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Source: Rangeland Ecology and Management, 76(1) : 1-11

Published By: Society for Range Management

URL: https://doi.org/10.1016/j.rama.2021.01.003

Rangeland Ecology & Management 76 (2021) 1–11

Contents lists available at ScienceDirect

Rangeland Ecology & Management

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

Forum: A Change in the Ecological Understanding of Rangelands in the Great Basin and Intermountain West and Implications for Management: Revisiting Mack and Thompson (1982)

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ARTICLE INFO

Article history:
Received 17 July 2020
Revised 20 October 2020
Accepted 6 January 2021

Key Words:
Ecosystem management
Great Basin rangelands
Intermountain West rangelands

ABSTRACT

Reevaluating assumptions about the ecology and management of sagebrush and salt desert shrub systems in the Great Basin and Intermountain West is a proper role for science. These are complex rangeland ecosystems, and our management applications need to account for this complexity. Understanding and reckoning this complexity is vital to the future existence of these rangeland systems and their ability to provide critical goods and ecosystem services to society. The most influential ecological claim of the past 40 yr is based on ideas presented by Mack and Thompson (1982), that Great Basin and Intermountain West plant communities evolved with few or perhaps no large hooved-grazing animals. Our thesis asserts that Mack and Thompson's position is based on 1) an oversimplification of complex, heterogeneous, and diverse ecosystems; 2) a poor understanding of science, both in 1982 and now; and 3) the attribution of all recent ecological changes to a single land use. We review the archaeological and historical record of vegetation and large grazing animals in the region and then revisit Mack and Thompson's (1982) interpretations of the rangeland plants and plant communities, forage quality and nutrition, and soil biotic crusts east and west of the Rocky Mountains, adding the information necessary for a more comprehensive interpretation. We finish by proposing an alternative paradigm to guide management and conservation of sagebrush and salt desert systems of the Great Basin and Intermountain West and beyond.

Introduction

There is an urgent need for a reevaluation of common assumptions about the ecology and management of sagebrush and salt desert shrub systems in the Great Basin and Intermountain West. These are complex rangeland ecosystems, and our management applications need to account for that complexity. Understanding and reckoning this complexity is vital to the future existence of these rangeland systems and their ability to provide critical goods and ecosystem services to society. A convincing case supporting the need of an ecologically based shift in management approach relies on identifying the foundation of our current paradigm, followed by a realistic assessment of where management has led us ecologically, with respect to the current status of ecological systems and successional trajectories. We argue that the current ecological status of many sagebrush and salt desert areas of the Intermountain West is, to a large degree, a direct result of outdated, misapplied, oversimplified, and incorrect ecological characterizations of those ecosystems. We contend that these two systems (and perhaps others) should now be viewed as novel ecosystems as a result of many factors (e.g., invasive species, increasing CO_2 levels, warming climate, increased anthropic fire ignitions), and novel systems require novel approaches to management and conservation. Oversimplified, one-size-fits-all, dichotomous, non-hysteresis-based management approaches (e.g., Beschta et al. 2013) are not useful (Porensky 2020).

The current ecological status of these two major Intermountain West ecosystems is also a product of management applications based on both ecological understandings and misunderstandings put in place decades prior. The most influential ecological claim of the past 40 yr is based on ideas presented by Mack and Thompson (1982), that Great Basin and Intermountain West plant communities evolved with few or perhaps no large hooved-grazing animals.

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https://doi.org/10.1016/j.rama.2021.01.003

The concept has been reinforced by numerous text and reference books (e.g., Archer and Smeins 1991; Hobbs and Huenneke 1996; Knick et al. 2011). This claim was expounded by others reaching the conclusion that virtually every undesirable change that has occurred in the Great Basin and Intermountain West since European settlement was the result of the introduction of novel, large domestic grazing animals into ecosystems that were not adapted to large herbivores (e.g., Cooperrider 1991; Fleischner 1994). Attributing the cause of the relatively recent ecological alterations of the region to the single land use of livestock grazing is unreasonable and unscientific. A myriad of human influences have played a role including the introduction of livestock (cattle, sheep, and horses); homesteading; cultivation; mining activities; energy development (including transmission corridors); road and railway construction; invasive species introductions; seeding programs; water diversion; elevated CO_2 levels; altered fire frequencies; and recreation pressures (Morris and Rowe 2014).

There is no question that major changes in plant community compositions have occurred as a result of European settlement (Burkhardt and Tisdale 1976; Young et al. 1987; Perryman et al. 2003). Legacy grazing practices of more than a century ago altered fire regimes that fostered downslope woody plant encroachment and the proliferation of invasive species (Miller and Wigand 1994; Miller et al. 2008; Tausch et al. 2009). Large segments of society have cited these effects as reasons for removing not only domestic animals from the region but also all human-induced disturbances in the hope that the systems will return to some semblance of what they were before European settlement. However, for semiarid systems it is well documented that the removal of disturbances like grazing does not initiate a return to the original ecological state (Westoby et al. 1989; Laycock 1991). Perryman et al. (2003) coined the term *pristine-management-paradigm* to describe the widely held concept that ecological systems are entities that can be held in a static condition if they are protected from burning, grazing, and other disturbances. The question must be posed: What is a productive role of science? Certainly, a periodic reassessment of ecological underpinnings and their associated management practices is a reasonable and appropriate function for the scientific community. We believe that Mack and Thompson's (M&T) hypothesis about rangelands east and west of the Rocky Mountains is an oversimplification of complex, heterogeneous, and diverse ecosystems, as well as an unrealistic framework for understanding and managing those systems, and should be replaced.

Our objective is to reevaluate M&T in light of current scientific knowledge and offer a new science-based vision for ecosystem management of the Great Basin, Intermountain West, and beyond. We begin by revisiting the archaeological and historical record of vegetation and large grazing animals. We then revisit M&T's interpretations of the rangeland plants and plant communities, forage quality and nutrition, and soil biotic crusts (SBCs) east and west of the Rocky Mountains adding the information necessary for a more comprehensive interpretation. We finish by proposing an alternative paradigm to guide management and conservation of sagebrush and salt desert systems of the Great Basin and Intermountain West and beyond.

Historical Vegetation Of the intermountain West

Phytogeographers universally agree that the native floristics of the Intermountain West today (with the notable addition of single-leaf pinyon pine, *Pinus monophylla* Torr. & Frém.) is essentially the same as it has been since the beginning of the Pleistocene (Cronquist et al. 1972; Tidwell et al. 1972; Barnosky et al. 1987), although local/regional extinctions, as well as elevational and latitudinal/longitudinal migrations, have occurred in response to climatic changes during glacial-interglacial periods (Miller and Wigand 1994; Nowak et al. 1994a, 1994b). The current suite of native species in the Great Basin is essentially the same collection of species that European explorers (Jedediah Smith, Peter Ogden, James Simpson) observed in the first 6 decades of the 19th century (Dale 1918; Cline 1974; Petersen 2008). Vale (1975) synthesized entries of 29 journals and diaries of European travelers (between 1822 and 1859) crossing the northern Intermountain West to assess the relative importance of herbaceous and woody plants. Vale concluded that the structure of these landscapes was dominated by woody shrubs. Johnson (1987) concluded that sagebrush "is" where sagebrush "was" at the time of European settlement. However, one significant characteristic not observed was the presence of nonindigenous, invasive annual grasses. Nonindigenous annual grasses may have certainly been present in California and the Pacific Northwest by the late 1800s, but their impactful migration eastward was still several decades away.

Historical Large Herbivores of the Intermountain West

The archaeological record reveals that Pleistocene megafauna were present in the Intermountain West and Great Basin areas throughout the Pleistocene period, only becoming extinct about 10 000 yr BP (Grayson 2016). There are documented megafauna remains dated to the late Pleistocene of at least 14 extinct large-bodied grazing animal species in the Great Basin. Furthermore, 7 out of 20 extinct megafauna genera (including predators) known to have populated the area during the late Pleistocene, have trustworthy last appearance dates indicating they survived until about 10 millennia ago (Grayson 2016). Notable within the archaeological record is the number of stratigraphic occurrences for horses, camels, and mammoths ($>$ 80, 60, and 60, respectively), indicating their relative prevalence throughout the area. At Mineral Hill Cave located about 100 km SE of the geographic center of Nevada, large, extinct radio-carbon dated grazers include Mexican horse (*Equus* cf. *conversidens*), large-headed llama *(Hemiauchenia macrocephala),* mountain deer *(Navahoceros fricki),* western horse (*Equus* cf. *occidentalis*), and yesterday's camel *(Camelops hesternus)* all dated within 30 000–55 000 yr BP (Hockett and Dillingham 2004).

We must acknowledge that the archaeological record only speaks to presence and distribution but not population sizes. Mack and Thompson (1982) claimed that the current lack of native dung beetles in the Great Basin and isolated specimens of large grazers from the archaeological record indicate only the presence of small sink populations of large grazers. However, the tentative plausibility of that assumption does not negate the fact that large herbivores were present and used the Great Basin for many millennia (enough time for natural selection pressure to modify forage plant responses to herbivory). There was most certainly a significant period of time between the megafauna extinction and migration of large Asian herbivores into the ecological vacuum that resulted from the extinction. An alternative and reasonable interpretation is that dung beetles became regionally extinct in the Great Basin due to reduced large herbivore populations after the megafauna extinction. Further, the environmental conditions at the time could also have led to a small archaeological record not generally representative of the actual large grazer populations that existed. Holocene Climate Optimum weather conditions (9 000–5 000 yr BP), for instance, could certainly have affected the preservation of large grazer skeletal remains in the region (Blau 2017).

The very presence of large predator remains (e.g., Southern Rocky Mountain wolf, *Canis lupus youngi*) in the archaeological record indicates that large-bodied, hooved grazing animal populations were sufficiently large to at least partially support predator populations over at least hundreds of thousands of years (Grayson 2016). If feral horses are used as the modern analog of Pleistocene horses in the Great Basin, we are suddenly struck with the realization that the current ecosystems of the Great Basin are (without the presence of predation factored in) certainly capable of supporting tens of thousands of horses (BLM 2020).

The presence of large herbivores and related predators means that forage and water sources were clearly abundant enough for these animals to survive and reproduce for millennia. But what were these animals foraging on? Because the case has already been made that native plant community compositions of Great Basin and Intermountain ecosystems today are essentially the same as they were during the Pleistocene, it stands to reason that current plant genera and their associated genetics have been subjected to natural selection by foraging/grazing animals for many millennia. Even with an increase in the amount of salt desert shrub systems now located where pluvial lakes once existed, archaeological research (Laudermilk and Munz 1934) on coprolites from sites like Gypsum Cave located east of Las Vegas indicate that Shasta ground sloths (*Nothrotheriops shastensis* Sinclair) were foraging on a list of plants that included Nevada ephedra (*Ephedra nevadensis* S. Watson), several members of the *Atriplex* genus, desert globemallow (*Sphaeralcea ambigua* A. Gray), rubber rabbitbrush (*Ericameria nauseosa* [Pall. Ex Pursh] G.L. Nesom & Baird), banana yucca (*Yucca bacata* Torr.), purple three-awn (*Aristida purpurea* Nutt.), and Utah juniper (*Juniperus osteosperma* Torr.).

Van Vuren and Deitz (1993) reported male and female *Bison* skull discoveries along the Humboldt River corridor in Nevada, and Grayson et al. (1982) concluded that bison were present in the Great Basin until protohistorical times. Butler (1976, 1978) and Van Vuren and Bray (1985) determined that bison were abundant in eastern Idaho and eastern Oregon from the beginning of the Pleistocene until historical times. The presence of large grazing animals in the Great Basin and Intermountain West during the Pleistocene, particularly the late Pleistocene, and early Holocene is well documented. Animal densities were certainly less than in areas east of the Rocky Mountains; however, breeding populations absolutely existed in the Intermountain West. A kill site in southwestern Idaho preserves a 7 000-yr record of human bison hunting activities that included 2 860 m of stone fence construction (Agenbroad 1978). A construction project of this temporal and logistical magnitude indicates the presence of substantial, stable bison populations.

Mack and Thompson's (1982) conclusion of few large, hooved animals in the Intermountain West during the Holocene has been the cornerstone of antigrazing policies (e.g., Donahue 1999) that have influenced how rangelands have been managed over much of the past 40 yr. The basic premise has been that the Intermountain West evolved with few large, hooved grazing animals, and therefore virtually every undesirable ecosystem change in the Great Basin and Intermountain West has been attributed to the introduction of domestic livestock (e.g., Cooperrider 1991; Fleischner 1994; Donahue 1999). However, Burkhardt (1996) made the case that attempting to understand these ecosystems based totally on a paucity of large Holocene grazers ignores the well-established fact that large grazers were present and using these same, floristically similar systems throughout the Pleistocene and early Holocene. Burkhardt converted the Pleistocene-Holocene period to an evolutionary year and calculated that the 10 000 yr or so when the Intermountain West was depauperate of large grazing animals was the equivalent of 31 hr out of the evolutionary year, less than a day-and-a-half or 0.35% of the period. Intermountain West plant communities coevolved with large herbivores during the previous 2.5 million yr. The animal community was consistent during that time, undergoing a relatively sudden general reduction (partial extinction) during the early Holocene. In the circa 10 000 yr before European contact, there was insufficient time for succession and evolution to fill the vacuum. The relative scarcity of large herbivores in the region comprised an evolutionarily insignificant amount of time, certainly an insufficient amount of time for forage plants to lose genetic adaptations to grazing developed during the Pleistocene. Great Basin and Intermountain plant communities coevolved with large grazing animals for at least 2.5 million yr. Does the evidence support the case that these plant communities should be managed as though they evolved with little or no adaptations for grazing pressure from large indigenous grazers? Should management strategies be based on an ecological anomaly? Clearly, historical evidence indicates the answer to both of those questions is *no*.

Rangeland Plants and Plant Communities

Mack and Thompson (1982) also attempted to use plant community characteristics of systems east (*Bouteloua* Province) and west (*Agropyron* Province) of the Rocky Mountains as evidence for a lack of large grazing animals west of the Rocky Mountains. It has never been disputed that the carrying capacities of the two areas are drastically different. The density and duration of water sources alone can account for major differences in useable, seasonal habitat.

East of the Rockies, grassland systems are influenced by not only Pacific weather but also that of the Gulf of Mexico, creating a two season precipitation pattern. Both cool- and warm-season forage plants comprise mixed-prairie and short-grass steppe plant communities. As cool-season (C_3) grasses mature and become less nutritious and palatable, warm-season grasses (C_4) begin their life cycle, extending the green forage period for up to 90 d. Elevational gradients are small, so late-Pleistocene and Holocene animals could simply move laterally to an area where more forage was available, usually applying extreme grazing pressure to the resource (Hart and Hart 1997). Rhizomatous grass species can dominate plant communities east of the Rockies, a characteristic that shields perennating buds and carbohydrate reserves below the soil surface, limiting access to large grazing animals. In the Great Basin and Intermountain West, systems are dominated by caespitose grasses that maintain perennating buds and associated carbohydrate reserves from just belowground (e.g., portions of buried root crowns) to just aboveground (base of last year's tiller at elevated portions of the root crown), providing easy access for exploitation by large grazing animals. We must point out that caespitose grasses are also common east of the Rockies and at least 12 of the 26 species of grasses listed as dominants or codominants in the reference states of eastern Colorado Major Land Resource Area (MLRA) 67B ecological sites are caespitose (USDA 2006). Blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), the namesake of the *Bouteloua* Province, is a caespitose grass.

Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) is often the model for caespitose grass grazing response in the *Agropyron* Province (Mack and Thompson 1982). Branson (1953) provided the first evidence that grasses with elevated apical meristems were more susceptible to ***intense*** grazing pressure than those that maintain all meristematic tissue near or below the ground surface. Flexibility in resource allocation also plays a significant role in plant responses to grazing. Caldwell et al. (1981) demonstrated that crested wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.), a caespitose grass also used as evidence by M&T, had better recovery from severe defoliation events than bluebunch wheatgrass (BBW) because of a higher capacity for new tiller formation, the rapid regrowth of new tillers that prevent depletion of the limited soluble carbon buffer, and flexibility in the allocation of resources by shifting supplies to regrowing tillers while simultaneously reducing root system growth. Differences between the two species were taken by M&T as evidence that BBW is poorly suited to large grazing animals, so there must have been few large-hooved grazing animals in the Intermountain West and Great Basin in times past. However, Caldwell et al. (1981) only addressed the effects of two clipping events initiated at the 4–5 leaf stage and repeated after a 2-wk period. Mueggler (1970, 1972) demonstrated that both Idaho fescue (*Festuca idahoensis* Elmer) and BBW have highly variable responses to defoliation when adjacent competing vegetation was also defoliated. Mueggler (1972) found that natural competition from surrounding vegetation severely restricted growth and vigor of BBW and that the beneficial effects of reduced competition obtained by clipping surrounding vegetation to ground level completely offset the adverse effects of heavy clipping of BBW. Additionally, the importance of differential grazing responses among different populations of BBW and other widely distributed species cannot be overlooked or minimized (Mukherjee et al. 2013).

Based on research and field experience, we suggest that BBW responds well after moderate to heavy defoliation events, especially when it occurs before elevation of active meristematic tissues, and there is enough soil moisture for regrowth coincident with a period of rest from grazing until dormancy is achieved (Stoddart 1946; Anderson and Frank 2003; Brewer et al. 2007) and if competition from invasive annual grasses is reduced (Harris 1967). Grazing BBW plants again after dormancy has little if any adverse effect (Daubenmire 1940; Laycock 1967; McClean and Wikeem 1985) and can provide a renewal of vigor by reducing dead or "wolfy" biomass and may provide compensatory growth if there are no limiting factors (McNaughton 1983). The demonstrable fact remains that BBW communities in the region have been grazed by livestock at various times, durations, and intensities for > 100 yr and yet BBW remains as a primary community component. Further, given our current understanding of a cooler-wetter climate during the Pleistocene and early Holocene periods, BBW could have been more abundant at lower elevations than its current distribution, where more foraging animals would certainly have taken advantage of that seasonal habitat.

The current geographic distribution of BBW leads to the question of why this species should serve as the M&T model for determining the adaptation of the Intermountain West to herbivory pressure in the first place? Sandberg bluegrass (*Poa secunda* J. Presl) is much more widely distributed geographically in the area that M&T call the *Agropyron* Province and occurs on many more ecological sites across the entire area. For this reason, BBW seems a poor choice to represent M&T's *Agropyron* Province.

One of many problems arising from such a "representative species" approach is the oversimplification of complex ecological dynamics that lead to false dichotomies. Livestock grazing is a complex ecological process, yet a false dichotomy has persisted in some peer-reviewed ecologically based literature for decades by authors who consider only two options: grazed and ungrazed. For a recent example, Williamson et al. (2019) concluded that there were strong effects of livestock grazing on cheatgrass (*Bromus tectorum* L.) occurrence and prevalence based on this false dichotomy, by characterizing areas solely as either grazed or ungrazed, with no information on how livestock grazing was managed (timing, duration, and intensity). Davies and Boyd (2020) recently highlighted this issue and effectively argue that grazing is not binomial, while Meiman et al. (2016) described this false dichotomy as treating livestock grazing as an on/off switch. Mack and Thompson (1982) move from the false dichotomy of one province being ***grazed*** for millennia and the other ***not grazed*** into "representative species" as evidence. Both are oversimplifications of reality.

Regardless of which grass species one might select, making broad, sweeping generalizations about the ecology of vast expanses of rangelands east and west of the Rocky Mountains based on very few species in each region (1 in each), as M&T attempted, is woefully inadequate and a gross oversimplification of complex, dynamic ecosystems. Mack and Thompson (1982) focus on the *Agropyron* Province (west of the Rocky Mountains) and the *Bouteloua* Province (east of the Rocky Mountains) as described by Daubenmire (1978). Based on Daubenmire's (1978) map of ecological provinces, we estimate the *Agropyron* Province occupies over 670 000 km^2 and appears to include rangeland ecosystems commonly described in rangeland ecology textbooks as Palouse prairie; cold deserts (salt desert shrubland and sagebrush grasslands, which are sometimes further divided into Great Basin sagebrush grasslands and sagebrush steppe); pinon-juniper woodlands; and mountain browse types (Holechek et al. 2010). The *Bouteloua* Province as used by M&T (adapted from Daubenmire 1978) appears to cover a land area > 1 million km^2 and includes rangeland ecosystems commonly described as the shortgrass prairie, northern mixed prairie, and southern mixed prairie (Holechek et al. 2010). Although a comprehensive characterization of rangeland ecosystems in the *Agropyron* and *Bouteloua* Provinces used by M&T is beyond the scope of this paper, it is important to appreciate how expansive and diverse these areas are. To illustrate this point, we provide a more detailed description of rangeland ecosystems, based on current U.S. land classification systems, in a relatively small portion of each region. The complexity revealed at this level of consideration sufficiently highlights the inadequacy of M&T's approach. Expanding consideration to the entirety of the regions east and west of the Rocky Mountains make M&T's approach even less appropriate.

Rangeland ecologists and managers in the United States commonly rely on a land classification approach that subdivides large landscapes into smaller, more homogeneous units called major land resource areas (MLRA). These are defined as "areas with comparable biotic potentials or limitations, identified as geographic areas with similar physiography, geology, climate, water resources, soils, biological resources and land use" (Salley et al. 2016). Based on descriptions of MLRAs for the United States (USDA NRCS 2006) and Daubenmire (1978), we estimate that M&T's *Agropyron* Province includes all or part of 19 MLRAs, and the *Bouteloua* Province includes all or parts of 41 MLRAs.

On the basis of the definition of MLRA offered earlier, one might assume that it would be easy to generalize the ecology of rangelands at the MLRA level, but that would be a faulty assumption. Within each MLRA are several to many ecological sites. An ecological site is defined as "a kind of land with specific physical characteristics that differs from other kinds of land in its ability to produce distinctive kinds and amounts of vegetation ***and in its response to management***." (emphasis added; Society for Range Management 1995). Finally, at the level of an ecological site, one can make reasonably accurate predictions and generalizations about the ecology of a site and its responses to management and disturbances. Recall that each MLRA typically contains many ecological sites; the *Agropyron* Province includes 19 MLRA; and the *Bouteloua* Province includes 41 MLRAs. One of the many MLRAs in the *Agropyron* Province is the Owyhee High Plateau (MLRA 25), a highly variable area that occupies ≈75 000 km^2 primarily in northern Nevada and Southern Idaho, ranging between 915 and 2 300 m elevation and 180 and 405 mm of winter-dominated annual precipitation (USDA NRCS 2006). There are somewhere between 60 and 70 ecological sites in MLRA 25 (Stringham et al. 2015). Across the ecological sites in MLRA 25, there are 31 different species of grass that are considered either dominant or subdominants in the reference states (historical climax plant communities) (USDA NRCS 2006). BBW is a member of this list, but so are 30 other grass species. Clearly, what is known of BBW is insufficient information to generalize to the ecology of MLRA 25, let alone the entire *Agropyron* Province. One of the many MLRAs in the *Bouteloua* Province is the Southern part of the Central High Plains (MLRA 67B) that occupies an area of ≈52 000 km^2 in eastern Colorado. There are 20–25 ecological sites in MLRA 67B, and there are

26 species of grass that are either dominants or codominants in reference states on those ecological sites (USDA NRCS 2006). Blue grama (*Bouteloua gracilis* [(Willd. ex Kunth] Lag. ex Griffiths) is a member of this list, along with 25 other grass species. What is known about blue grama is insufficient information to make accurate and useful generalizations about the ecology of MLRA 67B, let alone the entire *Bouteloua* Province. BBW does not occur as a dominant or codominant grass for ecological sites in MLRA 67B, but farther north in the *Bouteloua* Province, in MLRA 58B, BBW does occur as a dominant or codominant grass on some ecological sites.

Even though it is true that useful predictions about rangeland ecology and management responses can be made at the ecological site level (called range site in 1982), those predictions are ***NOT*** made by generalizing to the entire ecological site what is known about one or two species that might grow there. Rather, rangeland ecologists and managers consider different suites of species that co-occur under various combinations of natural and management inputs and the pathways of change among these different plant species assemblages. The consideration of ecological dynamics among suites of plant species that may exist on a given ecological site is not limited to grasses but also includes all plant lifeforms. It is also not limited to dominants and subdominants in the reference state, but rather considers species from all possible ecological states that span the range of relative abundances from rare to dominant. Mack and Thompson (1982) made broad, sweeping generalizations about the ecology of rangelands west of the Rocky Mountains based almost exclusively on selected information about BBW. Similarly, they made broad, sweeping generalizations about the ecology of rangelands east of the Rocky Mountains based almost exclusively on selected information about blue grama. In doing so, they ignored more than half a century of research, knowledge, and experience that formed the basis of the science of rangeland ecology and management.

In addition to ignoring the basic tenets of rangeland ecology and management, it seems that M&T were so confident in their position that they failed to acknowledge that some questions about the past will be forever unanswerable. Two important unanswerable questions are 1) the exact nature of the effect of legacy grazing practices that occurred before the birth of the science of rangeland ecology in the early 1900s and 2) the presence and extent of past plant associations strongly dominated by BBW that no longer exist in the Great Basin. If one is going to accept M&T's argument about BBW disappearing from the Great Basin solely due to legacy grazing, one must be prepared to explain why it still dominates many Great Basin plant communities today and why it continues to persist east of the Rocky Mountains. BBW literally grows side by side with little bluestem (*Schizachyrium scoparium* [Michx.] Nash) on ecological sites in northeast Wyoming and southeast Montana (*Bouteloua* Province), an area where immense numbers of bison were present over the past several millennia. Located in the heart of the *Bouteloua* Province, how did BBW persist on the edge of its ecological amplitude under the heavy grazing pressure of free-roaming bison?

Forage Quality and Nutrition

Mack and Thompson (1982) also made the case that the nutritional quality of the forage base in the *Agropyron* Province is a poor fit for the nutrient demand of large grazing animals. They argued that east of the Rockies, the mix of C_3 and C_4 grasses in the *Bouteloua* Province suits the nutrient demands of third-trimester and lactation periods much better. However, this is another gross oversimplification. At a given elevation, the period of green feed for grazing animals in the Intermountain West is much contracted in comparison with the area east of the Rocky Mountains. The initial phases of the Cascade-Sierra uplift occurred during the Pliocene, and the rain shadow effect became active during the later Pleistocene period. Indeed, Tidwell et al. (1972) determined that the uplift reduced annual precipitation and also altered the seasonality to winter-early spring dominance throughout the Pleistocene, just as it occurs today. In the Great Basin there is little or no influence from the Gulf of Mexico, so precipitation patterns are sharply winter dominated, giving rise to the dominance of deep-rooted, woody shrubs and caespitose grasses. Because there is no regionally significant summer precipitation to foster the presence of warm-season grasses, wildlife meet dietary needs by using lower-elevation riparian and subirrigated valleys and/or higher elevation resources to lengthen the green-feed period. Lower elevation riparian areas and subirrigated meadows are limited geographically but are locally significant in size (e.g., Humboldt River or the Malhuer Lake complex). For higher-elevation resources there are about 300 mountain ranges in Nevada alone, so summer habitat is never too distant for mobile species to access.

This observable, seasonal movement must also have been the case during the Pleistocene and early Holocene. Megafauna remains have been found at elevations above 8 000 ft. This is exactly where one would find large, free-roaming grazers such as antelope and feral horses today during mid- and late-summer seasons (Collins 2016). The availability of water is also greater at higher-elevation sites during the summer drought period typical of the *Agropyron* Province. It has been recognized for decades that seasonal habitats segregated by elevation are exploited by many wildlife species for nutritional reasons (Dyer et al. 2009). Even bison are known to migrate from lower-elevation winter range to higher-elevation summer range (Van Vuren 1983).

The Intermountain West and Great Basin are inherently short of summer seasonal habitat relative to winter habitat for many wildlife species, so many large grazing animals must and do move to higher-elevation habitats during summer, returning to lower-elevation habitats during winter to seek forage not covered with snow. The ratio of summer habitat to winter habitat in the Great Basin and Intermountain West is sharply in favor of winter habitat, logically leading to the concept of summer habitat as a limiting factor for many wildlife species today, as well as during the Pleistocene. Burkhardt (1996) derived the moniker "follow the green" to describe these seasonal, elevational movements.

Mack and Thompson (1982) also postulated that parturition dates for large grazers were not synchronized with the physiological stages of grasses in the *Agropyron* Province, thereby limiting forage plants to grazing exposure. In other words, if there was no green feed to consume during the birth season, there would be few or no grazing animals. However, in addition to not recognizing "following the green" behavior, they also failed to mention that breeding and parturition are highly correlated to day length or latitude (with plasticity) rather than forage phenology (Churcher 1993; Nuñez et al. 2010). Using the modern analogs of feral horses and bison that have birth windows beginning in March and April, respectively, at similar latitudes to the Intermountain West, we find that this timing corresponds implicitly with the typical annual forage green-up period for most lower and midelevation sites in the *Agropyron* Province. The associated lactation stage is the period when nutrient and forage demands are highest (Kellems and Church 2010). The first critical 60 d after parturition would then generally fall around the end of June, the period when green forages on lower and midelevation sites mature to lower nutrient quality. Therefore, the green period does correspond with peak lactation. At the end of June, wild, mobile grazing animals either move to or spend more time at low-elevation subirrigated ecological sites or move to higher-elevation ecological sites in order to continue foraging on green feed (Dyer et al. 2009; Dyer et al. 2010). Mack and Thompson (1982) failed to address these well-documented behavioral phenomena.

Additionally and of paramount significance, M&T also failed to account for the importance of palatable, nutritious shrub species in the Agropyron Province. Palatable shrubs add to the available forage during the dry summer and winter seasons, in essence subsidizing the grass portion of large, hooved herbivore diets throughout the Holocene period (Laudermilk and Munz 1934).

Soil Biotic Crusts

Mack and Thompson (1982) also argued that the distribution of SBCs was evidence that Great Basin and Intermountain West ecosystems have little naturally selected herbivory tolerance. They claimed that the Agropyron Province had high SBC cover and few large ungulates (Poulton 1955; Daubenmire 1970), while the Bouteloua Province had low SBC cover and abundant wild ungulates over many millennia (Shantz 1906; Hanson and Dahl 1957; Moir and Trlica 1976; Bouton et al. 1980). If polygons are drawn that inclusively connect the respective study areas from each of the six cited studies they referenced earlier, the total area enclosed would be about 14% and 3% of the Agropyron and Bouteloua Provinces, respectively (Fig. 1). Summarized, their evidence includes six geographically unrelated studies, with none designed to specifically assess the abundance of SBC. We must conclude that the disjointed evidence offered provides no definitive insight into the evolutionary development of herbivory tolerance in either Province.

Low SBC cover in the Bouteloua Province can be attributed to several causal factors. The list includes numerous small summer precipitation events (Osala and Lauenroth 1982; Osala, et al. 1992; Lauenroth et al 2009; Coe et al. 2012; Reed et al. 2012); a summer-dominated precipitation regime (USDA NRCS 2006; Bryce et al. 2012; Bowker et al. 2016); and low availability of soil manganese (Mn: $\leq$ 8 ppm) and zinc (Zn: $\leq$ 0.4 ppm) (Bowker et al. 2005).

Follett and Lindsay (1970) found Mn and or Zn levels less than these amounts in 26 of 37 soil A horizons across Colorado. Many ($n = 16$) were in the Bouteloua Province, an area widely known for Zn deficiencies [as are parts of the Agropyron Province] (Alloway 2008). The lack of SBC research across this expansive and heterogeneous ecoregion (Rosentreter and Belnap 2001; McCampbell and Maricle 2018), combined with existing factors known to limit the abundance of SBC, makes M&T's conclusion that the lack of SBC in the Bouteloua Province is due to a long coevolutionary history with large grazers, very tenuous at best.

Mack and Thompson (1982, p. 764), citing Daubenmire (1970) and Poulton (1955), stated "… in the most arid communities of the Agropyron Province, cryptogams cover all undisturbed soil surfaces not occupied by vascular plants and such cryptogam cover may exceed 50% on a unit area basis." This is a less than objective statement for portrayal of SBC cover in the steppe vegetation of Washington where Daubenmire worked, let alone the entire Agropyron Province. Daubenmire (1970) did not measure SBC cover, bare ground, or plant litter in any of the 15 habitat types he described, and he provided only qualitative statements about SBC for just 3 of the 15 habitat types (see Appendix 1). A review of Daubenmire's statements indicates that the amount of SBC cover, while potentially "continuous" in some settings, greatly reflects shade intensity, plant litter, soil characteristics (including stoniness), and, for mosses, the presence of a shrub canopy. Others have also noted the affinity of mosses for shrub canopies (Hilty et al. 2004; Bowker et al. 2005).

Mack and Thompson (1982) also failed to mention that while Poulton (1955) found relatively high SBC cover in *Artemisia tridentata/Pseudoroegneria spicata* plots (qualitatively described by Daubenmire—see Appendix 1, statement 1), he reported an actual mean SBC cover of 13%. A mean SBC cover of 13% creates a vastly different perspective than Daubenmire's (1970) qualitative statement about SBC having continuous cover between the bases of vascular plants. An important unanswered question is: What amount of Poulton (1955) SBC cover occurred under the sagebrush canopy, the microsite favored by mosses and liverworts? Furthermore, is SBC presence under shrubs due to microsite conditions unrelated to grazing? Cattle do not readily step on shrub plants (Balph and Malecheck 1985; Balph et al. 1989); thus, managed grazing is extremely unlikely to seriously harm SBC types largely found under shrub canopies. The > 50% cover of SBC stated in M&T was found in a minority of sites: one study plot of the *Artemisia tridentata/Stipa* association, the xeric phase of the *Agropyron-Poa* association (three total phases mentioned), and the pumitic soil of the *Poa Eriogonum* association, which at the association level had a mean SBC cover of 23%.

Poulton (1955) also reported that four habitat types he studied had 12% or greater bare ground, and in two habitat types bare ground coverage exceeded the cover of SBC. These data and others suggest that topography (Ponzetti et al. 2007), soil (Muscha and Hild 2006), vegetation (Tabeni et al. 2014), weather, and other factors (Poulton 1955, who mentioned burrowing animals) strongly influence crust cover. Daubenmire's (1970) qualitative statements, without quantitative data about crust cover, bare ground (potential crust habitat), and other factors known to influence SBC presence (Bowker et al. 2016), suggests that several to perhaps many factors interact to control SBC distribution and cover in the Columbia Basin and Plateau regions of the Agropyron Province.

Mack and Thompson (1982) did not mention research by Tisdale et al. (1965), which described three never-grazed habitat types within kipukas. Tisdale et al. (1965) noted that SBC cover in all three habitat types was < 5%, bare ground was between 31% and 53%, and shrub cover was between 13% and 15%. Likewise, this pattern of SBC cover, similar to or less than cover from bare ground, has been reported in eastern Idaho (Bork et al. 1998), southeast Oregon ($n = 106$ sites) (Davies et al. 2006; Davies and Bates, 2010), old growth juniper woodlands in central Oregon (Waichler et al. 2001), Wyoming (Muscha and Hild 2006), and 19 grassland communities (167 sites) in central and northeastern Oregon (Johnson and Swanson 2005). All of these authors described their sites as nearly pristine, largely undisturbed, not abusively grazed, or decades-old ungrazed exclosures. Collectively, these data suggest that SBC had microsites available for colonization, yet none reported SBC cover values similar to the levels measured by Poulton (1955). Factors beyond just grazing obviously control SBC abundance across the Agropyron Province.

In the Agropyron Province, both low and comparatively high SBC cover is often accompanied by large amounts of bare ground. This occurs on never-grazed sites, nearly pristine sites, grazed sites with no evidence of abusive grazing, and on sites withdrawn from grazing for decades and their paired, adjacent grazed areas. Collectively, the data do not support the M&T argument. Some communities described by Daubenmire (1970) and Poulton (1955) also occur in other areas of the Agropyron Province and show no evidence of unraveling when SBC cover is low but bare ground is high (Tisdale et al. 1965). This outcome leads one to legitimately question the thesis that large amounts of ground cover by SBC in the Agropyron Province (on what is actually a minority of the Province's total area) is due to a lack of relatively recent evolutionary history of grazing by large herbivores.

Mack and Thompson's claim that SBC abundance is due to a lack of coevolution with large herbivores in the Agropyron Province implies that SBCs are as important ecologically to the system as the predominant, deep-rooted perennial bunchgrasses. Perennial grasses are the recognized foundational life-form that holds sagebrush-grass plant communities together following disturbances that leave the bunchgrasses largely alive (Chambers et al. 2007; Chambers et al. 2014) and typically removes the

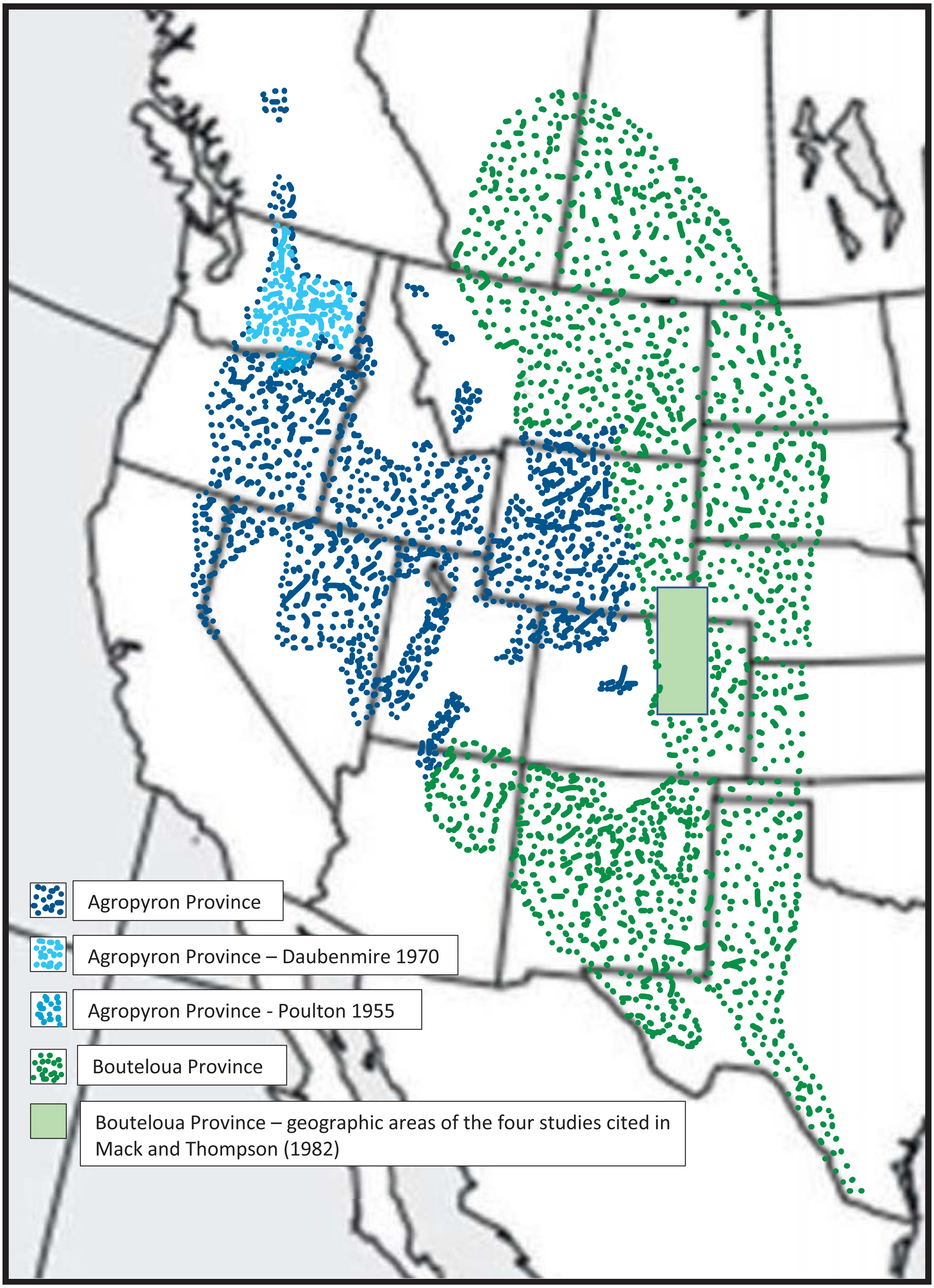

Fig. 1. Approximate boundaries of the Agropyron *(dark blue dots)* and Bouteloua *(dark green dots)* Provinces as adapted from Daubenmire (1978). The two studies cited by Mack and Thompson (1982) to portray soil biological crusts for the entire Agropyron Province occurred in the areas with the *lighter-colored blue dots.* The four papers Mack and Thompson (1982) cited to depict soil biotic crust abundance across the Bouteloua province occurred in the *solid light green polygon*.

nonsprouting sagebrush. Likewise, SBCs often decline dramatically and sometimes almost entirely after fire, in both grassland and shrub-grass fires (Antos et al. 1983; Johansen et al 1984, Hilty et al. 2004; Pyke et al. 2014; Root et al 2017). Grassland fires with low intensity appear less detrimental to SBC in unburned interspaces (gaps) between bunchgrass plants (Bowker et al. 2004), but Ponzetti et al. (2007) concluded that abundant SBC cover after fire depended upon a good stand of perennial bunchgrasses to prevent postfire invasion by annual grasses. These collective results strongly suggest that disturbance-resilient bunchgrasses (and associated multidimensional root systems) are much more important for sustaining plant communities in much of the Agropyron Province than high ground cover from SBCs, either early or late in the successional process. Mack and Thompson (1982) omitted available data from their paper, and additional research since 1982 further demonstrates the weakness in their hypothesis. Again, M&T offered an oversimplification of SBC distributions as evidence to support their claims.

The Alternative Paradigm

Two important points are clear: 1) on the basis of the entire body of scientific evidence, M&T's claim about rangelands east and west of the Rocky Mountains is oversimplified, untenable, and not supported by a reasonable interpretation of the totality of scientific evidence; and 2) current management should incorporate science that leads to realistic, desired future conditions or outcomes instead of rearward-focused management based on nonhysteresis assumptions. Mack and Thompson's (1982) oversimplification of highly diverse and heterogeneous landscapes undermined its validity and usefulness from the beginning. Even so, only about a decade after Mack and Thompson (1982) was published, calls were made by some researchers tangentially associated with the science of rangeland ecology to remove or reduce legally authorized livestock grazing uses from public lands (Fleischner 1994; Donahue 1999). Beschta et al. (2013) was a recent manifestation of this political movement and was answered with a broad-based scientific, evidentiary rebuttal (Svejcar et al. 2014). The movement is still operational in many lay publications and environmental advocacy group newsletters today. It was a major influence on some aspects of the Range Reform Proposal (1994) and its associated CFR Rule 43 Parts, 4, 1780, and 4100 (1995), which is still the legally mandated management framework the US Department of the Interior operates under.

Calls for livestock removals were based on Mack and Thomson (1982) and what Perryman et al. (2003) referred to as the pristine-management-paradigm (p. 33). Perryman et al. (2003) issued strong cautions against this paradigm, which implies that ecosystems would return to a mythical, past ecological state if only protected from stressors like fire and herbivory, which is completely implausible considering the impact of invasive species throughout the world, as well as alterations to the abiotic environment, such as elevated atmospheric CO_2 levels. Expanding this faulty logic into the future obviously leads to a homogenous condition of every ecosystem in the Intermountain West, eventually reaching a Clementsian climax condition—a veritable utopia. Again, what is a productive role of science? Is it reasonable for society to expect scientists and land managers to protect the region from disturbances such as fire and grazing with the goal of restoring it to some past ideological stage or homogenous ecological condition? Or is it the responsibility of scientists and land managers to lead society away from idealistic expectations for which there is limited ecological support and that are completely unachievable?

Rangeland science has embraced complexity in recent decades and continues to advance our understanding of rangeland ecology and management. Much evidence of this refinement exists, but only a few examples will be offered. Laca (2009) called for adaptive management of livestock grazing to incorporate concepts of heterogeneity in plant and animal components of ecosystems, event-driven dynamics, and nonlinear scaling, and Briske et al. (2011) emphasized the importance of adaptive management for complex systems. Fuhlendorf et al. (2017) further highlighted the importance of heterogeneity by stating that "Understanding heterogeneity in space and time should be central to the framework for advancing our discipline and progressing to solve problems that arise with changes in societal desires on rangelands." Fuhlendorf et al. (2017) also suggested that "Perhaps the greatest challenge for applying heterogeneity-based science in rangeland management is overcoming a century-old vision of rangelands as simple ecosystems." Another major development of rangeland science has been the increased incorporation of nonequilibrium ecology and resilience theory (Bestelmeyer et al. 2003; Stringham et al. 2003; Briske et al. 2008; Bestelmeyer et al. 2009; Briske et al. 2017).

As the science of rangeland ecology embraces complexity, management should do likewise. For instance, the two major grazing systems employed in the region are deferred rotation and rest rotation. Cutting-edge science for their time (decades ago), both approaches focus on meeting the physiological needs of grazed perennial grass species (Sampson 1913, 1951), but their implementation over decades throughout the region failed to address how annual invasive grasses would respond (Perryman et al. 2018). Both systems were developed on perennial grass ranges before invasive annual grasses held significant ecological roles. Science now recognizes that many sagebrush and salt desert shrub communities are no longer degraded forms of those monikers; instead, they are novel systems with mixed annual-perennial grass understories and remnant sagebrush or salt desert shrub constituents (Stringham et al. 2015), reinforced by new fire disturbance regimes. Hysteresis is operational in these systems and is of critical concern because hysteresis demands that ecological systems cannot, through removal of a stressor such as domestic livestock grazing, be easily returned to former states once the systems have become altered or changed (Westoby et al. 1989; Laycock 1991). Even ***IF*** domestic livestock were the singular cause of annual grass invasions, which is often claimed but not universally supported, hysteresis still tells us that removing domestic livestock grazing would not reverse the change (Davies et al. 2014). The addition of invasive annual grasses is such a change, which results in a threshold being crossed, and the need for additional energy inputs to cross back over the threshold, if that is even possible. Perryman et al. (2018) proposed managing these systems recognizing fuels management as a triage first step and highlighted fall cattle grazing as one measure to reduce annual invasive grass fuel load characteristics (Schmelzer et al. 2014) and cheatgrass seed bank potentials (Perryman et al. 2020).

Beyond the first step of fuels management, scientists and managers should recognize that livestock grazing must be included as an important tool for land management purposes (Svejcar et al. 2014). The permit process and much of the infrastructure needed to effectively manage domestic livestock grazing on public lands are already in place and do not depend on the vagaries of annual government funding like other useful tools do (e.g., herbicide applications, reseeding efforts). As to M&T's claim, it seems more reasonable to be concerned with how BBW, as well as all of the other plants that grow alongside of it and on sites that it may have once occupied, respond to ***current*** disturbance regimes and management actions, rather than searching backwards in time for responses of one or two species to legacy grazing practices. The first quantitative ecological assessments of public rangelands were based on comparisons to presumed climax vegetation compositions in relict or reference areas (Dyksterhuis 1949). Reference areas were places thought to be inaccessible to livestock during the legacy grazing period, such as butte tops and old cemeteries, or based on what was believed to be the best scientific opinion. Although innovative for the time and useful for context today, there was no consideration of plant community change based on things like the subsidence of Little Ice Age weather regimes, invasive species, changing atmospheric CO_2 levels, management effects of aboriginal people, and perhaps even a lack of grazing.

Current ecological assessments on Interior public lands are based on the Assessment, Inventory, and Monitoring (AIM) Strategy. This approach is an improvement over comparisons to past conditions that cannot be replicated and provides a framework for the Bureau of Land Management (BLM) to inventory and quantitatively assess ecological conditions and trends at regional scales through a series of system attribute indicators. However, AIM is still a measurement tool that informs decisions and should not be used as a management target or endpoint like its predecessor "climax condition" was used. Rather, a management target should be a vision of desired future conditions or outcomes. We conclude that plant communities, ecosystems, and landscapes should be managed in ways that maintain ecological processes rather than certain species compositions that may have existed in past times or in nonhysteresis systems. By maintaining ecological processes such as fire and herbivory (within appropriate or reasonable ranges of variation), we maintain our management and value options for the future. Managers should be given the flexibility to play more active roles rather than reacting to external forces. For instance, if fall livestock grazing in cheatgrass dominated areas is disallowed, cheatgrass fire cycles will continue to be fostered that negatively impact perennial grasses (Davies et al. 2016), the life-form that underpins the resilience of sagebrush communities. Over longer periods of time with limited perennial grass influence, the extent of sagebrush habitats will decline, leading to fewer management options and more compromised sagebrush obligate wildlife populations.

It is with these concepts in mind that we propose a new management paradigm for the Great Basin, Intermountain West, and beyond: management that repairs and maintains ecological processes as outcomes. These outcomes are necessary precursors to other activities and goals like the creation, fostering, and repair of seasonal wildlife habitats, as well as the reintroduction of the desired perennial and annual plant species that work in support of the multiple societal values associated with rangeland resources. Outcome-based management maintains our options for the future. To be successful, this management approach will require the flexibility to change inputs, schedules, and degrees or scales of use or intensities based on seasonal or annual opportunities identified by on-the-ground managers, for all the tools in the management tool box. Programmatic planning that provides management flexibility to react in a timely fashion to local and regional situations should be implemented. It should allow efficient applications of all available management actions including, but not limited to, fire rehabilitation efforts, targeted grazing and grazing prescriptions, vegetation monitoring, herbicide applications, water development projects, fuels management, prescribed fire, wild horse and burro management, conventional and virtual fencing, road building and maintenance, emerging technologies, and other restorative techniques. Maintaining ecological processes as outcomes increases the probability of ensuring for future generations the promotion of health, diversity, and productivity of public and private rangelands.

Declaration of Competing Interest

The authors declare no competing interests.

Acknowledgment

This work was supported in part by the USDA National Institute of Food and Agriculture, Hatch Project 1012851.

Appendix 1. Qualitative statements about soil biotic crust cover extracted from Daubenmire (1970)

Statement 1: about the *Artemisia tridentata* ssp. *tridentata/Pseudoroegneria spicata* habitat type—"areas not occupied by the bases of the vascular plants support a continuous … crust of mainly crustose lichens, tiny acrocarpous mosses, and occasionally liverworts."

Statement 2: for the *Festuca Idahoensis/Symphoricarpos* habitat type—"except where the overhead shade is very dense (mean shrub and herbaceous canopy cover was 269%) or the litter very deep, the ground is covered by lichens and pleruocarpus mosses …".

Statement 3: for the sparsely vegetated and rocky *Artemisia rigida/Poa secunda* habitat type (52% plant canopy cover, with 21% from shrubs) —"soils are always thin and stony" and "beneath the canopy of each *Artemisia* plant, the more vigorous growth of *Tortula* and other mosses."

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