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Sagebrush Ecosystems are More Than *Artemisia:* The Complex Issue of Degraded Understories in the Great Basin ☆

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ABSTRACT

Plant communities in a stable, long-term state with high sagebrush cover and low desirable perennial herbaceous cover and/or relatively high invasive annual cover are widespread across the Great Basin and distinct from areas affected by wildfire. Restoring these areas, collectively called "degraded sagebrush understories," and preventing future degradation are management challenges that require maintaining desirable levels of sagebrush cover while simultaneously increasing understory perennial abundance and diversity. Defining degradation based on a firm grasp of current and potential vegetation composition is a fundamental aspect of setting restoration goals and selecting methods. Assigning degraded status to any given site is also a considerable challenge in many sagebrush landscapes due to widespread (and long-standing) lack of intact herbaceous plant communities in some landscapes, as well as high interannual variation in herbaceous community composition (particularly cover). In this manuscript, we provide a workflow for defining degraded understories and present a framework for identifying restoration approaches emphasizing the pathways (causes) of degradation in this system, such as historical cultivation, inappropriate grazing, invasive species, and drought, as well as the size and extent of degraded areas. We also describe the relative paucity of well-documented successful restoration approaches for degraded understories, particularly for one-time restoration treatments. This lack of success may be due to lack of propagules, potential competition from sagebrush, invasive species, and/or altered soil conditions. Multiple restoration treatments in specific sequences and/or years may increase success; however, the effectiveness of these techniques is uncertain due to infrequent implementation and rigorous evaluation across a range of environmental conditions. Due to the extent of degraded understories in Great Basin sagebrush ecosystems, meeting biome-level conservation goals will likely require additional research to characterize the types and development pathways of the degraded understories, spatiotemporal recovery or ongoing degradation patterns, and targeted restoration techniques.

Introduction

Large areas of the cold desert sagebrush (*Artemisia* sp.) shrublands of North America, an increasingly threatened biome (Knick et al. 2003; Doherty et al. 2022; Smith et al. 2022), are categorized as "degraded understory" vegetation based on the combination of abundant native shrubs with a lack of desirable understory species, a state that is generally described as complex and difficult to restore and manage (West 2000; McIver and Starr 2001; McIver et al. 2010; Dunwiddie and Camp 2013; Pyke et al. 2015). This combination of intact native overstory with a depauperate understory presents particular management challenges in sagebrush ecosystems because conservation efforts in the region have focused on retaining and increasing sagebrush canopy cover. Sagebrush is highly vulnerable to fire (Ziegenhagen and Miller 2009) and recovery is slow and sporadic due to infrequent windows of favorable weather for recruitment at lower elevations (Knutson et al. 2014; Shriver et al. 2018). However, lack of native understory vegetation is also a particular management concern in sagebrush

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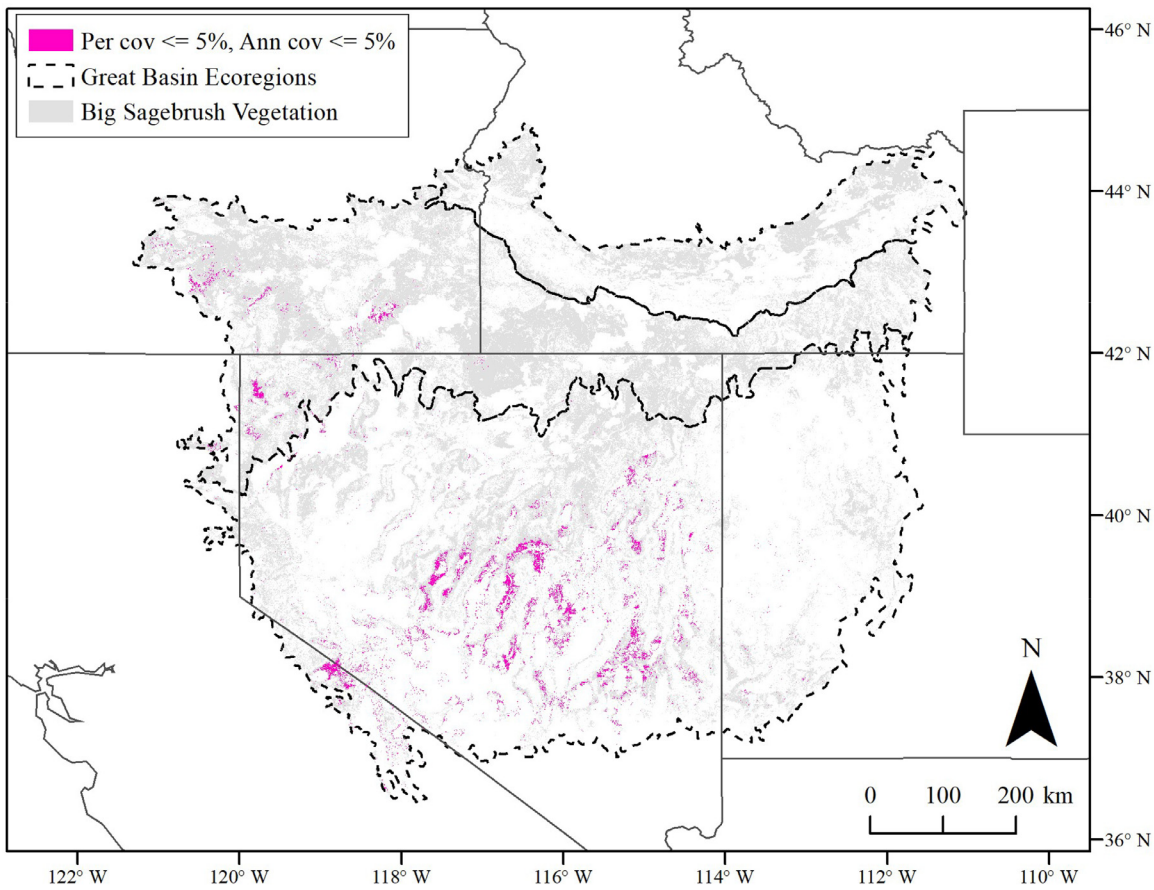

Figure 1. Sparse understory degraded sagebrush vegetation. Defined as high shrub cover and low tree cover, with sparse herbaceous cover (tree ≤ 5%, shrub ≥ 10%, perennial herb ≤ 5%, annual herb ≤ 5%, coordinate system: WGS84).

ecosystems because herbaceous understories are vital to wildlife habitat and livestock forage and provide the majority of plant diversity (Anderson and Inouye 2001; Pennington et al. 2016). Degraded sagebrush understories are predisposed to conversion to non-native annual grasslands if burned, due to lack of competition post fire from perennial herbaceous species (Davies et al. 2012; Boyd 2022), and are vulnerable to a positive feedback cycle between increasing annual grass invasion (Smith et al. 2022) and higher fire frequency (Balch et al. 2013).

Degraded understories may be extensive across Great Basin ecosystems, with more than 25 000 km^2 (13%) of big sagebrush (*Artemisia tridentata* Nutt.) vegetation meeting at least one type of degraded understory as defined here (Great Basin ecoregions, based on functional class cover estimates, range: 5 000–18 000 km^2, 3–9%, for details, Figs. 1–3). Other rough estimates have described the extent of degraded sagebrush as even higher (50%, West 2000). However, as described in subsequent sections, defining the problem of degraded understories, let alone addressing the issue, is complex and associated with multiple knowledge gaps. For example, the development of persistent degraded understories are linked to lack of fire and disturbances, such as inappropriate grazing or cultivation, but may also be the result of historical interactions with soil and climate factors and/or current trends in climate change and annual grass invasion (West 2000; McIver and Starr 2001; McIver et al. 2010; Dunwiddie and Camp 2013; Pyke et al. 2015; Doherty et al. 2022; Smith et al. 2022). Given the extensive areas affected, improving understory composition in these degraded communities may be a key element in maintaining and enhancing habitat for sagebrush associated species, such as greater sage-grouse *(Centrocercus urophasianus),* and reducing risk of conversion to invasive grass or bare ground states. However, restoring degraded understories may be more complex than typical post-fire restoration, given the presence of a functional shrub overstory, and unknowns with respect to site potential following disturbance (Dunwiddie and Camp 2013).

Despite the importance of this vegetation state for biome management in sagebrush ecosystems, “degraded understory” is defined in various ways. Here, we define degraded understories as *areas with long-term (stable) community composition with moderate to high abundance of sagebrush species* (*Artemisia* L.) *and low relative and/or absolute desirable herbaceous species abundance compared to reference sites* (Fig. 4). Non-*Artemisia* species may be part of the high overstory shrub cover in some circumstances. We also allow for a broad definition of desirable herbaceous species based on reference site composition and possibly management goals. For example, both annual and perennial herbaceous species may be included in the “desirable” category in some circumstances, whereas perennials alone may be considered in others. Non-native seeded (as compared with invasive) species, generally perennial grasses, may be considered desirable or neutral in some management scenarios. Divergence in community composition relative abundance and/or species identity, not just functional group abundance from reference sites, may also be an indicator of degraded states in specific areas. For example, high relative cover of disturbance-tolerant perennial grass (e.g., Sandberg’s bluegrass, *Poa secunda* Vasey) compared with the later successional, typically dominant larger perennial grasses (e.g., bluebunch wheatgrass, *Pseudoroegneria spicata* [Pursh] A. Löve) could suggest understory degradation even

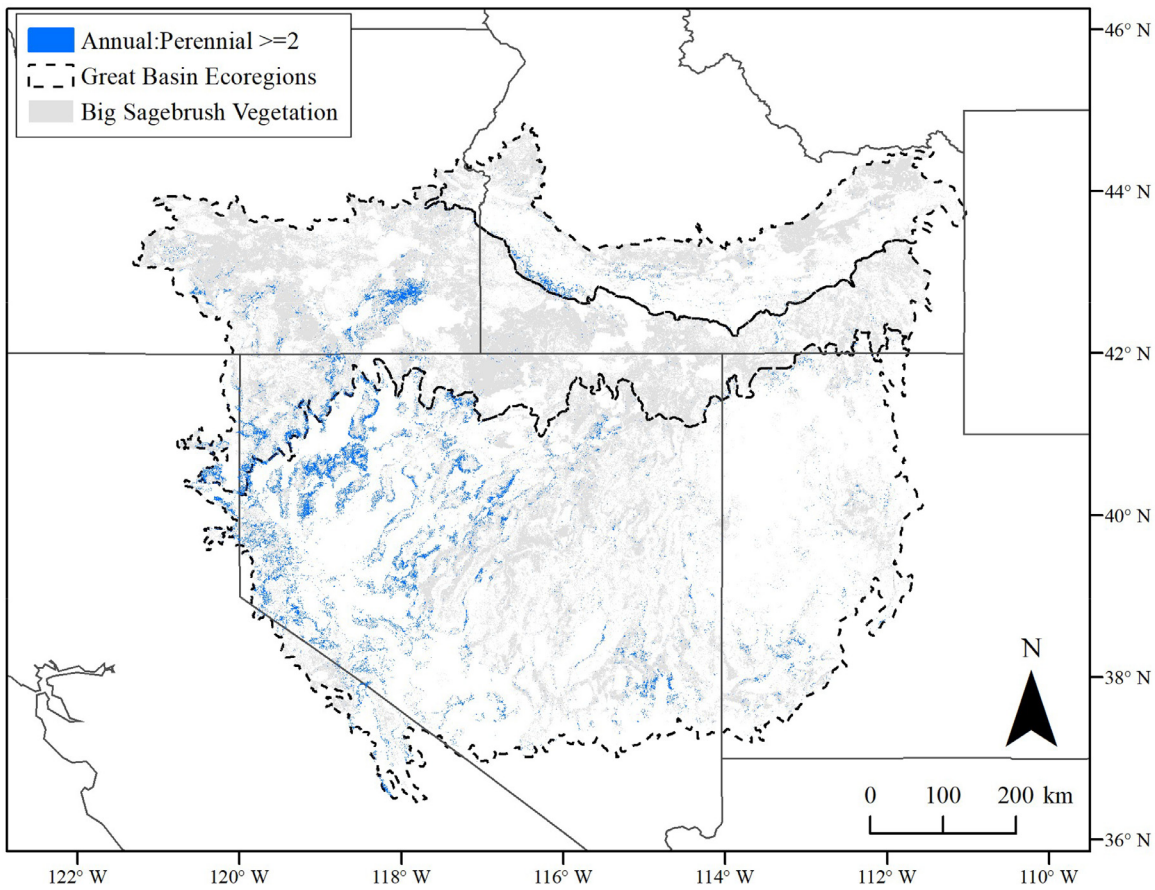

Figure 2. Annual-dominated understory degraded sagebrush vegetation. Defined as high shrub cover and low tree cover, with high relative abundance of annual species (tree ≤ 5% shrub ≥ 10%, annual herb–perennial herb ≥ 2). This definition is linked to the earlier threat-mapping definitions in Oregon sagebrush steppe with similar methods but uses a higher threshold for the annual-to-perennial ratio (annual–perennial ≥ 1, Creutzburg 2021; Oregon SageCon Partnership 2021, coordinate system: WGS84).

with high total perennial herbaceous cover. We focus on three subtypes of degraded states included in previous research with unique characteristics based on the total herbaceous cover and invasion: 1) sparse understories (low herbaceous cover, mostly bare ground); 2) annual invasive-dominated understories (based on relative annual to perennial abundance, irrespective of total herbaceous abundance); and 3) annual invasive-dominated understories with extremely low perennial cover (Dunwiddie and Camp 2013; Johnson et al. 2019).

Our objectives are to 1) describe why the understory degradation concept in sagebrush ecosystems must be anchored in comparison with reference conditions specific to that site's environmental characteristics and based on stable (rather than transitory) states. 2) We also illustrate how differing definitions affect efforts to quantify the problem of degraded understories. However, definitions and mapping, while important steps at the biome scale, are not sufficient to meet conservation goals. Therefore, we 3) demonstrate that this complex issue requires that managers and researchers consider the causal factors leading to degradation via different pathways, trends suggesting recovery or further degradation, and changes in site potential due to altered soils or climate change. We also 4) present a simple framework for restoration decision making based on historical factors, current site potential, and spatiotemporal scale. Finally, we explain how acknowledging the complexity of understory degradation in sagebrush ecosystems is more likely to lead to effective and transferable restoration and management approaches with associated positive impacts on biome-wide conservation.

"Degraded understories" must be stable and altered relative to reference conditions

Planning restoration attempts and/or changes in management for suspected degraded understory sites in sagebrush ecosystems should involve defining degradation based on long-term degraded states and comparison to reference sites (see Fig. 4), as generally recommended for ecological restoration planning (Aronson et al. 1993; SER International Science & Policy Working Group 2004; Miller and Hobbs 2007). Mischaracterizing sites as degraded (or not degraded) has the potential to lead to wasted resources given the large areas of potentially degraded vegetation in the sagebrush biome. However, climate and soil factors drive widespread variation in composition and functional cover across intact big sagebrush vegetation (Passey et al. 1982; Pennington et al. 2017; Pennington et al. 2019), which complicates the task of locating suitable reference communities. Even at smaller ecological or spatial scales, understory herbaceous communities can diverge widely. For instance, intact higher-elevation big sagebrush (ssp. *vaseyana* [Rydb.] Beetle) communities have 4.0 and 1.8 times the perennial forb canopy cover and diversity of intact lower-elevation big sagebrush (ssp. *wyomingensis*) in eastern Oregon (Davies and Bates 2010a; Davies and Bates 2010b). In the same region, topography and soils combine to influence orders of magnitude variation in native perennial grass (13–24%) and forb (0.3–5%) abundance even within lower elevation big sagebrush (ssp. *wyomingensis*) communities (Davies et al. 2006; Davies et al. 2007; Bates and Davies 2019).

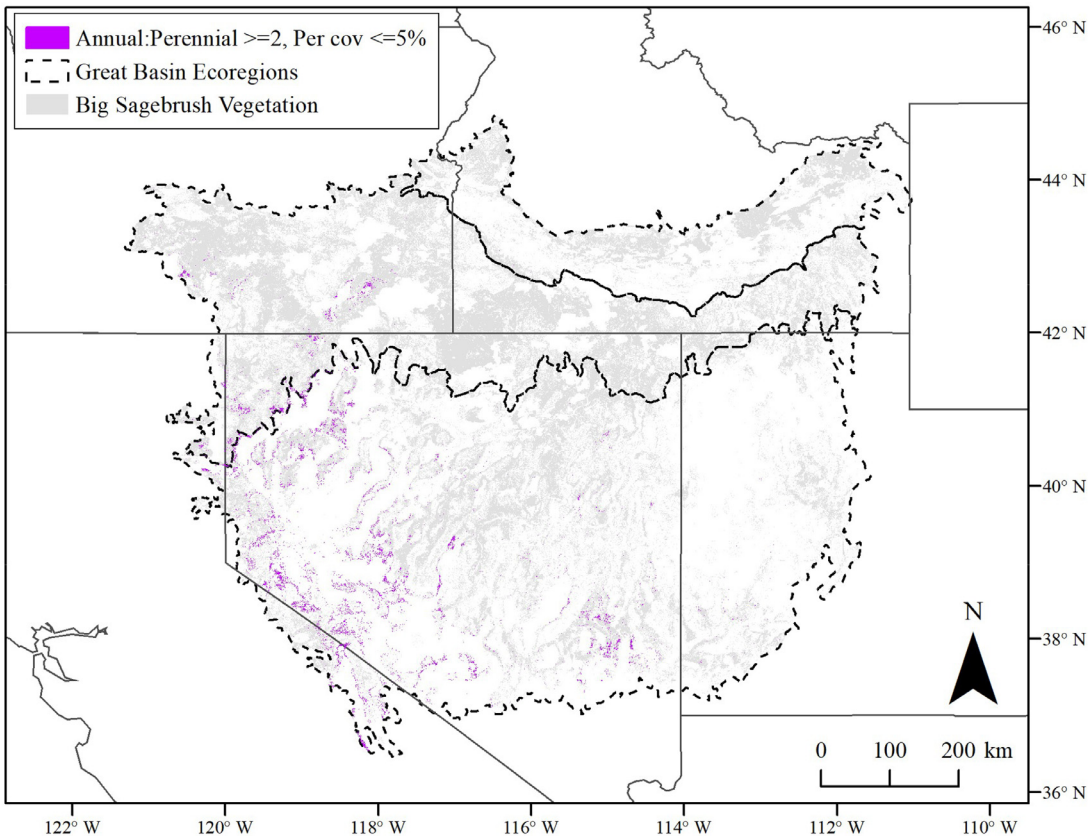

Figure 3. Annual-dominated understory degraded sagebrush vegetation with low perennial abundance. Defined as high shrub cover and low tree cover, with high relative abundance of annual species, as in Figure 4, but with the additional limitation of low (absolute) perennial abundance (tree ≤ 5%, shrub ≥ 10%, perennial herb ≤ 5%, annual herb−perennial herb ≥ 2, coordinate system: WGS84).

For some sites and regions, locating appropriate reference conditions based on soil and climate for direct comparisons may be difficult to impossible, due to lack of nearby intact sagebrush vegetation, particularly for large degraded lower-elevation sagebrush areas and/or less common soil or vegetation types. In these cases, ecological site descriptions and local knowledge may assist with generally describing site potential cover for a specific geographic location, soils, and climate (Bestelmeyer et al. 2016). Functional group cover values from remote sensing platforms may also be helpful in defining degradation (e.g., Rangeland Analysis Platform, Allred et al. 2021). As remote-sensing tools improve and allow for finer-scale and species-specific maps, understory composition is likely to become easier to track over time and space at smaller spatial resolutions and with greater accuracy. However, interpreting these data to identify degraded sites will still require managers and researchers to articulate their assumptions regarding historical reference conditions by constraining expectations based on relevant environmental variables (such as soils and climate).

High weather-driven variation in herbaceous abundance and diversity across years is common in sagebrush ecosystems even in the absence of disturbance (Passey et al. 1982; Sneva 1982), leading to the potential for inaccurate classification (degraded or nondegraded) with one-time measurements. For example, monitoring in 1 dry yr could lead to anomalously lower abundance and cover estimates for herbaceous species compared with long-term averages (Passey et al. 1982; Copeland et al. 2022). Monitoring at inappropriate windows during the growing season is also problematic and likely to underestimate perennial forbs, particularly early season and/or geophyte species (Endress et al. 2022), which are the majority of herbaceous diversity in sagebrush ecosystems and critical habitat components for sagebrush obligate wildlife like sage-grouse (Pennington et al. 2016). Other understory species, like bunchgrasses, may be more readily observed across seasons than forbs, (though cover will vary). Weather-driven cover fluctuations can be partially accounted for by identifying year effects with long-term monitoring in similar sites (Applestein et al. 2021) and/or remote sensed functional group cover variation (e.g., Rangeland Analysis Platform, Allred et al. 2021). Slow recovery trends post disturbance may be difficult to identify given high weather-driven variation in sagebrush ecosystems (Anderson and Inouye 2001), suggesting that defining stable degraded states could require a minimum of several monitoring years with different weather conditions.

Variable definitions alter estimates for degraded understories across sagebrush ecosystems

Here we show how vastly different estimates of the extent and distribution of degraded vegetation within sagebrush ecosystems result from the three general types of degraded understories described earlier: low herbaceous cover, annual invasive-dominated, and the subset of annual invasive-dominated sites with extremely low perennial cover. To ground our perspective on current frameworks used in sagebrush management planning, we closely followed definitions used in recent landscape-level estimates (Creutzburg 2021; Doherty et al. 2021; Johnson et al. 2019) created with remote-sensing estimates of functional group cover (2016−2020, 30-m pixels, Rangeland Analysis Platform, Allred et al. 2021). We limited our estimates to Great Basin ecoregions (US Environmental Protection Agency 2013; EPA Level III, Northern Basin and Range, Central Basin and Range, Snake River Plain, NatureServe 2018) and big sagebrush (*Artemisia tridentata* Nutt.) vegetation

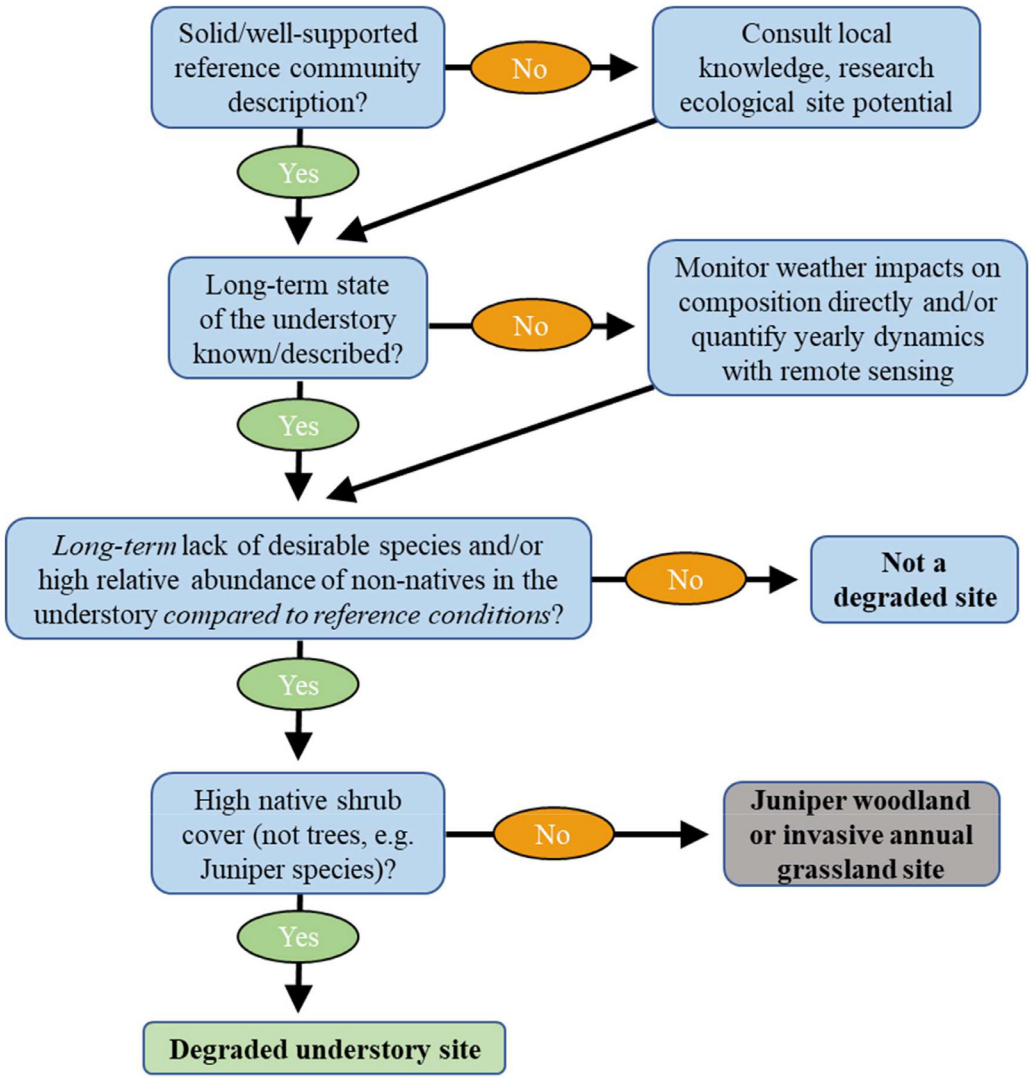

Figure 4. Workflow for defining a degraded understory site.

(LANDFIRE Existing Vegetation Types, Intermountain Basins Big Sagebrush Shrubland, Intermountain Basins Big Sagebrush Steppe, Inter-Mountain Basins Montane Sagebrush Steppe, *Artemisia tridentata* ssp. *vaseyana* Shrubland Alliance, Wildland Fire Science 2016). We excluded areas with tree cover to avoid including areas altered by juniper invasion (> 5%). We selected areas with relatively high shrub cover (≥ 10%) and either 1) a sparse understory (≤ 5% annual and/or ≤ 5% perennial herbaceous cover, Fig. 1) or 2) high relative annual to perennial cover (Fig. 2, total annual–total perennial herbaceous cover ≥ 2), or 3) high relative annual cover combined with low perennial cover (Fig. 3, total annual–total perennial herbaceous cover ≥ 2 and perennial herbaceous cover ≤ 5%). Note that the annual–perennial ratio threshold employed here (2:1) is conservative (an underestimate potentially) compared with the 1:1 annual–perennial proportion used for sage grouse habitat quality in Oregon (Johnson et al. 2019; Creutzburg 2021; Doherty et al. 2021). Google Earth Engine (Gorelick et al. 2017) was used for all calculations.

With those methods, about 13.3% of the sagebrush vegetation in the selected ecoregions fit one or more of the degraded understory definitions, and the three definitions led to a wide range of extents and locations of degraded areas (Figs. 1–3). Approximately 8 300 km^2 or about 4.4% of the sagebrush biome met the 'sparse' understory definition compared with approximately twice the amount, 17 600 km^2, or 9.3% of the biome, based on annual dominance alone (≥ 2 annual–perennial ratio). Constraining the annual dominated definition to areas that also had low perennial herbaceous cover (≤ 5%) reduced the estimated area by 72% to 4 900 km^2, or 2.6% of the biome. While this remote sensing analysis illustrates the sensitivity of outcomes to definitions for degraded, it does not address the need to include site potential, based on soil and climate (Bestelmeyer et al. 2009), in "degraded understory" definitions. The need to incorporate more ecosystem-specific baselines for characterizing understory states is urgent, as increasingly large-scale efforts are likely needed to address declines in sagebrush ecosystems (Doherty et al. 2022). Remote sensing cover estimates are able to illuminate decadal trends with consistent measurements over broad scales, such as the increasing area of degraded understories, with high relative annual cover, over the past 25 yr in some parts of the eastern Oregon sagebrush steppe (Creutzburg 2021), increasing invasive annual grass cover at higher elevations in the Great Basin (Smith et al. 2022), and vegetation responses to treatments across western US Bureau of Land Management lands (Kleinhesselink et al. 2023). While relatively coarse in spatial scale (30 m), remote-sensing estimates of vegetation condition can be fine-tuned to site potential (e.g., Rigge et al. 2021). More detailed mapping may be particularly needed to identify the emergence of smaller degraded areas located within or adjacent to intact sage-

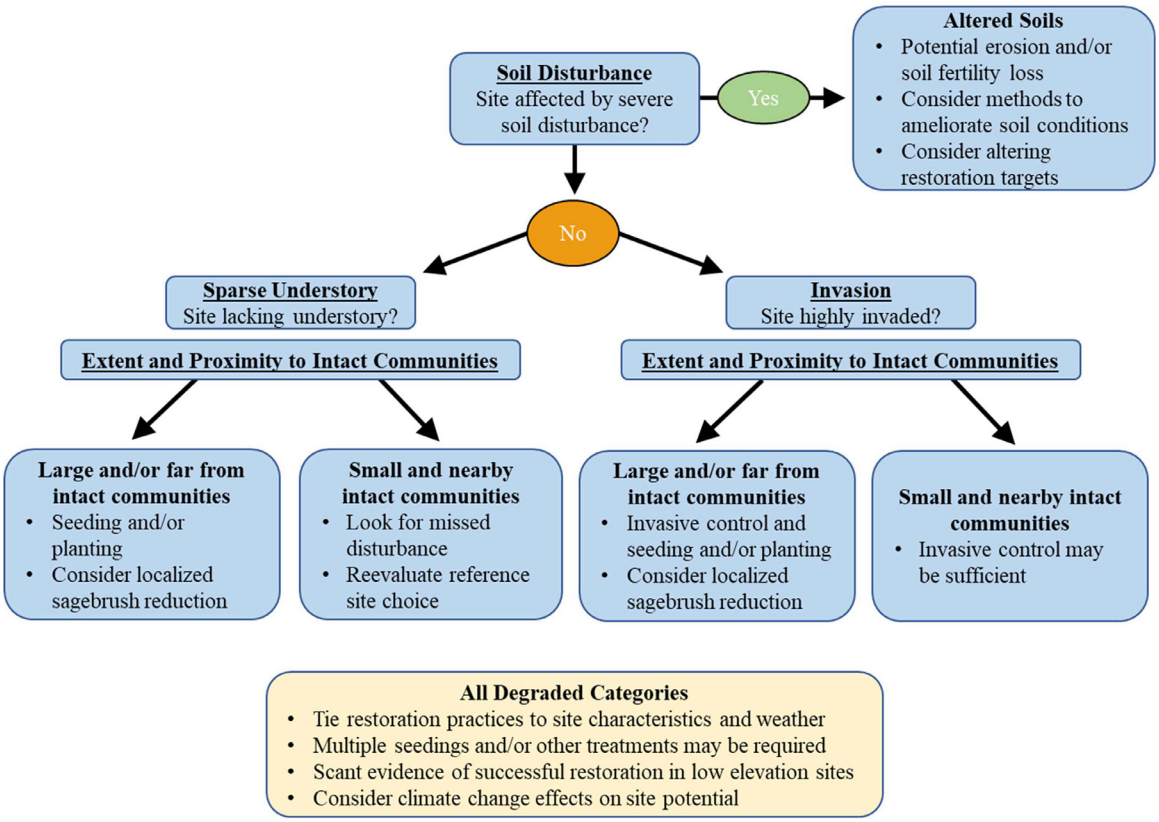

Figure 5. Framework for assessing restoration options for different types of degraded understory sagebrush sites.

brush habitat that may be priorities for protection and/or treatment (Creutzburg et al. 2022).

Pathways to degraded understory states

Low understory perennial abundance in sagebrush communities could be due to a number of individual and combined factors, including long-lasting impacts of historical disturbances, especially those that cause major shifts in soil fertility, texture, or structure (McLendon and Redente 1990; McLendon et al. 2012; Gasch et al. 2014) with pathways indicated by community characteristics, particularly invasive annual dominance (Johnson et al. 2019; West 2000). Degraded understories are also likely to arise from different conditions than those associated with loss of dominant shrubs in sagebrush, such as wildfire or other human and natural agents leading to widespread die-offs of specific shrub species, such as *Aroga* moth outbreaks (Kirkland 1972; Bolshakova and Evans 2016), flooding (Ganskopp 1986), or various sagebrush/woody removal treatments. Identifying potential mechanisms or pathways and separating degraded states by their key characteristics are important because they may indicate different effective management interventions (Fig. 5).

Soil disturbance from tilling and plowing

Soil disturbances related to an array of land-use and management activities, including plowing, discing, drill seeding, chaining, mining, and energy development construction, are associated with understory degradation in Great Basin sagebrush ecosystems (Rickard and Sauer 1982; Morris and Rowe 2014; Avirmed et al. 2015; Morris et al. 2016; Monaco et al. 2018; Kulmatiski and Beard 2019; Dunham-Cheatham et al. 2020). Cultivated agriculture is one documented source of long-lasting imprints on vegetation composition and structure in the Great Basin, due to widespread failures in dryland agriculture in the early 1900s (Morris et al. 2011; Morris and Rowe 2014). Soil disturbance legacy effects can be difficult to recognize where land use and ownership has changed, such as in cases where cultivated homestead properties were returned to federal ownership, although historical records for certain types of transfers are available (Morris 2011). Soil disturbances such as plowing associated with seeding and/or sagebrush removal dating from the 1940s are also widespread on federal lands in the Great Basin, such as those managed by the Bureau of Land Management (Land Treatment Digital Library, Pilliod and Welty 2013; Pilliod et al. 2017). Historical land use involving substantial soil disturbance may be more likely to be a factor in degraded areas with flatter topography, increasing access and feasibility for seeding equipment, and signs of historical seeding such as stands of non-native perennial grasses.

Improper grazing

A frequently mentioned mechanism for understory degradation is inappropriately heavy, repeated growing season livestock grazing (West 2000; McIver and Starr 2001). Livestock grazing can limit recruitment and increase mortality rates for herbaceous species if improper stocking rates and timing of use result in repeated removal of vegetative and reproductive plant tissues, leading to elevated mortality rates and decreased recruitment in bunchgrasses (Laycock 1967). Additionally, soil disturbance from heavy trampling and increased bare ground with loss of perennial cover can lead to erosion, with long-term effects on soil properties, particularly in sites with combinations of soil and climate factors such as erosion-prone soils, low plant cover, and dry climate like those found in southeastern Utah (Neff et al. 2005; Fernandez et al. 2008; Duniway et al. 2018).

Long-lasting degradation due to the combined impacts of direct (herbivory) and indirect (soil-related) disturbance factors is particularly associated with legacy, historical grazing patterns in the sagebrush ecosystem (Laycock 1967; Yeo 2005). Current and historical grazing management approaches in the Great Basin differ broadly in terms of livestock species (sheep, cattle, and horses); stocking rate; and timing, all of which are related to whether or not livestock grazing is associated with degradation (Holechek 1981). Similar rates of herbaceous recovery in exclosure and currently grazed areas after shifting to more moderate livestock grazing demonstrate the differences between historical and current practices (Courtois et al. 2004; Copeland et al. 2021).

Interactive effects of climate, soil type, and disturbance on degradation

Temporally or spatially variable factors, like weather extremes and soil type, may amplify the effects of disturbance. For instance, drought could amplify the effects of higher grazing intensity on sagebrush understory communities (Anderson and Inouye 2001). Alternatively, site factors like soil type may largely control the effects of disturbance. For example, a comparative study of paired cultivated and uncultivated sites showed that ecological site, associated with soil type, largely affected long-term forb community recovery (Morris et al. 2011). These interactions may be difficult to disentangle yet important for assisting in management to prevent or reverse degradation.

Shrub interactions with understory vegetation

While sagebrush is a desirable native species in sagebrush ecosystems, at high densities *Artemisia* species may maintain degraded states by competing with understory plants, particularly grasses (Cook 1963; Boyd and Svejcar 2011). Consistent with variable effects of shrubs on understory restoration observed in other systems (Gomez-Aparicio 2009), sagebrush canopy effects on understory species range from positive to negative in various circumstances (Huber-Sannwald and Pyke 2005; Poulos et al. 2014; Holthuijzen and Veblen 2015; Koutzoukis et al. 2023). Competitive versus facilitative effects of sagebrush on understory abundance are associated with combinations of sagebrush cover (Huber-Sannwald and Pyke 2005), abiotic environment, such as rainfall (Holthuijzen and Veblen 2015), and understory species identity (Koutzoukis et al. 2023).

Framing the options for restoration and recovery of degraded understories

We suggest at least four elements to include in a framework for selecting management approaches for degraded understories (see Fig. 5). Sites with a history of severe *soil disturbance* should be identified because adjusted restoration targets and/or methods to ameliorate altered soil properties may be required. Areas should be separated based on *invasion* by competitive non-native species as opposed to areas with sparse, but native dominated, understories, because these are separate conditions, potentially arising from different site disturbance histories, and often requiring different restoration approaches. Finally, the *extent* and *proximity to intact sagebrush communities* are related, and important, considerations given dispersal constraints for many native species. Seeds from native understory species are much more likely to arrive, and at higher rates, into small degraded sites surrounded by intact vegetation. In contrast, native species dispersal into degraded sites at long distances from intact vegetation, such as within large degraded landscapes, is likely to be low. Definitions for the size (large vs. small) of degraded areas and their distance from intact sites are not simple, given limited information on dispersal distances for sagebrush understory species. Big sagebrush, for example, disperses relatively rarely to distances > 20 m, despite the production of tens of thousands of seeds per individual shrub (Applestein et al. 2022).

Reestablishing high-quality herbaceous communities in degraded understory sites may require multiple, coordinated management interventions including both shrub reductions and seedings (Davies and Bates 2014; Davies et al. 2021), perhaps in patches or strips within larger areas (Hulvey et al. 2017), and is seldom attempted (Dunwiddie and Camp 2013). Restoration treatments mentioned as potentially effective include various combinations of mechanical, herbicide, and selective grazing (e.g., fall sheep grazing) methods for sagebrush reduction combined with multiple seedings of herbaceous species and herbicide treatments for invasive species (Laycock 1991; McIver et al. 2010). However, each type of treatment involves choices among many potential methods and associated variability in outcomes and uncertainty regarding effectiveness (Munson et al. 2020; Shaw et al. 2020). Multiple coordinated treatments in an adaptive management framework may be successful, for instance, in encouraging desirable perennial species over annual species via a series of herbicide and seeding treatments (Sheley et al. 2006) and/or timing of seedings with weather conditions like high soil moisture during establishment (Chambers et al. 2014; Schantz et al. 2019; Young et al. 2017). Such sequential and/or targeted approaches are not broadly adopted or standardized (e.g., uncommon in documented large-scale Bureau of Land Management treatments, Pilliod et al. 2017), perhaps due to the timeframes and costs required combined with a lack of well-supported, consistently favorable outcomes. However, less complex restoration methods for degraded sagebrush understories are often unsuccessful. For instance, attempts to restore degraded sagebrush by reducing sagebrush cover and seeding with heavy equipment increased invasive annual abundance, though perennial herbaceous species also increased slowly (Davies and Bates 2014; Davies et al. 2021). At lower-elevation sites, increases in fine fuels with sagebrush reduction may increase fire risk and potential for conversion to an invasive annual grassland (Chambers et al. 2021). Little information is available on the effectiveness of high-diversity seedings, which may be required for degraded understory habitats, particularly for forbs, and at relevant scales and methods for landscape level restoration (but see Ott et al. 2019; Davies and Boyd 2021; Ott et al. 2022). Additional research on effective methods for seeding diverse seedmixes is urgently needed as the use of native species in the region steadily increases (Pilliod et al. 2017) in tandem with efforts to increase native seed availability for largescale use (McCormick et al. 2021).

Sagebrush reduction in particular may be an effective method for restoring understories in localized areas, as well as specific sites, though results vary. This management option also contrasts with regional goals to increase sagebrush cover where frequent, large fires have led to widespread losses. Sagebrush cover reductions with various mechanical or herbicide methods are not novel and were a common method for improving forage cover in sagebrush vegetation over many decades in the Great Basin (Pilliod et al. 2017) and adjacent ecosystems (Copeland et al. 2018). However, historic sagebrush reduction treatments were intended to improve livestock forage and/or address soil erosion and frequently combined with seeding non-native grass species (e.g., the landscape-scale treatments, southeastern Oregon, Vale Rangeland Rehabilitation Program, 1952–1973, 2 050 km^2, Heady and Bartolome 1977), in contrast with more recent sagebrush reduction treatments linked to more complex goals, including restoring diverse understory communities (Utah Watershed Restoration Initiative, Riginos et al. 2019). Widespread sagebrush

reduction for forage has been largely replaced in recent decades by large-scale attempts to increase sagebrush cover via seeding and transplants in response to widespread losses with increasing wildfire frequency and severity. Big sagebrush is a focus of postfire restoration efforts because the species is readily killed by fire and has a short-lived seedbank, with episodic and often limited recovery (Ziegenhagen and Miller 2009) tied to favorable weather conditions (Shriver et al. 2019; O'Connor et al. 2020). The effects of sagebrush reduction on wildlife habitat range from unfavorable (Smith and Beck 2018) to neutral (Davies et al. 2021) to positive (Olson and Whitson 2002; Riginos et al. 2019). Negative impacts of sagebrush reduction treatments appear to be more likely in the short term (Copeland et al. 2019) and in drier compared with wetter big sagebrush communities (Wilder et al. 2019). Outcomes of sagebrush reduction may also depend on the potential of herbaceous species to respond, which is likely to vary with functional group and site characteristics (Boyd and Svejcar 2011; Pyke et al. 2014; Riginos et al. 2019; Chambers et al. 2021).

Recovery and the spatiotemporal scale of understory degradation and change in site potential

The shape and temporal scale of both degradation and recovery trajectories remain unclear in sagebrush ecosystems, particularly given climate change and the increasing abundance of highly competitive invasive species. Great Basin sagebrush understories are dominated by perennial herbaceous species, some with decadal lifespans (Liston et al. 2003; Lauenroth and Adler 2008) represented at only relatively low abundance in seed banks, particularly after disturbance such as historical cultivation (Bernards and Morris 2017a) or fire and/or significant invasion by annual grasses (Humphrey and Schupp 2001; Martyn et al. 2016; Barga and Leger 2018). Degraded understories may eventually recover over long timescales in the absence of ongoing disturbance (passive restoration) and invasive annual grasses, with rate of recovery dependent on site abiotic characteristics and historic soil disturbance (Morris et al. 2011; Morris and Leger 2016; Bernards and Morris 2017b; Monaco et al. 2018; Condon et al. 2020; Copeland et al. 2021). Weather trends during key periods related to establishment are likely to be especially influential for recovery of some species, particularly in drier sites (Anderson and Inouye 2001). However, even if recovery is occurring, it may be unacceptably slow to meet management objectives in landscapes where degraded understories are widespread and persistent. For example, several years to a decade of cattle grazing removal was not associated with recovery in degraded understory herbaceous communities (Davies et al. 2014; Davies et al. 2016; Thomas et al. 2022). However, recovery did occur over decades in another site where legacy heavy-grazing practices led to a degraded understory (Sneva et al. 1984; Copeland et al. 2021). This contrast in results could suggest either extremely slow recovery trends (not detectable in shorter-term studies), due to low dispersal rates and depauperate seed banks, or limited recovery associated with the ongoing dominance of big sagebrush. Waiting for recovery (passive restoration) may also be undesirable because degraded understory sites may persist on borrowed time, a wildfire away from rapid conversion to an annual grassland, an undesirable state with additional barriers to recover ecosystem function (Davies et al. 2012). In contrast, competitive understory species like large perennial bunchgrasses in intact understories can prevent or limit annual grass dominance post fire (Chambers et al. 2007; Wainwright et al. 2020). Many sagebrush understory species may require dispersal to align with suitable environmental conditions in order to successfully colonize degraded sites, due to their infrequency in the seed bank, particularly following long time periods of absence. As a consequence, the size and spatial arrangement of degraded understory areas may be influential, with recovery of larger degraded areas likely to take longer than in smaller areas adjoining intact sagebrush plant communities with diverse and abundant herbaceous understories.

Climate change and the contemporary presence of invasive annual grasses in most sites may have altered site potential in parts of the sagebrush ecosystem (Palmquist et al. 2021), particularly in the presence of more frequent fire (Ellsworth et al. 2020). Many understory species can resist invasion by annual grasses and are resilient to severe weather, and even directional climate change trends once established. It is unclear, however, if changed environmental conditions allow for reestablishment of formally suitable species in many sites and to what extent divergent functional or species composition benchmarks are needed. Vegetation shifts in sagebrush ecosystems linked to climate change include increasing annual herbaceous cover and production across broad areas (Kleinhesselink et al. 2023) and the movement of invasive annual grasses to higher elevations (Tang et al. 2015; Smith et al. 2022). Predictions for future climate change impacts include widespread losses in perennial C_3 grasses and perennial forbs in sagebrush ecosystems (Palmquist et al. 2021). Vegetation targets for understories chosen for future climate, as opposed to past climate, may be more achievable. Benchmarks based on climate change futures might alter restoration approaches in degraded sites by, for example, suggesting species for seeding based on suitability for current and future climate (Butterfield et al. 2016).

Altered soil conditions (e.g., shallow soils) due to tilling or other causes of soil erosion can have severe, long-term implications on site potential and recovery trajectories (Morris et al. 2011; Bernards and Morris 2017a) and are unlikely to improve quickly due to millennial timescales of soil development in the Great Basin (Harden et al. 1991). Therefore, the outcomes of passive recovery in sites with altered soil conditions are unlikely to quickly mirror undisturbed reference sites (McLendon and Redente 1990; Morris et al. 2011; Avirmed et al. 2015). Legacy effects such as differences in soil nutrient concentrations and heterogeneity can remain for decades (Morris et al. 2011; Morris et al. 2013; Morris et al. 2016). Restoration approaches may need to account for these changed conditions via species selection, amelioration methods for altered soils, and adjusted restoration goals.

In general, sagebrush ecosystem understory communities diverge by climate and edaphic gradients at various spatial scales (Passey et al. 1982; Davies et al. 2006; Davies et al. 2007; Davies and Bates 2010b; Pennington et al. 2017; Pennington et al. 2019). Some native perennial species are less tolerant to certain types of disturbance than others; for example *Phlox hoodii* Richardson a woody low-growing species with aboveground growth points, was particularly slow to recover from historic cultivation (Morris et al. 2011). Similarly, some native species may be much more dispersal limited than others, and most perennial native species in sagebrush steppe do not appear to be highly persistent in seed banks (Martyn et al. 2016; Bernards and Morris 2017a; Barga and Leger 2018). This variation in response to altered environmental conditions and disturbance among species implies that in sites where understory diversity and abundance are especially low compared with reference sites, multiple conditions are likely interacting to prevent understory vegetation from recovering. Similarly, treatment methods that fail to consider this variation in species characteristics are likely to be only partially successful.

Preventing further degradation

Given limited capacity for broad-scale restoration of degraded understory communities (due to the intensive efforts that would be required), preventing additional degradation of the sagebrush ecosystem should be a management emphasis (Davies et al. 2011). For example, managers may want to avoid widespread soil distur-

bance in sites susceptible to long-lasting soil alteration and associated lack of recovery (Morris et al. 2011; Duniway et al. 2015). Proactively identifying and correcting negative trends in understory condition, for instance, with recent remote-sensing trends at early stages could prevent the need for the intensive management effort required to address severe and widespread degradation.

Conclusion

Overall, the state of knowledge regarding degraded understories in the sagebrush ecosystem may be insufficient to suggest concrete management approaches to the problem. For example, little is known regarding the relative role of seed dispersal distance and environmental thresholds for natural recovery in the sagebrush ecosystem, particularly in the context of widespread invasive species. Larger areas of stable (persistent) degraded understory sagebrush may require special attention, particularly where adjacent to intact, higher-diversity plant communities. Nonweather factors limiting herbaceous native perennial colonization and growth may be indicated where degraded understory states persist for long time periods including over multiple favorable weather periods for native perennial species recruitment. Identifying these factors is likely an important step for deciding among potential restoration strategies, as well as managing this vegetation state in general. For instance, altered soil properties and/or invasive annual grass competition could lead to lower site potential, representing an environmental threshold that is difficult to reverse (Harris et al. 2006; Bestelmeyer et al. 2009). However, correctly identifying such thresholds is a complex and uncertain task (Suding and Hobbs 2009; Bestelmeyer et al. 2013), particularly in dryland systems, like Great Basin sagebrush vegetation, where recovery trends are relatively slow. In contrast, degraded understory sites where slow recovery is taking place may require little to no active restoration, though large areas may require island seedings (Hulvey et al. 2017) if dispersal limitation is playing a significant role (Marlette and Anderson 1986).

Research is needed to understand divergent pathways related to various types of degraded understory in the sagebrush ecosystem, given their extent and associated importance to conservation of the sagebrush biome. Site factors like spatial configuration (relative to intact understories), disturbance history, invasive abundance, and current site potential for herbaceous community composition may lead to distinct states, requiring divergent management approaches, such as natural recovery versus active restoration. Whether current degradation patterns and processes will resemble historical pathways is a particularly pressing question for research. Present-day sagebrush ecosystems are experiencing shifts in climate, including increasing temperatures and both higher precipitation and drying in different parts of the region (Tang and Arnone III 2013; Tang et al. 2015; Xue et al. 2017; Snyder et al. 2019; Zhang et al. 2021), and ongoing annual grass invasion (Smith et al. 2022). These altered environmental characteristics may mean that novel degraded states are possible, further complicating efforts to understand effective management and restoration. Even in the face of change and uncertainty, embracing the inherent complexity of species composition, associated environmental gradients, and land-use patterns is the best path toward identifying effective targeted approaches to promote resilient, diverse, and abundant understory vegetation in sagebrush ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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