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ABSTRACT

Understanding historical ecosystem diversity and wildlife habitat quality can provide a useful reference for managing and restoring rangeland ecosystems. We characterized historical ecosystem diversity using available empirical data, expert opinion, and the spatially explicit vegetation dynamics model SIMPPLLE (SIMulating Vegetative Patterns and Processes at Landscape ScaLEs) for a landscape of approximately 946,000 ac in eastern Wyoming. We used SIMPPLLE to simulate plant community dynamics as a result of historical disturbance events (for example, fire, bison grazing, and prairie dog activity), climate, and landscape elements (for example, ecological site, proximity to water, and elevation) and their interactions to derive estimates of the historical range of variability for each grass/shrub ecosystem. For each NRCS designated ecological site we defined the historical states that occurred in the presence of grazing by native herbivores and fire, and identified the processes for movements among states within each site. For each historically occurring state within the delineated landscape we determined the mean ac it occupied and the range of variability (in other words, minimum and maximum ac a state occupied). Comparisons of historical grass/shrub ecosystem diversity of the area with existing conditions indicate that there have been significant changes, most notably the lack of representation of ecosystems dominated by grass species that typically decrease with grazing, the widespread presence of introduced species especially annual brome, and alterations to fire regimes. Through comparisons of historical ecosystem diversity with existing conditions, we identified specific plant communities that are underrepresented and in need of restoration to maintain ecosystem diversity and wildlife habitat.

INTRODUCTION

It has been suggested that loss of evolutionary habitats, or the environments in which species evolve, is one of the greatest threats to biological diversity (Templeton and others 2001). In an effort to address this threat many conservation planning initiatives have sought to identify historical reference conditions of ecosystems for assessment of existing conditions and identification of management goals or conservation priorities (Forbis and others 2007; Haufler and others 1996). Historical reference approaches represent one type of coarse filter strategy for biological diversity conservation (Haufler 1999). This approach is based on the premise that the ecosystem diversity that occurred in an area over the past several hundred to thousand years defined biodiversity at the ecosystem and landscape levels, and provided the habitat that supported the species and genetic diversity of a landscape (Haufler and others 2002; Poiani and others 2000). This coarse filter approach has the primary objective of providing adequate ecological representation of all historically occurring ecosystems especially in the context of providing adequate wildlife habitat for species of concern.

Historical references describe ecosystem conditions that resulted from natural disturbance (in other words, fire, grazing, etc.) and human-influenced disturbance (in other words, native American), which created the dynamic conditions that supported the native species of an area prior to the influences of European settlement. Historical references are usually confined to a period less than 1000 years prior to European settlement, as these reflect the habitat conditions most relevant to the species that are present today (Morgan and others 1994). Historical disturbance regimes are the patterns of frequency and intensity that can be quantified using ecological evidence. Historical reference conditions are typically characterized using the Historical Range of Variability (HRV), which emphasizes that many ecosystems varied in amount, composition, and structure due to historical variations in climate and stochastic events (Aplet and Keeton 1999).

The most common approach used to characterize historical reference conditions are field assessments that quantify biological attributes of sites identified as being relatively free from anthropogenic alterations and where the ecological processes that a site evolved with are relatively intact (Stoddard and others 2006; USDA/NRCS 2003). Although this approach to characterizing historical reference conditions provides very useful information, appropriate references sites are often lacking because of historical disturbance regime modification and land conversions (Nilsson and others 2007). Furthermore, relict reference sites are typically found in inaccessible areas characterized by rugged terrain, rocky outcrops, and areas of shallow soil depth (Shinneman and others 2008), which are rarely characteristic of the type of sites in the surrounding landscape. These types of reference sites also

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have higher probabilities of having site conditions indicative of late historical states because of their protected landscape position.

Lack of appropriate reference areas are especially a problem in many rangeland systems where modern grazing practices, fire management policies, and wildlife "pest control" policies have resulted in very different ecosystem dynamics. Modern livestock operations often control the timing, duration, and level of utilization by livestock and most operations include infrastructure developments like water, fencing, and attractants to promote even utilization and homogeneous structure (Fuhlendorf and Engle 2001). In many areas of the Great Plains, fire suppression activities and land use practices that have reduced the probability of fire spread have drastically decreased the occurrence of fire compared to historical fire regimes resulting in modification of ecosystem structure and function (Bragg and Hurlbert 1976; Hoch and others 2002; Sieg and others 1999). Pest control (for example, prairie dog poisoning) has also had an impact on the amounts of this historical disturbance (Miller and others 1994). As an alternative to field assessments, simulation modeling efforts have been used to develop reference conditions in forested systems (Barrett 2001; Chew and others 2004), and LANDFIRE model components have been used to provide reference conditions in grass and shrub ecosystems in Nevada (Forbis and others 2007).

Most modern restoration efforts do not attempt to return landscapes to conditions that occurred prior to the influences of European settlement. Non-indigenous species and anthropogenically modified disturbance regimes characterize most modern landscapes and complicate restoration efforts. However, providing an understanding of the ecosystem diversity that occurred during an identified timeframe prior to European settlement provides critical reference information for defining and quantifying a baseline of what should be considered "natural" for an area. Below we describe the primary disturbances that historically influenced ecosystems within the Thunder Basin region and we describe the historical ecosystem diversity, including an estimate of the historical range of variability of ecosystems within a delineated, 946,000 ac area in Converse, Campbell, Weston, and Niobrara Counties in eastern Wyoming.

Review of Evolutionary Disturbance Mechanisms in Eastern Wyoming

Prior to Euro-American settlement, natural disturbance processes such as fire and grazing were primary influences on the ecosystem diversity that occurred in eastern Wyoming (Knight 1994). Additional disturbances included herbivory and burrowing activities of prairie dogs (Kotliar and others 1999). Native Americans interacted with and influenced ecosystem diversity for thousands of years, but typically in ways that used naturally occurring disturbance processes to benefit their subsistence strategies, such as using fire to create better wildlife habitat for hunted species or maintaining travel corridors in more open conditions (Williams 2005).

Fire

As in much of the Great Plains grasslands, fire was a relatively common disturbance event in eastern Wyoming prior to European settlement (Daubenmire 1968; Fisher and others 1987; Hann 2003; Perryman 1996; Perryman and Laycock 2000). Historically, fires were started by lightning (Higgins 1984; Komarek 1964) and the activities of Native Americans (Higgins 1984; Williams 2005). Native Americans used fire throughout the year. In contrast, fires started by lightning occurred mostly in hot and dry summer conditions, late growing season, or during the dormant season (Komarek 1964; Perryman and Laycock 2000). Within fire maintained landscapes, microhabitats that prevent or slow fire spread existed in riparian zones, badlands, ravines, and other fire-protected locations like prairie dog colonies (Anderson 1990). Furthermore, fire return intervals were also influenced by climate and by previous grazing disturbance. Fire effects on grassland ecosystems are a function of fire frequency, intensity, and timing, as well as the interaction of these factors with herbivory (Engle and Bidwell 2001). Fire can influence grassland vegetation in a number of ways including changes to productivity, composition, and structure (Engle and Bidwell 2001).

Bison Grazing

Great Plains grasslands were grazed by many herbivores, however, no species was more influential than bison in shaping the grassland ecosystems of Wyoming (Knapp and others 1999). Intensity of bison grazing was influenced by actively growing plants (McNaughton 1985), juxtaposition to water sources and recent fire events. Bison, like most herbivores, require a regular supply of water. Sites surrounding rivers, lakes, and ponds typically receive a disproportionate amount of heavy grazing. In contrast, sites farthest from water sources typically receive lower levels of grazing (Soper 1941). Many researchers have found that a recently burned site will attract bison (Bamforth 1987; Biondini and others 1999; Coppedge and Shaw 1998; Frank and others 1998). The release of soil nutrients and the corresponding rapid new growth represents high-quality forage for several seasons following a fire event. At the landscape level, historical fire and grazing disturbance regimes interacted to provide a mosaic of structural and successional conditions across grassland ecosystems (Fuhlendorf and Engle 2001). Fire and bison grazing interacted because recently burned sites attracted bison grazing, and subsequently the amount of forage removed from a site and its distribution in the landscape determined the probability and intensity of the next fire event (Fuhlendorf and Engle 2001). Thus, the combination of fire and grazing yielded the dynamic habitat mosaic and landscape heterogeneity to which prairie wildlife species were well adapted (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004).

Black-tailed Prairie Dogs

Prior to European settlement, black-tailed prairie dogs occurred extensively throughout eastern Wyoming (Wuerthner 1997). Black-tailed prairie dogs are considered an historical disturbance component in Wyoming due to the effect of their colonies on grassland ecosystems. Prairie dogs alter prairie ecosystems by creating above and below ground disturbances that produce large and unique habitat patches and thereby alter the structural and functional properties of grassland ecosystems (Whicker and Detling 1988).

METHODS

Description of Historical States

We described all the terrestrial ecosystems or "states" that historically occurred (in other words, the ecosystem diversity) in Thunder Basin as a function of the different abiotic factors (for example, soils, climate, etc.) and disturbances that historically occurred (for example, fire, grazing, prairie dog activities) (Haufler and others 1996; Haufler 2000). We utilized the Natural Resources Conservation Service's (NRCS) ecological site classification system that uses soils as the basic mapping unit (USDA/NRCS 2003). Ecological sites provide valuable information on abiotic conditions and they provide information on the potential states that could occur on each site. This information must then be further developed to quantify the actual historical states and their amounts that occur across any specific ecological sites. Thus, we included fire and large herbivore grazing (in other words, bison) as the primary disturbance mechanisms that historically operated in grass and shrub ecosystems of eastern Wyoming and described the historical states occurring on each ecological site (see figure 1 for an example of the descriptions of historical states that occurred as a function of historical disturbance regimes). We predicted fire and grazing disturbance transitions for each ecological site using the best available information on ecosystem and plant species response. For example, we used canopy cover of plant species that typically increase or decrease with different levels of grazing pressure as indicators of historical states driven by different grazing regimes. We identified plant species likely to occur in a particular ecological site and how those species typically respond to grazing from NRCS developed ecological site descriptions, as well as, input from a team of range ecologists knowledgeable of the plant dynamics of the area. We used canopy cover of big sagebrush (*Artemisia tridentata*) as an indicator of historical states driven by short or long interval fire regimes, where some states were classified as being characteristic of long fire return intervals if they had >10 percent big sagebrush cover. We characterized the historical fire regime for this area by using information developed for the fire regime condition class Interagency Handbook Reference Conditions (Hann 2003), as well as, supplemental literature (Perryman 1996; Perryman and Laycock 2000). We estimated plant dynamics and rates of change for each plant species included as indicators of either fire return interval or grazing level based on input from the team of rangeland ecologists and species information.

Determining the Historical Reference: Modeling Historical Ecosystem Diversity

We modeled historical grass/shrub vegetation dynamics in Thunder Basin using a spatially explicit landscape model SIMPPLLE (SIMulating Patterns and Processes at Landscape scaLEs) (Chew and others 2004). We used SIMPPLLE to simulate plant community dynamics as a result of natural disturbance events (for example, fire, bison grazing, and prairie dog activity), climate, and landscape elements (for example, ecological site, proximity to water, and elevation) in the delineated planning area in eastern Wyoming. Although SIMPPLLE has a variety of potential applications, we specifically used SIMPPLLE to derive the historical range of variability (HRV) for each grass/shrub ecosystem and we represented the HRV as the average, minimum, and maximum number of ac that each historical state occupied in our simulations.

Within the planning area we divided the landscape into 10 ac cells and assigned each cell as a specific vegetation unit defined by its ecological site and by its historical state which was based on its vegetation composition. We identified starting points (in other words, historical states based on plant species composition) for each 10 ac cell using generalized vegetation descriptions included in historical public land survey records (PLSRs) conducted in the 1880s. The 1880 PLSR information provided general descriptions of the dominant plant types (for example bunchgrass, sagebrush, etc.) and was prone to surveyor bias, however, this information offered at least a generalized starting point for the modeling effort that was based on spatially reported data from the 1880s.

Landscape features that were static components in each simulated area included ecological sites, aquatic areas, riparian areas, estimated locations of historical prairie dog colonies, and elevation. To map ecological sites for the planning area, which occurred within the Northern Rolling High Plains Major Land Resource Area (MLRA 58B), we used the NRCS ecological site classification system that uses soils as the basic mapping unit (USDA/NRCS 2003). We used National Hydrography Data and NRCS ecological sites to map wetland, riparian, and aquatic areas and digital elevation models to map elevation within the project area.

The approximate locations of historical prairie dog colonies were derived from a prairie dog suitability assessment conducted for this area that was based on preferred soils, other terrain features, and knowledge of existing prairie dog colonies.

The response of key plant species to climate (in other words, precipitation) and disturbance (in other words, fire and grazing) were tracked annually in SIMPPLLE for each 10 ac cell. Within a given year plant species within each cell were subject to change based on climate (for example, above average, average, or below average precipitation), grazing (for example, light, moderate, or heavy grazing), and the occurrence of fire. Subsequently each 10 ac cell was given an ecosystem classification that placed it into a historical state within each NRCS designated ecological site based on its species composition. That is, classification rules were developed that used percent cover of species within a cell to identify what historical state it belonged to, and over time climate and disturbance induced changes in plant species composition caused shifts among historical states. We based the plant species response parameters to climate and disturbance, as well as shifts among historical states on expert opinion from a team of rangeland ecologists, and on scientific literature.

Fire starts were caused by lightning strikes in this model and were stochastically selected, resulting in variations designed to simulate historical variations in lightning caused fires over time. The number of lightning strikes was adjusted in the model to cause increases or decreases in the number of fire starts, but the overall influence of fire was more dependent on the burn patterns than on the number of fire starts. Once a fire started in a given cell it had the opportunity to spread to adjacent cells until it encountered cells that reduced the ability of fire to spread (see below), or encountered a stochastic weather ending event. The probability of fire occurrence was influenced by the climate (precipitation and temperature) in a given year and the grazing history on individual units (for example, a heavily grazed 10-ac unit in a given year had a lower probability of burning, whereas a lightly grazed 10-ac unit had a higher probability of burning). Fire spread probabilities were also influenced by fixed landscape features, such as prairie dog colonies, gullied land, and aquatic/riparian areas that provided natural fire breaks. Terrestrial ecological sites that had low probability of fire because of sparse fine fuel included the following ecological sites; saline upland, very shallow, badlands, and gullied land which combined represented 84,253 ac within the planning area. The remaining terrestrial ecological sites clayey, shallow clayey, loamy, shallow loamy, sands, sandy, shallow sandy, and shallow hilly representing 810,978 ac, had a fire return probability of 11 years that ranged from approximately 3 to 15 years, with some areas exhibiting low fuel levels burning infrequently or never.

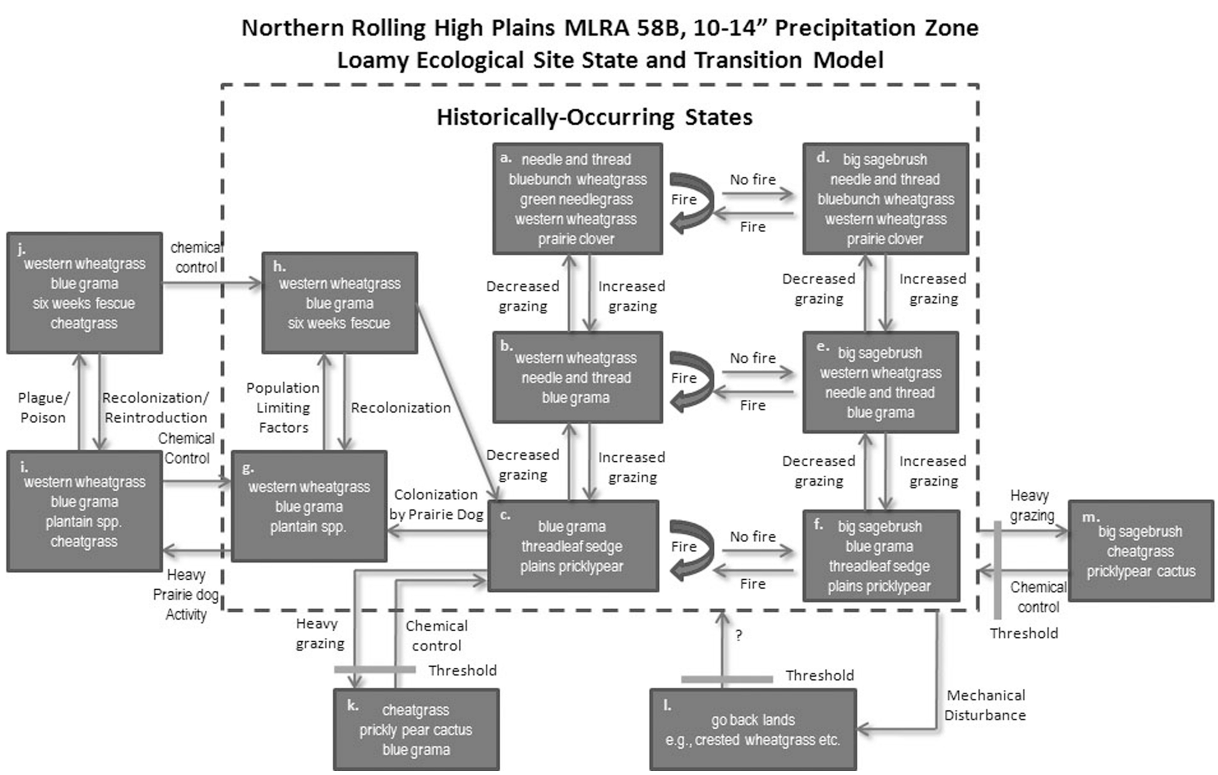

Figure 1–Expanded state and transition model highlighting the states, disturbance pathways, and transitions that historically occurred on loamy ecological sites within the Northern Rolling High Plains Major Land Resource Area (MLRA 58B).

Bison grazing intensity was dependent on the proximity of the 10-ac vegetation units to water and the fire history of the vegetation units within the areas simulated. For instance, based on knowledge of bison grazing behavior it was assumed that the closer the 10-ac vegetation units were to water and the more recently burned the vegetation units were, the heavier bison would graze. Vegetation units located between 0 to 5,280 feet away from water had a higher probability of receiving heavy bison grazing, whereas vegetation units located between 5,281 to 15,840 and 15,841 or greater feet away from water had increasingly higher probabilities of receiving moderate or light grazing, respectively. Likewise, the probability of heavy grazing on 10-ac vegetation units 1 to 2 years after a fire was higher, whereas 3 to 5 years and 6 or more years after fire the vegetation units had a higher probability of moderate and light grazing, respectively. Five simulations, each representing 85 years, were performed in SIMPPLLE following an initial 250 year run of the model. The initial 250 year run was designed to allow the modeling landscape to acclimate to the disturbance regimes, an important feature considering the starting ecosystem conditions of the landscape were based on generalized descriptions of the PLSR. In each of the simulations, climate (in other words, precipitation and temperature) patterns were varied within the range of climate patterns recorded for the Thunder Basin area. Following the simulations the results were summarized by the historical states within each ecological site occurring within the planning area.

RESULTS AND DISCUSSION

Terrestrial plant community states for the Northern Rolling High Plains, Major Land Resource Area are fully described in Haufler and others (2008). These state descriptions include information about the species composition, structure, productivity, and the characteristic disturbances that occurred within each historical state. The average, minimum, and maximum number of ac historically occupied by each historical state in the Thunder Basin region can be found in table 1. A majority of the terrestrial ecosystems in this area, 80.30 percent, were in vegetation conditions described by the short interval fire regime (table 2) generally experiencing a fire at least once every 25 years. A smaller component of the terrestrial ecosystems (19.70 percent) were classified as having long fire return intervals (table 2). Of this, 9.75 percent of the grass/shrub ecosystems were sparsely vegetated, independent of grazing regimes, and would not support short fire return intervals (table 2).

Table 1–Results of the Historical Range of Variability (HRV) analysis for ecological sites within the Thunder Basin planning landscape in eastern Wyoming. The mean, minimum, and maximum number of acres historically occupied by a given state is presented for each ecological site.

Fire Return Interval (FRI)/ Grazing Regime	Ecological Site										
	HRV	Clayey	Shallow Clayey	Loamy	Shallow Loamy	Sands/ Sandy	Shallow Sandy	Shallow Hilly	Very Shallow	Saline Upland	Badlands/ Gullied Land
Short FRI											
Light Grazing	Mean	40,470	44,690	90,235	20,566	20,285	10,327	9,435			
	Min	30,710	32,612	73,170	14,125	15,545	6,308	6,480	—[a]	—	—
	Max	47,969	53,490	102,646	25,538	25,024	13,914	11,716			
Moderate Grazing	Mean	44,161	65,569	77,307	17,628	21,043	10,575	8,087			
	Min	40,113	59,184	70,326	15,312	17,252	7,421	7,025	—	—	—
	Max	52,017	75,404	88,684	22,148	26,162	14,780	10,161			
Heavy Grazing	Mean	31,543	59,357	70,844	16,837	12,007	7,297	7,724			
	Min	22,140	47,106	55,330	12,713	7,267	4,391	5,832	—	—	—
	Max	43,327	76,612	91,269	22,205	18,705	11,008	10,187			
Long FRI											
Light Grazing	Mean	2,381	2,071	11,983	1,413	7,141	2,257	648	913	4,160	
	Min	952	690	6,981	452	3,665	155	207	518	3,353	N/A[b]
	Max	4,642	3,969	17,582	2,995	11,880	6,648	1,374	1,210	5,136	
Moderate Grazing	Mean	357	518	7,239	17	1,959	340	8	1,007	7,173	
	Min	0	173	6,464	0	632	0	0	710	3,523	N/A
	Max	1,309	1,553	10,601	57	4,108	2,041	26	1,444	12,309	
Heavy Grazing	Mean	119	345	1,034	45	758	124	21	682	31,113	
	Min	0	0	259	0	126	0	0	406	25,552	N/A
	Max	714	1,035	2,844	226	2,022	1,237	104	1,056	35,230	
Sparsely Vegetated		6,606	51,811	9,745	6,041	1,490	4,270	4,348	189	3,456	6499

[a]Ecological sites that did not have short fire return intervals because of sparse fuel.
[b]Information not available.

Historical vegetation conditions reflective of light, moderate, and heavy grazing regimes were found in near equal proportions in the Thunder Basin planning area with 31.36 percent, 30.85 percent, and 28.04 percent of plant communities classified as having compositions characteristic of light, moderate, and heavy grazing respectively (table 2). Of the terrestrial ecosystems classified as having a short fire return interval, 27.54 percent where characteristic of light grazing regimes, 28.74 percent were characteristic of moderate grazing regimes, and 24.02 percent were characteristic of heavy grazing regimes (table 2). For the terrestrial ecosystems classified as having a long fire return interval, 3.82 percent were characteristic of light grazing regimes, 2.11 percent were characteristic of moderate grazing regimes, 4.02 percent were characteristic of heavy grazing regimes, and 9.75 percent were sparsely vegetated regardless of grazing regimes (table 2).

The results of this historical range of variability simulation (tables 1 to 2) provide estimates of the historical ecosystem diversity within the Thunder Basin planning area. These results along with the model input information provide an estimate of reference conditions for historical states for each ecological site occurring in the Thunder Basin planning area. Various parameters within the SIMPPLLE model can be adjusted which would influence the model's results and thus the estimated amounts of plant community states. For example, increasing the number of lightning strikes will increase the number of fire starts. While the primary influence of fire was more related to its ability to spread across the landscape, changes in number of lightning strikes would result in some change in the percentage of the landscape in long or short-interval fire regimes. Similarly, changes to weightings for probabilities of grazing pressure would result in shifts in the percentages of the landscape in light, moderate, or heavy grazing regimes. The number of bison and other grazers that historically occurred in the landscape is not known. Therefore we estimated possible grazing effects to maintain some representation of all regimes. The specific amounts of each grazing regime that occurred historically may have differed from our estimates, but we have attempted to simulate a likely landscape configuration based on the best available information we complied.

Comparison of historical ecosystem conditions of this area with previously assessed existing ecosystem conditions (Ganguli and others 2008) reveal several interesting differences, most notably the widespread presence of exotic plant species especially *Bromus tectorum* and *Bromus arvensis*, the lack of native plant species that typically decrease with increasing grazing pressure, and the alteration of fire regimes. Through comparisons of historical ecosystem diversity with existing conditions we identified specific plant communities that are underrepresented in the Thunder Basin planning area and in need of restoration to provide desired wildlife habitat and other altered ecosystem services. We have identified the information required to develop a coarse filter approach for conservation planning efforts and suggest that private and public land managers within the Thunder Basin planning area consider an integrated coarse and fine filter approach as they develop specific conservation objectives and a management plan for this area.

Table 2—Summary of the SIMPPLLE historical range of variability model simulation illustrating the percent of the Thunder Basin planning area that was classified, based on plant species composition, as being characteristic of disturbance (i.e., fire and grazing) induced historical states or states that are naturally sparsely vegetated.

	Fire Return Interval	
Grazing Regime	**Short**	**Long**
	% of the landscape	
Light	27.54	3.82
Moderate	28.74	2.11
Heavy	24.02	4.02
Sparsely Vegetated		9.75

Coarse filter and fine filters are terms that have been widely used to characterize different conservation strategies. Coarse filter strategies focus on providing an appropriate mix of ecosystems or ecological communities across a planning landscape, while fine filter strategies focus on providing for the needs of individual or multiple species within a landscape (Haufler 1999; Marcot and others 1994; Schwartz 1999; The Nature Conservancy 1982). The fundamental difference in the two conservation approaches in whether the primary basis of a strategy is focused on ecosystems or species. Coarse filter approaches assume that providing adequate ecosystem representation will maintain ecosystem integrity, habitat needs, and future persistence of all native species. However, simply providing specified amounts of each native or historically-occurring ecosystem in a landscape may not be sufficient because the size, juxtaposition, or distribution of the habitat patches provided by the representation conditions might not meet the needs of many species. Various conservation planning initiatives have moved towards using a combination of coarse and fine filter approaches to address their objectives so that both ecosystems and species are considered in the planning process.

IMPLICATIONS

Given the difficulty of identifying appropriate native ecosystem reference sites that are free of modern anthropogenic influences, spatially explicit landscape-scale modeling efforts can provide valuable information that can be used in conservation planning and management of grass and shrub ecosystems. A modeling tool like SIMPPLLE allows users to define the spatial scale (in other words, grain and extent) appropriate for a given modeling exercise and incorporate the best available information for an area. SIMPPLLE can also be used in simulations of current or future conditions allowing for investigations of plant community response to disturbance regime modification, climate change, and invasive plant species. In fact, SIMPPLLE has recently been used in a collaborative modeling effort to address landscape impacts to alternative management scenarios (Turner and others 2008). Tools like NRCS Ecological Site Descriptions and associated state and transition models often provide valuable information that can be used to characterize the SIMPPLLE model for simulations aimed at characterizing reference conditions. Furthermore, the integration of model-derived reference sites with information from ecological site descriptions can provide a useful resource for ecosystem restoration planning. To aid management and conservation planning efforts future development and modification of Ecological Site Descriptions should include as much information as possible about native or historical ecosystems that occurred as a function of historical disturbance regimes. Ecological site descriptions should also be further developed to provide better wildlife habitat information for historical and existing ecosystem states.

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