community structure is susceptible to alterations caused by rangeland disturbances (e.g., livestock grazing, fire), which not only directly apply successional pressures but also facilitate exotic plant invasion (see Fig. 2).

Fire

Effects of wildfire on AMF vary with severity and likely mirror the effect on the aboveground community. Reduction in AMF hyphal networks occurs in rangelands after high-intensity fires, which eliminate aboveground vegetation along with host plant root presence (O'Dea, 2007a). Fire has been shown to decrease AMF spore diversity (presumably because of higher soil temperatures), although subsequent alteration of soil chemical and physical properties may influence AMF community reassemblage (Allen et al., 2011). Some studies have shown fire to have little effect on overall AMF spore abundance (Eom et al., 1999) and inoculum potential (Longo et al., 2014). Xiang et al. (2015) recorded a decrease in AMF spore density a year post fire in a semiarid coniferous forest in northern China; however, the AMF community structure and spore numbers returned to prefire levels after 11 yr. A reduction in spore numbers after fire may be less important than the loss of the AMF hyphal network, at least in terms of inoculum potential (Martins and Read, 1997). In a measure of mycorrhizal inoculum potential in *Bouteloa*-dominated grasslands of Arizona, AMF inoculum decreased significantly after soils were subjected to low-intensity prescribed burns (O'Dea, 2007a). The same author (O'Dea, 2007b) stresses the importance of reestablishing the AMF community after fire in order to stabilize soil that might otherwise be eroded. However, depending on soil type and severity, fire may have at least a temporary positive effect on soil aggregate stability (Mataix-Solera et al., 2011). This may be in part due to increases in glomalin-related soil proteins in postfire soils (Sharifi et al., 2018); however, factors such as organic matter content and texture may be more important in shaping postfire soil aggregation (Mataix-Solera et al., 2011).

Although it is unclear whether AMF may confer some level of fire tolerance to individual host plants, it is possible that AMF contribute to the maintenance of fire-resilient plant communities via increased plant water status of individuals, increased moisture holding capacity in soils, and increased competitive effects against annual grass invaders (fine and contiguous fuels). The impact of fires on AMF may vary, but it is highly likely that fire will reduce AMF inoculum potential via reduction of spores, external hyphae, or host colonized roots and decrease AMF species richness. There is a significant lack of research on AMF and fire in sagebrush steppe, with more North American fire-AMF studies conducted in the Central Plains prairies. Fire effects on fungal communities in general likely vary between ecosystems (Dove and Hart, 2017) due to different soils, fire tolerances of plants, and aboveground fuel loads contributing to fire severity.

Grazing

The response of mycorrhizal plants to grazing varies, and it likely depends on a combination of plant species-specific grazing tolerances and host plant responsiveness to AMF colonization (Allsopp, 1998). Eom et al. (2001) found grazing to stimulate AMF root colonization in C4 grasses located in the Flint Hills prairie in northeast Kansas; however, lower root colonization can occur in some plants due to lower photosynthetic rates and reduced translocation of carbon to roots (Ilmarinen et al., 2008). A study of the grazing effects on root colonization rates in 20 sagebrush steppe species revealed significant decreases in colonization after grazing, as well as the apparent loss of one species of AMF from the community (Bethlefalvay and Dakessian, 1984). Medina-Roldan et al. (2008) found no long-term effect of grazing on AMF root colonization in the grazing-tolerant species, *Bouteloa gracilis* (Willd. ex Kunth.) Lag. ex Griffiths, while Allsopp (1998) found grazing to have a smaller impact on extraradical hyphal length in grazing-tolerant plant species than in grazing-intolerant plants. When studying the grazing-intolerant sagebrush steppe species bluebunch wheatgrass and Idaho fescue (*Festuca idahoensis* Elmer) Walling and Zabinski (2006) recorded smaller plant sizes after simulated grazing in AMF-colonized plants than in noncolonized plants of the same species grown in sterile soils. These results suggest that AMF may temporarily gain more benefits than they confer to grazing-intolerant host plants when photosynthetic rates are low. Host plant responses to grazing also depends on fungal species identity, as shown when some species, or combinations of AMF species, appeared to increase subsequent root and shoot biomass gain after clipping *Bromus inermis* Leyss. more than other AMF species that were colonizing these plants (Klironomos et al., 2004). Grazing must also be viewed as a syndrome comprising multiple types of disturbance (trampling, herbivory, nutrient deposition) with individual and combined effects on AMF symbiosis dependent on severity and timing of grazing, as well as plant host and AMF identity (Allsopp, 1998). In general, nitrogen application is assumed to decrease AMF colonization in soils with adequate phosphorus levels but increase colonization in low phosphorus soils (Johnson et al., 2003). Bentivenga and Hetrick (1992) studied the effects of burning combined with mowing and fertilization (as surrogates for grazing effects) on AMF spore abundance, colonization rates, and soil inoculum potential in tallgrass prairie. By yr 3 of the study, nitrogen application in unburned plots had significantly increased spore numbers in randomly sampled soils. Increases in nitrogen may also decrease root colonization and inoculum potential if applied during the growing season (Bentivenga and Hetrick, 1992). Trampling in the absence of defoliation may increase AMF abundance (Liu et al., 2015), as trampling may encourage reallocation of plant resources to roots. Disturbance of the soil surface through trampling may also increase spore dispersal but may have a disruptive effect on CMNs (van der Heyde et al., 2017). Consumption of AMF-colonized roots or spores by grazers may also disperse AMF, as shown in a study at Yellowstone National Park where bison dung was used to successfully inoculate soils with AMF (Lekberg et al., 2011). Yellowstone is also the site of a 40-yr-old ungulate exclosure, which allowed Murray et al. (2010) to detect a positive effect of buffalo grazing on AMF diversity but a negative effect on spore abundance. A recent study in an Australian rangeland found grazing had both positive and negative effects on the relative abundance of AMF among fungal functional groups, with effects differing between grazing type (Eldridge and Delgado-Baquerizo, 2018). Historic cattle, rabbit, and kangaroo grazing had a negative effect on relative abundance of AMF, current cattle and kangaroo grazing resulted in increases in relative abundance, and sheep grazing had no significant effect (Eldridge and Delgado-Baquerizo, 2018). Overall, the role of AMF in plant responses to grazing is likely to be dependent on other plant physiological adaptations to grazing stress such as partitioning and storage of carbon and mineral nutrient resources. It also appears that at least certain species of AMF are better adapted to survive and disperse in environments subjected to some level of grazing, and further study of the impact of grazing on AMF ecology is necessary.

Although it is important to consider fire and grazing as natural aspects of some rangeland ecosystems, it is equally important to consider the combined impacts of disturbance and invasion on AMF functionality. Figure 2 illustrates the potential shift in plant communities from one reliant on AMF to one devoid of mycorrhizal hosts, through disturbance and subsequent exotic plant invasion. Importantly, the role of AMF in rangeland ecosystems and the potential shifts in AMF community composition and inoculum potential are subject to the severity of the initial disturbance and mycorrhizal host status of the native and invading plants.

Plant-AMF Associations in Prominent Sagebrush Steppe Plant Species

AMF-Associated Keystone Shrub–Artemisia tridentata

Artemisia tridentata (big sagebrush) may be the most important plant species in sagebrush steppe ecosystems (Davies et al., 2007). As a keystone evergreen shrub, it provides habitat for a variety of fauna such as sage-grouse, while below its canopy, it supports the establishment and persistence of bunchgrasses and forbs, especially at sites experiencing greater heat and drought stress (Davies et al., 2007; Reisner et al., 2015). Historic removal of big sagebrush to extend grasslands for grazing, combined with invasion of exotic annuals and the associated change in fire regimes, have led to a reduction of big sagebrush in the intermountain west, and restoration and reestablishment can be difficult due to small seed size, competition with annual grasses, and drought-associated mortality (Meyer, 1994). Recently, Davidson et al. (2016) reported varying results from sagebrush inoculation trials, but a meta-analysis of two mesocosm and two field experiments revealed a 42% increase in seedling survival, as well as 84% increase in root colonization in inoculated seedlings (Davidson et al., 2016). Interestingly, Davidson et al. (2016) found no effect of AMF inoculation on plant shoot biomass. Stahl et al. (1998) highlighted the ability of AMF to mitigate drought stress in big sagebrush, as mycorrhizal sagebrush seedlings survived in soils with water potentials as low as −3.22 MPa while nonmycorrhizal seedlings survived only to water potentials as low as −2.77 MPa. These mycorrhizal benefits incurred by big sagebrush are striking considering that the environmental stresses (e.g., temperature and drought) facing seedling establishment may become even greater due to climatic shifts. Increased fire frequency and disturbance-associated stressors such as competition from annual grasses in soils with lowered inoculum potential may also provide a scenario in which sagebrush seedlings require inoculation before planting (i.e., shift to AMF obligate).

Ambiguity does exist concerning the mycorrhizal responsiveness of big sagebrush and the use of AMF inoculum in sagebrush restoration. Dettweiler-Robinson et al. (2013) analyzed survival rates for Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) planted in eastern Washington and assessed the efficacy of (among other things) the use of a commercial AMF inoculum. Although application of hydrogel (a method to reduce drought-induced stress) had a significant positive effect on sagebrush survival, growing the seedlings in soil amended with a commercial inoculum did not increase survival rate after outplanting. The number of samples (10 500 sagebrush plants) and period of observation (8 yr) was impressive, but the authors pointed out that initial plant quality and weather variability were not accounted for (Dettweiler-Robinson et al., 2013). Furthermore, it is possible that the commercial inoculum simply was not effective, as there was no record of root colonization. In a study of 7 sagebrush steppe plant species (Rowe et al., 2007), two different commercial AMF products (one a single species and another a mixture of several species) were ineffective in colonizing roots and initiating plant growth responses when compared with native AMF inoculum. An earlier study by Stahl et al. (1988) suggests that multiple soil factors need to be addressed before simply inoculating soils with AMF to allow for successful reestablishment. Sagebrush seedlings grown in the greenhouse in disturbed soil gained little benefit from AMF after inoculation with native AMF species, while those seedlings grown in undisturbed soil with the same propagule density resulted in greater colonization and 30% more biomass (Stahl et al., 1988). Busby et al. (2011) did not observe a significant response in big sagebrush shoot biomass to inoculation with field soil (versus plants grown in sterile soil), while Reinhart et al. (2017) observed a decrease in shoot biomass versus plants grown in sterile soil. A decrease in shoot biomass, however, may actually be beneficial to a plant's survival under drought stress (Smith et al., 2010).

AMF-Associated Keystone Bunchgrass—P. spicata

P. spicata (bluebunch wheatgrass) is a native perennial, considered a foundation bunchgrass in sage steppe ecosystems due to its dominance and contribution to habitat quality for animals (forage and shelter) and plants. This tussock-type bunchgrass forms habitats for small birds and mammals, facilitates the growth of heterospecific plants (Jackson and Caldwell, 1993), and has been shown to confer invasion resistance under some conditions in sagebrush steppe (Davies, 2008). Studies on AMF associations with bluebunch wheatgrass are limited, but root colonization has generally been low (< 20% of root length) (Thorne et al., 1998; Walling and Zabinski, 2006). Information on bluebunch wheatgrass' responsiveness to AMF is limited (no effect seen in Reinhart et al., 2017); however, research indicates bluebunch wheatgrass gains potential competitive benefits from soil fungal interactions (Callaway et al., 2004). Bluebunch wheatgrass may condition soils in a way that positively affects the growth of heterospecific plants in clayey soils and negatively affects conspecific plants in silty loams (Perkins and Nowak, 2013). Meiman et al. (2006) recorded a positive effect of soil biota associated with bluebunch wheatgrass on the emergence of spotted knapweed (*Centaurea maculosa* auct. non Lam.) but a negative effect on diffuse knapweed (*Centaurea diffusa* Lam.). In a similar study, diffuse knapweed cover decreased from 18% when grown in soils conditioned by weedy species including itself and cheatgrass to 5% cover when grown in soils conditioned by bunchgrass steppe community members including bluebunch wheatgrass, needle-and-thread grass (*Hesperostipa comata [Trin. & Rupr.]* Barkworth), and species of the genus *Lupinus* L. (Kulmatiski et al., 2004). Bluebunch wheatgrass has also, in competition, negatively affected spotted knapweed growth to a greater degree than other bunchgrasses in the community, such as Idaho fescue and prairie June grass *(Koelaria macrantha)* (Callaway et al., 2004). While research indicates bluebunch wheatgrass is associated with AMF, we encourage quantification of mycorrhizal dependence of this species due to its considerable contribution to the ecosystem, current status as a top competitor with certain invasive plants, and potential use in restoration seeding or out-plantings.

Although big sagebrush and bluebunch wheatgrass are arguably two of the most important plant species in sagebrush steppe ecosystems, intact (i.e., uninvaded) sagebrush steppe plant communities can be highly diverse and forb diversity especially has been implicated as an important aspect of habitat quality for sage-grouse (see Pennington et al., 2016). Early studies of AMF in sagebrush steppe focused on identifying colonization of, and AMF species associated with, plants in the community (see Wicklow-Howard, 1994), but few studies have attempted to gain a broad understanding of mycorrhizal responsiveness of sagebrush steppe plants. One such study (Reinhart et al., 2017) aimed to determine the mycorrhizal responsiveness of 68 plants of the Northern Plains. Although their study examined responsiveness outside of plant competition and in a single environmental setting (i.e., no stress variation), it is a starting point that provides potential outcomes and future comparisons of plant-AMF interactions in sagebrush steppe. Although this information is useful, strengths and trajectories of responses (including no response) in single-plant, single-condition mycorrhizal responsiveness studies are context dependent. Factors that may affect mycorrhizal responsiveness for a given plant host include competition from other plants (Marler et al., 1999; Carey et al., 2004), nutrient availability (Johnson et al., 1997; Hoeksema, 2010), water availability (Augé et al., 2015), light availability (Ballhorn et al., 2016), salinity (Caruso et al., 2018), plant host age (Li et al., 2005), AMF species identity and community composition (van der Heijden et al., 1998), and AMF inoculum source (Rowe et al., 2007).

Facultative Invasive Annual Grass—Bromus tectorum

One of the most widespread invaders of sagebrush steppe is cheatgrass *(Bromus tectorum),* an exotic annual grass that creates vast stands and decreases fire return intervals (D'Antonio and Vitousek, 1992). Considered a facultative AMF host, cheatgrass biomass increases are not correlated with AMF root colonization (Allen, 1984), and in some cases AMF colonization may actually decrease cheatgrass performance (Owen et al., 2013; Reinhart et al., 2017). Owen et al. (2013) compared the impact of mycorrhizal colonization on cheatgrass and the native bunchgrass squirreltail (*Elymus elemoides* [Raf.] Swezey) when grown in soils subjected to differing levels of disturbance and found that cheatgrass shoot biomass was weakly negatively correlated with AMF colonization. The correlation was even less pronounced in burn pile — disturbed soils, which were low in AMF hyphae and spore abundance and diversity (Owen et al., 2013). Although increases in some environmental stressors (i.e., warming and drying) may not affect cheatgrass competitiveness (Larson et al., 2017), salt shrub deserts may be more susceptible to cheatgrass invasion (Haubensak et al., 2014). AMF root colonization of rangeland plants decreases with increasing soil salinity (Aliasgharzadeh et al., 2001), and cheatgrass genotypes sampled from salt shrub desert communities were less colonized on average than cheatgrass genotypes found in sagebrush grasslands (Haubensak et al., 2014). AMF community composition in the soil differs between sites invaded by cheatgrass and sites dominated by native plant species (Hawkes et al., 2006; Busby et al., 2013). The root endophyte community of neighboring plants may also be affected by cheatgrass presence (Gehring et al., 2016). Although the autecology of cheatgrass may be similar to other exotic winter annual invasive grasses such as medusahead and ventanata (*Ventanata dubia* [Leers] Coss.), little is published of their mycorrhizal associations or effects on AMF communities (but see Gornish et al., 2016 for a medusahead study).

AMF-Associated Invasive Forb—Centaurea maculosa

Centaurea maculosa aka *stoebe* (spotted knapweed) is an invasive short-lived perennial forb that is highly responsive to AMF colonization (Reinhart et al., 2017). Spotted knapweed relies on AMF to assist in its competitive dominance, at least against native bunchgrasses such as Idaho fescue and bluebunch wheatgrass (Marler et al., 1999; Callaway et al., 2004). In a plant competition study, Carey et al. (2004) grew Idaho fescue and blue grama in the presence and absence of both AMF and spotted knapweed. Using stable isotopes, they estimated that 15% of spotted knapweed's carbon was supplied by Idaho fescue. However, a subsequent study by Zabinski et al. (2002) found no carbon transfer occurring and instead attributed AMF-colonized spotted knapweed's increase in biomass when in competition with a grass to increased phosphorus uptake. Interestingly, spotted knapweed contains much higher foliar phosphorus levels than bunchgrass steppe native plants yet increases available soil phosphorus in some invaded soils (Thorpe et al., 2006). Although increased soil phosphorus may alter the relationships between native plants and AMF, it also implies that spotted knapweed is not outcompeting neighboring plants via AMF-mediated soil phosphorus depletion. Spotted knapweed has also been shown to alter AMF colonization and alter fungal community composition in neighboring plant roots (Mummey et al., 2005; Klein et al., 2006). Further evidence of spotted knapweed's reliance on AMF for competitive dominance came when Callaway et al. (2004) conducted a combination field (competition) and greenhouse (plant-soil feedback) experiment manipulating soil fungi and recorded decreased facilitation by some neighboring bunchgrasses after fungicide application. In the presence of AMF and in competition with *Festuca idahoensis* and *Koeleria cristata,* spotted knapweed biomass increased significantly compared with being grown alone (Callaway et al., 2004). When grown in soil treated with the fungicide Benomyl, spotted knapweed biomass decreased in competition with *F. idahoensis* and *K. cristata* versus being grown alone (Callaway et al., 2004). Spotted knapweed may also benefit from an altered soil AMF community correlated with its own invasion (Mummey and Rillig, 2006). This alteration is not always represented as a negative shift in diversity, as AMF diversity may increase or decrease in soil conditioned by spotted knapweed depending on the initial AMF community (Lekberg et al., 2013; Bunn et al., 2014). The combination of competitive mycorrhizal benefits and fitness conferring root exudates makes this invasive forb difficult to defend against and may be an example where increasing soil phosphorous levels may ameliorate the competitive benefits of knapweed over native species.

Nonmycorrhizal Invasive Forbs—Sisymbrium species

Sisymbrium species such as *S. officinale (L.) Scop., S. loeselii* L., and *S. altissimum* are annual or biennial exotic forbs that invade disturbed areas and roadsides throughout the Intermountain West. *S. altissimum* stands create large seed banks in soil, and at one time they were considered the second most invasive species in the Great Basin after cheatgrass (Howard, 2003). *Sisymbrium* species belong to what is considered a nonmycorrhizal plant family, the Brassicaceae, or mustard family (Brundrett, 2009). However, it is possible that some Brassicaceae in the genera *Biscutella* and *Thlaspi* may form mycorrhizal associations during certain life stages (Orlowska et al., 2002; Regvar et al., 2003). Many mustards, including species of *Allaria, Sisymbrium, Thlaspi, Brassica,* and *Cardaria,* produce glucosinolates, which release toxic isothiocyanates (when acted upon by the co-occurring enzyme myrosinase) that are antifungal (Schreiner and Koide, 1993). *Sisymbrium officinale,* or hedge mustard, and tall hedge mustard *(Sisymbrium loesili)* increase their competitiveness through allelopathy resulting from isothiocyanates and other toxic breakdown products of glucosinolates (Bainard et al., 2009; Blažević et al., 2010). Glucosinolate degradation products identified from numerous mustard plants have suppressed spore germination of AMF, and S. *loeselii* was shown to reduce the AMF inoculum potential in field soils (Schreiner and Koide, 1993; Bainard et al., 2009). Seed germination and growth of native bunchgrass steppe perennials, as well as the invasive spotted knapweed, were also reduced by *S. loeselii* (Bainard et al., 2009). In addition, Fontenla et al. (1999) reported that AMF root colonization in *Pisum sativum* L. was reduced when grown in competition with *Sisymbrium officinale,* but only if *S. officinale* had conditioned the soil for 30 d and reduced the AMF inoculum potential before planting pea. However, root colonization in *Medicago sativa* L. was not altered by *S. officinale* preconditioning in the same study, indicating that AMF or their host plants do not respond the same to a similar loss of AMF abundance in soil (Fontenla et al., 1999). The allelopathic and antifungal properties of mustard plants should encourage land managers to assess the potential toxic effects of these invasive plants on native plant species and AMF alike before further restoration actions.

Nonmycorrhizal Invasive Forb—Salsola tragus

Plant species in the family Chenopodiacea (Chenopods) are often considered nonmycorrhizal (Brundrett, 2009). Although there is evidence of colonization by AMF hyphae, and even vesicles in some Chenopods, colonization by arbuscules or arbusculate coils is rare (Zhao et al., 2017). While a few Chenopods are native in the salt desert rangelands in North America (growing in highly saline and alkaline soils) (Mata-

González et al., 2017), the exotic forb Russian thistle (*Salsola tragus* aka *S. kali)* is a common invader of heavily disturbed areas such as roadsides or abandoned cropland (Mata-González et al., 2012). Unlike the invasive mustards, Russian thistle has not been found to exude fungicidal chemicals in soil. Russian thistle may be allelopathic to some extent (Lodhi, 1979), which could be related to the variety of phenolic acids present in its roots and foliage (Anna et al., 2009); however, it has been used as forage due to high palatability when young and has a high protein content (Beckie and Francis, 2009). In some invaded areas Russian thistle has developed a resistance to several herbicides (Beckie and Francis, 2009), including a recently discovered glyphosate resistance in northeastern Oregon (Barroso et al., 2018). As with some nonmycorrhizal species, AMF appear to have a negative effect on the growth of Russian thistle, with the plants exhibiting reduced stomatal conductance when grown in competition with bunchgrasses and AMF (Allen and Allen, 1984). Russian thistle grown in mining tailings with AMF inoculum exhibited decreased growth when the soils were amended with high levels of phosphorus (Johnson, 1998), and this species responds as if AMF were pathogenic as roots colonized by AMF hyphae quickly turn yellow and detach (Allen et al., 1989). However, in a meta-analysis of weed plant community responses to tillage systems in Canada, Thomas et al. (2004) classified Russian thistle as a weed that is most likely to invade a zero-till system, which is counterintuitive because zero-till systems should be high in AMF inoculum potential. Russian thistle may also potentially increase AMF spore production in the rhizosphere of recently disturbed soils low in inoculum potential (Schmidt and Reeves, 1984); however, it seems unlikely that its presence would benefit AMF site reestablishment outside of its native range due to the plant's invasive nature in North America and poor host status.

Implications for Research and Management

Advancing Understanding and Utilization of AMF Ecology in Sagebrush Steppe Restoration and Management

It is increasingly clear that plant community restoration and management strategies will benefit from synthetic understanding of belowground and aboveground community biotic and abiotic conditions and interactions (Heneghan et al., 2008; Kardol and Wardle, 2010; Koziol and Bever, 2016). However, the current body of research regarding the role of AMF in assisting or conferring resistance against exotic plant invasion in the Intermountain West suggests that a deeper and more explicit integration of knowledge about mycorrhizal fungi and their impact on the different plant species in this system is necessary in order to confidently complement existing aboveground-oriented approaches to invasive species management with AMF management techniques. Conceptually, a mycologically based approach to invasive plant management would seek to systematically understand and harness the role of AMF in stress amelioration and competitive interactions, as well as to understand the soil conditioning effects of invasive plants as they relate to ecosystem function (see Fig. 2) and alterations of native plant community maintaining ecological feedbacks (see Fig. 1). For AMF, hypotheses that address questions concerning the degree of reliance on AMF for plant species' fitness and community resilience, as well as the potential shifts in AMF community structure and inoculum potential occurring due to disturbance and invasion, should be pursued (Fig. 3). In the following section we outline a framework to specifically understand what role AMF may or may not play in mitigating invasions in sagebrush steppe ecosystems. While conceptual frameworks are in place to guide research concerning AMF contributions to plant invasion, generally (Pringle et al., 2009), this framework is an applied approach, targeted to rapidly assess the role of AMF in rangeland plant invasion and to direct management toward more effective restoration that will increase native community resilience and resistance.

Assessment 1: Mycorrhizal Host Status

Although information about the mycorrhizal status of the plants of interest at a particular site may be present in the literature, the first assessment for a plant of unknown mycorrhizal status is to determine the extent of root colonization (e.g., using the simple grid line method). This assessment can be refined to include measures of different fungal structures in the roots (particularly arbuscules) that can provide some added clues about potential nutrient exchange between the plant and associated AMF (Schreiner and Scagel, 2016). We stress the need to carefully identify roots by tracing back to crowns when collecting AMF colonization data from mixed plant communities and also to sample at multiple times over the active growing season. Root colonization data are also useful when assessing inoculum potential of a commercial, or locally sourced inoculum, or potentially degraded soil. Four separate outcomes exist when comparing the host status of one native and one invasive plant: A) both plants are colonized, B) only the native plant is colonized, C) only the invasive plant is colonized, and D) neither plant is colonized. If none of the plant species of interest are colonized by AMF (outcome D, Fig. 3), then research should focus on understanding the roles that other factors play in influencing competition such as plant functional traits (Kunstler et al., 2016). AMF could potentially play a role in the plant community dynamics from outcomes A, B, or C, leading to the assessment of mycorrhizal benefits under competition.

Assessment 2: Mycorrhizal Benefits

The second tier of assessments should focus on mycorrhizal benefits to understand whether AMF influence competition among the native and invasive plants at the site in question. These assessments should be conducted with the native and exotic plants grown in competition, with and without the influence of AMF (locally sourced), and under varying nutrient concentrations (Johnson et al., 1997) and environmental conditions, such as drought, heat, salinity, or grazing stress. Cryptic contributions of AMF to plant fitness, such as effects of "hidden" phosphorus uptake (Smith et al., 2010), protection from pathogens (Wehner et al., 2010; Hohmann and Messmer, 2017), contributions to seed abundance or viability (Hartnett et al., 1994), and amelioration of mortality-inducing stress (e.g., extreme heat, cold, drought) (Davidson et al., 2016) may not be measured as an increase in biomass, but rather an increase in survival. The metrics used for mycorrhizal benefit studies are commonly measures of total biomass, as well as root-to-shoot ratio, and specific leaf area; however, to more accurately assess AMF contributions to plant fitness (i.e., AMF dependence), measures of reproductive structures and survival and/or recruitment rates of offspring should be considered (Hartnett et al., 1994; Jones and Smith, 2004). We stress the importance of conducting such assessments under conditions as close as possible to the site, if not actually in the field (outplanting inoculated seedlings or experimentally applying fungicide), to avoid overestimating the impacts of individual species, which may be negated in a more diverse community setting than the greenhouse (Heinze et al., 2016). If conducting greenhouse experiments, plants should be grown in soil collected from the site and, if necessary, inoculated with AMF species present in the field (see Fig. 3, assessment 3). Possible hypotheses for assessments of mycorrhizal benefits incurred in competition are 1) the native plant performs better with AMF, 2) the invader performs better with AMF, or 3) AMF does not alter the outcome.

Although host and nonhost invasive plants may alter AMF community composition in the soil, it is of particular importance to understand the soil-conditioning effects of nonmycorrhizal invaders. If the native plant of interest is colonized but the invader is not (Fig. 3, outcome B), then mycorrhizal growth benefits should be assessed for the native plant when it is grown in both soil from a noninvaded site and soil dominated by the invasive plant, preferably from a multigenerational monoculture. If the plant grown in native soil performs better than the plant grown in invaded soil and there is a difference in either colonization rate or AMF community composition in the roots, then it is likely the invader has decreased soil inoculum potential or altered AMF community

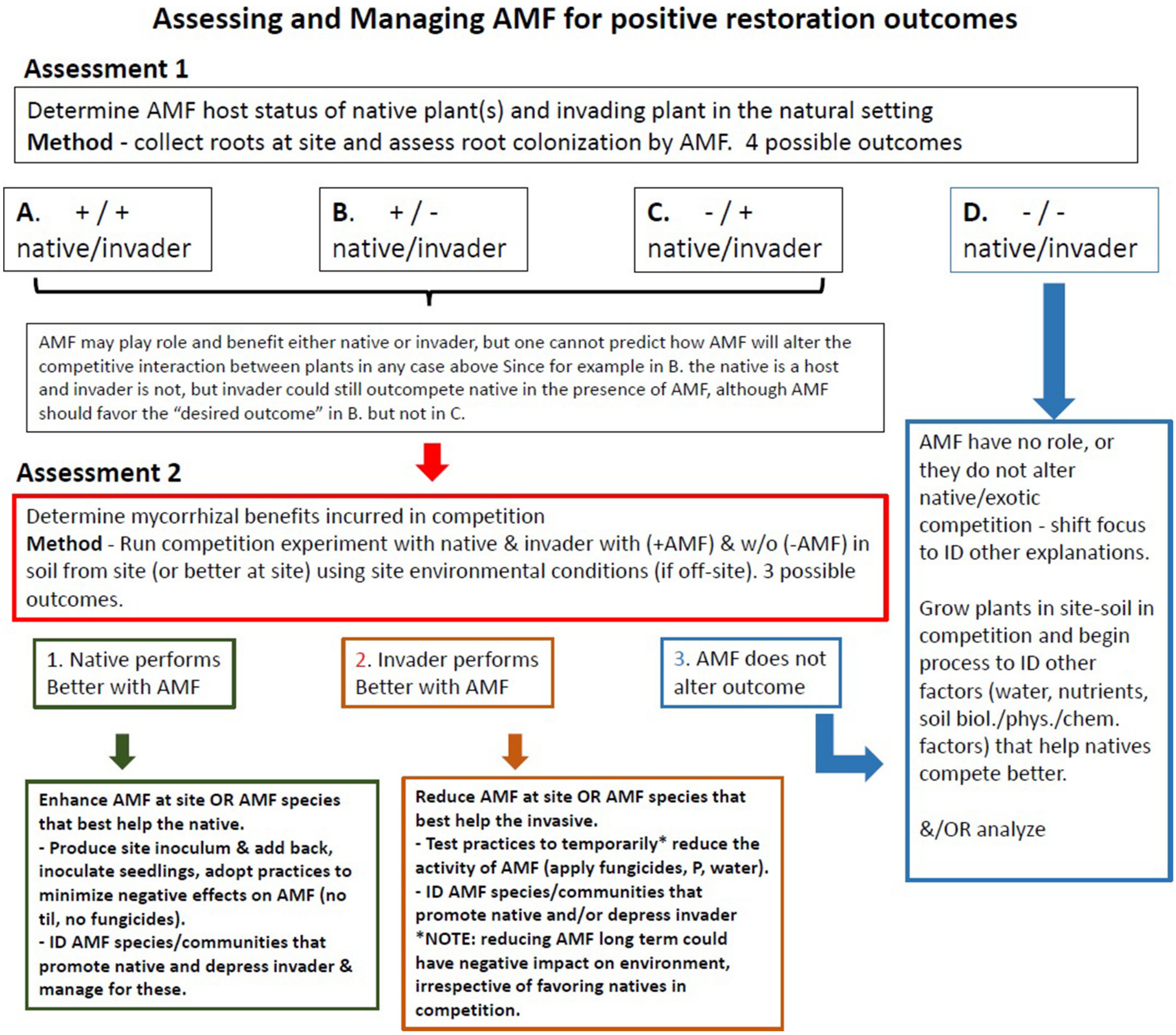

Figure 3. Flow chart outlining the assessments, methods, and outcomes to understand the role of arbuscular mycorrhizal fungi in plant invasion at a given site. Emphasis is placed on assessing results of interactions between dominant native and invasive plant species of varying colonization status (+ = colonized by AMF; - = non-mycorrhizal) in the presence and absence of AMF inoculum in the soil. A mycologically-based approach to invasive plant management seeks to understand mycorrhizal fungi mediated interactions between native plants, invasive plants and the environment in order to conserve, promote, and restore native plant community maintaining fungal feedbacks and will complement current above-ground oriented paradigms.

composition in the soil. In this case, reestablishment of the native plant community may be hindered and further restoration actions to reestablish preinvasion AMF community structure should be considered.

Assessment 3: AMF Community Composition

Assessing AMF community composition in the soil and plant roots can be useful to determine if an invasive plant has altered the AMF community in the soil or neighboring native plant roots or a native or invasive AMF obligate is benefitting from a particular AMF community or species. Advancement in molecular research concerning AMF communities, including the creation of species-specific primers (i.e., Krüger et al., 2009; see Kohout et al., 2014 for a comparison of primer sets) and a decrease in cost of genetic analysis (Lindahl et al., 2013), has made these assessments viable options for researchers, but the methods are still unlikely to be of direct interest to rangeland managers. High-throughput next-generation sequencing (i.e., Illumina) allows for quick, inexpensive analysis using short amplicon lengths but high numbers of reads (Lindahl et al., 2013). Amplicon length of previously established series for 454 pyrosequencing may be inadequate for Illumina sequencing, and currently, shorter amplicon lengths based on NS31 and AML2 primers are emerging (J. Zhang et al., 2016). Alternatively, broader fungal primers may be necessary to capture the breadth of mycorrhizal endophytes, which could include members of the phylum Ascomycota such as dark septate endophytes (DSE). In this instance, the broad fungal primers used in the past have been ITS1 and ITS4; however, recent use of ITSoF7 and ITS4R has achieved genus-level identification of both AMF and DSE (Kohout et al., 2014; Gehring et al., 2016).

Another common measure of AMF community structure is the identification of spores present in soils through extraction and identification by microscopy (Walker, 1992). The taxonomy of AMF is based on spore morphology and has been largely supported by molecular phylogenies (Redecker et al., 2013). Furthermore, spore microscopy may result in similar results when compared with some molecular methods of AMF community analysis (Gamper et al., 2008; Wetzel et al., 2014). However, identifying AMF spores or fungal DNA in soil samples does not mean that the species identified will colonize the plant roots at the site in question or provide quantifiable benefits (Hempel et al., 2007).

Restoration Actions

If native sagebrush steppe plants perform better against invaders in the presence of AMF, then restoration actions should focus on increasing

AMF colonization of desired plant species, especially with AMF species that are most beneficial. Restoration of sagebrush steppe, especially of big sagebrush communities, can be wrought with failure due to factors such as competition with native seeded bunchgrasses (Rinella et al., 2015), competition with exotic annual grasses in areas of inadequate precipitation (Davies et al., 2011; Arkle et al., 2014; Knutson et al., 2014) and slow recovery times (Arkle et al., 2014; Mata-Gonzalez et al., 2018). Although, as mid to late seral components of the system, it would make sense for big sagebrush to require specific soil characteristics (e.g., nutrients, soil depth, soil moisture, soil biota) to compete successfully against early and midseral plants, so far AMF inoculation has not been as successful in increasing restoration success for big sagebrush (e.g., Dettweiller-Robinson et al., 2013) as it has been for late seral species in more AMF dependent systems such as the Great Plains (Koziol and Bever, 2017).

If the restoration area requires removal of invasive species, methods will be site specific, but limiting severe soil disturbances such as topsoil removal, chaining, and tilling (especially deep tillage) is paramount in maintaining an intact CMN (Kabir, 2005). Once undesired plants have been removed, seeding or planting with little to no fallow time will help preserve soil inoculum potential levels (Thompson, 1987). Prescribed fire is a natural plant removal method and, depending on the severity, may have a low impact on the AMF community (see Disturbance section earlier). The herbicide glyphosate, if accidentally applied to native plant foliage, can decrease AMF and DSE colonization (Druille et al., 2016). Glyphosate applied to the soil can decrease spore viability in grassland systems (Druille et al., 2013) and may lead to decreases in colonization of subsequent plantings (Ronco et al., 2008). The forb-specific herbicide Picloram appears to have no negative effect on AMF, even when applied directly to mycelium (Lekberg et al., 2017). However, depending on the mycorrhizal status of the removed invasive and remaining species in the plant community, an indirect effect of herbicide application may be an altered AMF community (Lekberg et al., 2017). However, even after removal, invasive plant species such as spotted knapweed, which are highly colonized by a diverse AMF community (Mummey et al., 2005), may leave an AMF legacy less in need of restoration than a poorer AMF host invader (Lekberg et al., 2013; Lekberg et al., 2017) and negate the necessity of restoration methods such as inoculation.

Successful restoration of site-appropriate inoculum (i.e., AMF species that benefit natives over invaders) is the goal. This may be accomplished by amending the restoration site with AMF inoculum (which could or could not be native to the site), transplanting AMF with soil from a similar ecosystem (Carbajo et al., 2011), planting seedlings that are already colonized by AMF, or seeding the site before the restoration planting with a plant host that promotes the desired increase in soil inoculum potential (Lekberg and Koide, 2005). AMF inoculum is currently being used in restoration efforts across ecosystems in order to increase establishment and growth of planted natives (Torrez et al., 2016; Koziol and Bever, 2017; White et al., 2017) and may be of greater importance in restoration of late-successional plant species in AMF-dependent systems like the Great Plains (Koziol and Bever, 2016). Koziol and Bever (2017) reintroduced native AMF species cultured from a similar ecosystem by inoculating early and late-seral "nurse" plants in the greenhouse and then outplanting to a prairie restoration site in Indiana. Some late-seral plant species appeared to be highly dependent on inoculation with AMF from a local source and did not survive without the treatment. Commercial inoculum that may consist of only one, or a handful of more generalist AMF species, may not be the most effective strategy when seeding or planting late seral plant species after a disturbance (either natural or restoration associated) since the desired outcome may rely on specific AMF species and soil characteristics (Stahl et al., 1988; Rowe et al., 2007). Furthermore, allochthonous (i.e., not cultured from the site) inoculum may introduce AMF species or genotypes that compete with in situ AMF for root space (and other resources) in inoculated plants and their in-field neighbors (Janoušková et al., 2017). Maltz and Treseder (2015) conducted a meta-analysis on 28 mycorrhizal inoculation field studies conducted in ecosystems ranging from tropical forests to desert shrublands and found locally sourced (site-specific) inoculum increased root colonization of AMF greater than commercially sourced inoculum. Locally sourced inoculum is likely to be more useful and poses less risk of introducing a new species of AMF to a site with unknown consequences. However, care must be taken to not also transplant pests or pathogens along with local AMF.

Maintaining appropriate plant hosts and the associated soil characteristics (e.g., texture, chemistry) to which the native/desired AMF are adapted through revegetation and soil amendments is also of importance. While bypassing succession during postdisturbance replanting of native species is commonplace (i.e., outplanting or seeding desired late successional species vs. early seral), considering an initial planting of highly colonized, quickly growing native plants (e.g., early or midseral forbs) might be beneficial in more closely recreating the preinvasion/disturbance AMF community and CMN (Busby et al., 2011). This strategy proved somewhat successful for Duponnois et al. (2011) when they planted the AMF-dependent shrub *Lavandula stoechas* L. (French lavender) alongside outplantings of the rare tree species *Cupressus atlantica* (mountain cypress). The lavender plants seemingly conditioned the soil (including the AMF community) to the benefit of mountain cypress, but these benefits were only apparent 3 yr after planting and were not greater than benefits incurred from direct inoculation of mountain cypress seedlings with AMF. For larger-scale projects, restoring the soil to a condition that favors AMF presence through organic matter amendments (specific to desired AMF community soil habitat requirements) may be more viable than large-scale broadcast inoculation (Johnson, 1998). Biochar application, more common in agricultural systems, has been recommended for use in rangelands (Stavi, 2012) and may be a possible amendment strategy to increase nutrient availability, carbon sequestration, and mycorrhizal colonization (see Lehmann et al., 2011). However, the effects of biochar amendment on nitrogen availability may actually benefit invasive species more than natives, but this effect is likely system dependent (Adams et al., 2013; Laungani et al., 2016).

If an undesired plant community is currently gaining competitive benefits from a mycelial network (Fig. 3, outcome 2), altering soil nutrients, such as adding phosphorous to the soil, may decrease the undesired advantage. McCain et al. (2011) demonstrated a fungicide application management strategy when promoting forb establishment in a C4 grass—dominated tall-grass prairie; however, long-term reduction of AMF may be detrimental to soil structure and function and may have unforeseen consequences in plant competition. It is also possible that the invading plant would benefit less from an alternative AMF community, in which case planting native AMF nurse plants that are known AMF community drivers,or inoculating with alternative AMF species (alternative seral stage mix, or competitive generalist monoculture) may provide the invader with less of an advantage.

Conclusion

The potential for AMF to contribute to resilient rangeland ecosystems could occur because AMF ameliorate environmental stress, particularly from drought, improve soil structure and function (i.e., stability and moisture holding capacity), and mediate plant competition between natives and invaders. While increased rate and severity of disturbance, as well as subsequent exotic plant invasion, threaten to alter both plant and AMF communities, the impact on AMF and their role in invasion are less certain and depend on the type and severity of the disturbance, the AMF community composition and soil inoculum potential, as well as the AMF host plant status and relative dependency (or responsiveness) of the native and invasive plant species. In sagebrush steppe ecosystems, while two of the most ecologically important plant species (big sagebrush and bluebunch wheatgrass) are AMF hosts, their responsiveness to AMF in the field while in competition with, and relative to that of the invading plant, is not predictable. Invasive plant species' AMF host status, dependency levels, and impact on AMF communities varies significantly; therefore, restoration approaches that include AMF need to be tailored to the specific invasive plant and the native ecosystem in question. Restoration practices aimed at increasing mycorrhizal benefits for native plant species should likewise only be applied when the response of the plant community is fully understood and aligns with management goals. Ultimately, AMF restoration is likely most impactful on small scales at sites identified as high-priority links, remnants, or restoration islands.

Although this review is rangeland centric, all plant communities are susceptible to climatic shifts, abiotic and biotic stresses, and exotic plant invasion. Although soils in more mesic ecosystems may be less susceptible to aboveground shifts in alternative stable states (Bansal and Sheley, 2016), with less impact on AMF functions and community composition, it is possible that shifts in global climate and land use patterns will create locally novel stress and disturbance scenarios analogous to those driving state-transition dynamics in arid ecosystems (i.e., megadisturbances) (Millar and Stephenson, 2015). The current challenges are to understand the complex interactions between native plant and AMF communities including the mycorrhizal benefits incurred under scenarios of varying levels (i.e., along a gradient) of stress, disturbance, and invasion. This will require the use of molecular analyses tools to fully understand the specific AMF species or combinations of species on which plants are most dependent; however, the bulk of the initial research should focus on competition studies in the presence and absence of AMF.

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