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ABSTRACT

*Use of reference conditions to compare current conditions what managers believed represented healthy and functioning systems has become a common approach to evaluate vegetation and habitat conditions and aid development of land management plans. Often reference conditions attempt to describe landscapes as they existed and functioned prior to about 1850, and often largely rely on expert opinion. We developed reference conditions for sagebrush (*Artemisia *spp. L.) ecosystems in eastern Oregon based on ecological site descriptions, soil surveys, climate data, wildfire records, expert opinion, and literature using a state-and-transition (STM) modeling framework. Using ecological site descriptions for the Malheur High Plateau Major Land Resource Area (MHP), we divided sagebrush communities into four groups based on grass productivity in low, average and high productivity years. Literature helped us determine which disturbance factors to include, the community phases for each model, and associated seasonal habitat for greater sage-grouse (*Centrocercus urophasianus*). We developed successional timelines in the absence of disturbance, and determined the probable outcomes of a given type of disturbance event. We used fire records and climate data to develop disturbance event probabilities and periodicities. Contrary to our expectations, fire did not appear to be the most important factor influencing sagebrush ecosystems under reference conditions in our models. The modeled historical abundance of sage-grouse breeding and brood-rearing habitat was within range of or greater than the amount recommended by sage-grouse biologists, but the abundance of wintering habitat was less. By using objective criteria as much as possible, our approach should also be repeatable in other locations. Since we used climate criteria to define most disturbance probabilities, our models provide an opportunity to examine how changes in climate could affect plant communities, disturbance regimes, and the quality and quantity of sage-grouse habitat in future modeling efforts.*

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INTRODUCTION

Sagebrush (*Artemisia* spp. L.) ecosystems provide many important economic and social values in the Intermountain West, such as livestock forage, water, recreational opportunities, and habitat for a variety of wildlife species. Changes to sagebrush ecosystems over the last 150 years threaten their ability to provide many of these values in the future (Connelly et al. 2004; Miller and Eddleman 2000). Human-related disturbances, invasive species, expansion of conifer woodlands, changes in fire regimes, and changes in climate have all been involved in reducing the area occupied by sagebrush ecosystems by an estimated 14.8 million ha across the western United States (USDI BLM 2004). Habitat for the greater sage-grouse (*Centrocercus urophasianus*), a candidate species for listing under the Endangered Species Act, is of great concern in many areas of the interior West (Bunting et al. 2002; Connelly et al. 2004; Knick et al. 2003).

Under current ecosystem management practices, federal land managers compare current conditions to reference conditions to evaluate changes in land health and probable causes of those changes. Generally, reference, or historical, conditions are based on some measure or description of conditions present around 1850 in the western United States. However, the lack of detailed descriptions and suitable surrogates, such as tree ring studies, and the lack of stand or patch-scale vegetation modeling tools in rangelands mean that expert opinion often forms a large part of the basis for the reference condition descriptions. In the absence of intact reference areas to serve as a basis, different experts may form very different opinions of the reference conditions and what factors were important in creating those conditions.

State-and transition modeling frameworks (STMs), such as the Vegetation Dynamics Development Tool (VDDT) (ESSA Technologies Ltd. 2007), offer the promise of developing reference conditions that are more objective and repeatable, using a process that is transferable to other landscapes. These modeling frameworks can be used at a scale suitable for land use planning, can incorporate management actions and relevant natural disturbances, and fit directly with current rangeland ecology paradigms (Briske et al. 2006; Stringham et al. 2003; Westoby et al. 1989). Since STMs are probabilistic instead of mechanistic, they can operate with a combination of empirical data and expert opinion where empirical data are lacking; a common condition in rangeland management. Climate variables can form the basis of event probabilities to predict plant community changes.

Our goals in this study were to evaluate the use of climate variables as a basis for event probabilities and to evaluate how historical disturbances may have influenced reference conditions in sagebrush communities, with an emphasis on the quantity and quality of sage-grouse habitat. Our primary objective was to develop VDDT-based models that could 1) simulate the effects of natural disturbances on plant community dynamics using fire, soils, and climate data, 2) incorporate available information from the scientific literature on sagebrush-steppe ecosystems, and 3) use selected rules used in mechanistic vegetation models. We used the literature, climatic records, and a limited amount of expert opinion to develop probabilities of disturbance and successional pathways and rates for four sagebrush groupings. Sagebrush groupings were based on ecological site descriptions. We estimated the amount of each community phase and the resulting quantity of sage-grouse habitat within each sagebrush group and for the landscape as a whole. Terminology follows that used by the state-and-transition literature (Bestelmeyer et al. 2009).

STUDY AREA

The study area was the 4-million ha Malheur High Plateau (MHP) major land resource area (NRCS 2006) in southeastern Oregon (figure 1). Much of the area lies between 1190 m and 2105 m elevation, with Steens Mountain reaching 2967 m. The area contains no major rivers and little surface water but has numerous springs, shallow lakes, and playas. Perennial streams and small rivers are mostly located on the periphery. Using soil series descriptions (http: /soils.usda.gov/technical/classification/osd/index.html) we estimated that 98 percent of the soils in the sagebrush ecological types of the MHP are Mollisols and Aridisols. Soils are primarily loamy to clayey, well-drained and shallow (25 to 50 cm) to moderately deep (50 to 90 cm) in uplands, and poorly to well-drained and deep to very deep (>90 cm) in basins.

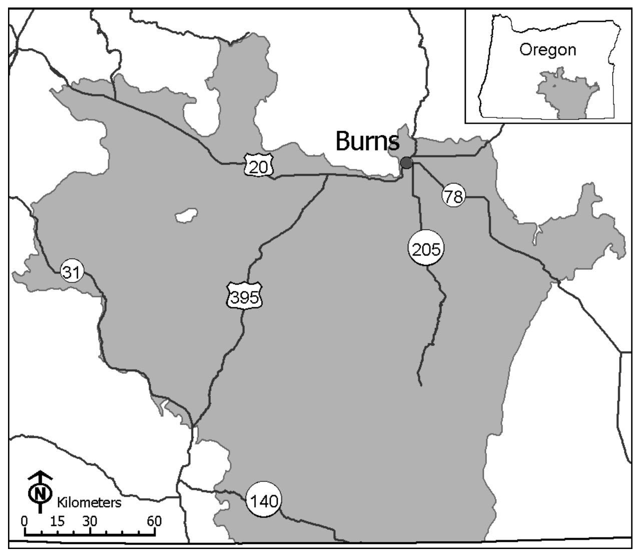

Figure 1. Location of the study area in Oregon. The High Desert Province Ecological Province and the Malheur High Plateau Major Land Resource Area occupy approximately the same area, with the exception of the area to the east of Steens Mountain. The Malheur High Plateau Major Land Resource Area includes some area to the east of Steens Mountain while the High Desert Ecological Province does not. The area to the east of Steens Mountain lies within the rain shadow of the mountain and has a different climate. The town of Burns is the largest community within the study area.

The average annual precipitation ranges from 105 mm to 305 mm over most of the area. Winter and spring are the wettest periods with most precipitation falling in November, December, January and May, while summer is the driest. January is the coolest month, averaging -2°C, and July the warmest, averaging 19°C. Sagebrush-steppe (*Artemisia* spp. L. and cespitose grasses) is the dominant vegetation type with salt desert shrub (*Sarcobatus vermiculatus* (Hook.) Torr.-*Grayia spinosa* (Hook.) Moq.) on saline soils in basins, western juniper (*Juniperus occidentalis* Hook. var. *occidentalis*) expanding out from rockier areas, and aspen (*Populus tremuloides* Michx.) at the higher elevations.

Model Design and Assumptions

We selected 1350 to 1850 as our historical reference period, a period commonly known as the Little Ice Age. Although the climate was cooler and wetter than present, it had shifted into a winter-dominant precipitation regime with plant communities very similar to present (Miller and Wigand 1994). Prior to this period, climate was warmer and drier than present with less dominance of winter precipitation and different disturbance regimes (Cook et al. 2004; Miller and Wigand 1994).

We used instrument-based climate records to develop rules for determining the frequencies of climate-related events (Neilson et al. 1992), using these frequencies in combination with other information sources and expert opinion to estimate the probabilities of several disturbance types and establishment rates for sagebrush. Data sources included temperature and precipitation records for Oregon Climate Division 7 (OCD7) (http: //www7.ncdc.noaa.gov / CDO/CDODivisionSelect.jsp) organized by water year (October through September) for 1894 to 2007; snow data from the Reynolds Creek Experimental Range for 1967 to 1996 (Hanson et al. 2001; Marks et al 2001), and local remote area weather stations (RAWS) (http: //www.raws.dri.edu/index.html). Although the Reynolds Creek Experimental Range lies outside the study area, the climate is similar (Hanson et al. 2001) and detailed snowfall data are available for this location that are not available for OCD7.

We used ecological site descriptions for the MHP (http: //esis.sc.egov.usda.gov) to divide the sagebrush-grass plant communities into four groups based on grass productivity in low, average, and high production years. We designated these groups as Warm-Moist Sagebrush (WM Group), Cool-Moist Sagebrush (CM Group), Warm-Dry Sagebrush (WD Group), and Shallow-Dry Sagebrush (SD Group). Since site productivity influences recovery rates following fire (Bollinger and Perryman 2008; Boltz 1994; Lesica et al. 2007; Wambolt et al. 2001), we assumed the same applied equally well to other disturbances. We used grass production of 672 kg ha^{-1} as the threshold for these divisions since that level of production is considered the minimum needed to support fire spread in bunchgrass fuels under moderate burning conditions (Bunting et al. 1987; Gruell et al. 1986).

The WM Group, the most productive group, typically resided on xeric, mesic, deep to very deep soils. Water storage capacity was high and many sites were subirrigated. This group occurred mostly in swales, terraces, and near or in riparian areas below 1220 m elevation. It occupied an estimated 11 percent of the MHP, based on soil surveys (http: //www.or.nrcs.usda.gov/pnw_soil/or_data.html). The modal community was basin big sagebrush (*Artemisia tridentata* Nutt. ssp. tridentata)/basin wildrye (*Leymus cinereus* (Scribn. & Merr.) A. Löve). We included fire, drought, and insects as the important disturbances in this group.

The CM Group was found on xeric, frigid, moderately deep to deep soils mostly above 1220 m elevation. Soils had a high water storage capacity, but subirrigation was rare to nonexistent. This group typically occurred on ridges, northerly aspects at lower elevations, and all aspects at higher elevations, and occupied an estimated 16 percent of the MHP. The modal sagebrush community was mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle)/Idaho fescue (*Festuca idahoensis* Elmer). We included fire, drought, insects, freezekill, snow mold, and voles as major disturbances.

The WD Group was found on aridic, mesic, moderately deep to shallow soils up to 1400 m elevation. Water holding capacity was moderate to low and sites tended to become quite dry by mid to late summer. This group occurred mostly on southerly aspects at higher elevations, well-drained soils, and relatively shallow soils in basin bottoms and terraces, and occupied approximately 61 percent of the province. The modal plant community was Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young)/bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve)-Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth). Factors included in this group were fire, drought, insects, and pronghorn browsing.

The SD Group, the least productive sagebrush environment, occupied aridic, mesic to frigid, shallow to very shallow soils at any elevation. Soils typically had low water storage capacity and high evaporation rates from temperature, wind, or both and became quite dry by late spring or early summer. The SD Group covered an estimated 12 percent of the MHP. The modal plant community was low sagebrush (*Artemisia arbuscula* Nutt.)/Sandbergs bluegrass *(Poa secunda* J. Presl). Factors included in this group were fire, drought, insects, and pronghorn browsing.

We built STMs for all four groups using VDDT version 6.0.9 (ESSA Technologies ltd. 2007). All models used four community phases (figure 2). Grasses and forbs dominated the early seral (ES) community phase. In the midseral open (MSO) phase, mature sagebrush was present but ecologically subdominant, and grasses and forbs were dominant. Sagebrush, grass and forbs co-dominated in the late seral open (LSO) community phase. Sagebrush was dominant in the late seral closed (LSC) community phase. We used sagebrush cover as the indicator of movement from one community phase to the next.

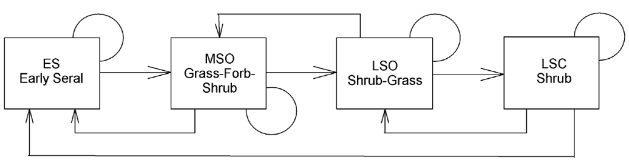

Figure 2. Model structure. Arrows pointing to the right indicate deterministic transitions resulting from succession. Arrows pointing to the left indicate probabilistic transitions to an earlier community phase. Circles indicate probabilistic transitions that remain in the same community phase. ES = early seral, MSO = midseral open, LSO = late seral open, LSC = late seral closed.

We assumed sagebrush density and cover were initially low following a high severity disturbance then increased until the site reached full occupancy (Daubenmire 1975; Harniss and Murray 1973; Johnson 1969; Lesica et al. 2007; Perryman et al. 2001) and that soil moisture availability in spring and early summer were key to sagebrush establishment (Boltz 1994; Daubenmire 1975; Johnson and Payne 1968; Lomasson 1948; Meyer 1994). Sagebrush establishment in the CM, WD, and SD groups was based on various combinations of spring precipitation, temperature and season length intended to represent adequate soil moisture. We assumed establishment in the WM Group was based on random weather factors we could not assess through the available data, such as the specific timing of precipitation events and any heat waves or cold snaps. We estimated the time needed to reach sagebrush cover breakpoints between each community phase based on sagebrush crown measurements and growth rates from published studies involving common gardens and wild plants (Anderson and Inouye 2001; Johnson 1969; McArthur and Welch 1982; Miller and Eddleman 2000; Pringle 1960; Tisdale et al. 1965; Wambolt and Sherwood 1999; Wambolt et al. 2001; Winward 1991).

An extensive review of the sagebrush and wildlife literature combined with preliminary model testing indicated we should include fire (Connelly et al. 2004; Knick et al. 2003; Knick et al. 2005), drought (Allred 1941; Ellison and Woolfolk 1937; Pechanec et al. 1937), freezekill (Hanson et al. 1982; Walser et al. 1990), snow mold (Nelson and Sturges 1986; Sturges and Nelson 1986; Sturges 1986, 1989) and herbivory as major disturbances. Native herbivores of most importance to local sagebrush ecosystems included pronghorn (*Antilocapra americana)* (Hansen and Clark 1977; Howard 1995; MacCracken and Hansen 1981; Verts and Carraway 1998), voles (*Microtus* spp.) (Hubbard and McKeever 1961; Mueggler 1967), and several species of insects (Allred 1941; Gates 1964; Hall 1965; Welch 2005) of which aroga moth (*Aroga websteri* Clark) appeared to be the most ecologically significant.

We used monthly or seasonal temperature, precipitation or snow depth to estimate probabilities for fire, freezekill (DeGaetano and Wilks 2002; Hanson et al. 1982; Hardy et al. 2001, Walser et al. 1990), snow mold (Nelson and Sturges 1986; Sturges and Nelson 1986; Sturges 1989), severe pronghorn browsing (Bilbrough and Richards 1993; Hoffman and Wambolt 1996; McArthur et al. 1988, Smith 1949), and vole-related sagebrush mortality (Frschknecht and Baker 1972; Mueggler 1967; Parmenter et al. 1987). We created variability modifiers for fire and pronghorn impacts by estimating the percentage of years in different severity categories (low, average, high, and extreme), the average number of hectares per event in each severity category, and the ratio of hectares affected in each severity category. We based fire variability on the variability of fire season severity in modern fire records from Bureau of Land Management (BLM) for Burns and Lakeview Districts and from the US Fish and Wildlife Service (FWS) for

Hart Mountain Refuge. Pronghorn variability was based on a very simple model of pronghorn population dynamics to estimate the frequency of population peaks and lows based on winter conditions (Kindschy et al. 1982; O'Gara and Yoakum 2004; Smyser et al. 2006; Yoakum 2006).

We reduced climate-based estimates of fire occurrence to account for the lack of ignitions when sufficient fuel is present. We also partitioned fire into two different burn patterns – a mosaic (heterogeneous) burn pattern and a stand-replacing (homogeneous) burn pattern. These burn patterns are approximate equivalents of mixed severity and high severity fires in forests. We assumed homogeneous fires resulted from high winds and used frequency of high winds in August based on hourly data from local RAWS to estimate the occurrence of homogeneous burn patterns. We then assumed that heterogeneous burn patterns occur in low, average, and high years, and homogeneous burn patterns occur in high and extreme years. Once a site reached the LSC phase, only homogeneous fire occurred to account for the effects of sagebrush density and cover on fine fuel abundance (Bradford and Laurenroth 2006; Daubenmire 1975; Derner et al. 2008).

We based drought probability on the estimated frequency of droughts as severe as that in the 1930s (Cook et al. 1999; Cook et al. 2004; Gedalof and Smith 2001; Graumlich 1987; Stahle et al. 2007), the only drought with documented big sagebrush mortality (Allred 1941; Ellison and Woolfolk 1937; Pechanec et al. 1937). Insect outbreak frequencies were based on a forest defoliator as a surrogate due to the lack of detail on aroga moth dynamics, the primary insect affecting sagebrush (Gates 1964; Hall 1965; Hsaio 1986). We selected Pandora moth (*Coloradia pandora* Blake) to represent probable frequencies and variability (Gates 1964; Hall 1965; Hsaio 1986; McBrien et al. 1983; Speer et al. 2001). We used a combination of the vole population cycle (Frischknecht and Baker 1972; Murray 1965) and frequency of severe winters (Frischknecht and Baker 1972; Parmenter et al. 1987) to estimate the probability of vole-related mortality. Because vole populations also depend on the abundance of grass, we varied the probability of vole impacts by community phase.

Table 1. Habitat suitability (low, moderate, high) for greater sage-grouse by model and community phase based on descriptions from Call and Maser 1985; Connelly et al. 2000, 2004; Crawford and Gregg 2001; Goodrich 2005; Braun et al. 2005; and Gregg 2006.

	Leks	Pre-laying hens	Nesting	Early brood-rearing	Late brood-rearing	Wintering
Warm moist sagebrush group						
ES[a]	Low	Moderate	N/A	Low	Moderate	N/A
MSO[b]	N/A	Moderate	Low	Moderate	High	N/A
LSO[c]	N/A	Low	High	High	High	High
LSC[d]	N/A	N/A	Moderate	Low	Low	Moderate
Cool moist sagebrush group						
ES	Low	High	N/A	Low	Moderate	N/A
MSO	N/A	High	Low	Low	High	N/A
LSO	N/A	Moderate	High	High	High	High
LSC	N/A	N/A	Moderate	Moderate	Moderate	Moderate
Warm dry sagebrush group						
ES	Moderate	High	N/A	Low	Low	N/A
MSO	Low	High	N/A	High	Low	Low
LSO	N/A	Moderate	High	High	Low	High
LSC	N/A	Moderate	Moderate	Moderate	Low	High
Shallow dry sagebrush group						
ES	High	High	N/A	High[e]	Moderate	High[f]
MSO	Moderate	High	N/A	High[e]	Moderate	High[f]
LSO	Low	High	N/A	High[e]	Low	High[f]
LSC	N/A	High	N/A	High[e]	Low	High[f]

[a] Early seral. [b] Midseral open. [c] Late seral open. [d] Late seral closed. [e] High along edges, dropping to low in interior. [f] High until or unless buried by snow.

Table 2. Ranking of disturbance types in each sagebrush model based on the estimated disturbance rotation period.

Warm moist sagebrush group	Cool moist sagebrush group	Warm dry sagebrush group	Shallow dry sagebrush group
Insects	Snow mold	Pronghorn	Pronghorn
Fire	Voles	Insects	Insects
Drought	Insects	Fire	Fire
	Freezekill	Drought	Drought
	Fire		
	Drought		

We used the descriptions of the different types of sage-grouse habitat provided by Connelly et al. (2000) to evaluate the potential effects of the disturbance variables on sage-grouse habitat suitability. Breeding habitat included lekking, pre-laying hen, and nesting habitat, and brood-rearing habitat included early and late habitats. We based habitat quality ratings on similarity to described habitat characteristics (Barnett and Crawford 1994; Braun et al. 2005; Call and Maser 1985; Connelly et al. 2004; Connelly et al. 2000; Crawford and Gregg 2001; Goodrich 2005; Gregg 2006). Each community phase was rated as none, low, moderate, or high quality habitat for each seasonal habitat based on sagebrush cover, assumed forb abundance and timing of senescence, and expected duration of the habitat in the absence of disturbance (table 1). We then summarized the amount of moderate- and high-quality seasonal habitat available for each group and habitat element and the four groups collectively.

Analysis Methods

Each model began with an equal proportion of the four community phases. We ran each model 50 times for 500 years and recorded the abundance of each community phase every 10 years. To allow ample time for the models to come into dynamic equilibrium, we analyzed only the last 250 years of data. We conducted sensitivity tests to evaluate how the mix of community phases might change if we altered event probabilities from those initially developed. After finalizing the models based on the sensitivity testing, we estimated the amount of historical seasonal habitat for sage-grouse in each sagebrush group and on the landscape as a whole and compared the results to the amount of habitat recommended by Connelly et al. (2000). We compared the predicted fire rotation in models to estimated fire frequencies published in the literature. Because community phases were not normally distributed in most cases we analyzed medians rather than means.

Fire, drought, and insect outbreaks affected the full area occupied by the sagebrush groups. Freezekill, snow mold, and vole-related mortality occurred where snowpacks are deeper and more persistent (Frischknecht and Baker 1972; Hanson et al. 1982; Mueggler 1967; Nelson and Sturges 1986; Parmenter et al. 1987; Sturges and Nelson 1986; Sturges 1989; Walser et al. 1990), limiting them to a portion of the CM Group. Wintering pronghorn tended to move to where snowpacks were lowest and preferred habitat with long sightlines (Kindschy et al. 1982; O'Gara 1978; Verts and Carraway 1998); therefore, we assumed pronghorn impacts were restricted to a portion of the WD and SD Groups. We modeled fire, pronghorn browsing, freezekill, and snow mold as random events and drought, insects, and voles as cyclical events.

Our models accounted for the impacts to sagebrush only and not to other species or life forms. Homogeneous fire was the only stand-replacing event in all models, resetting any community phase back to ES. All other events were modeled as thinning events, resetting a community phase back to its beginning or moving it back one or two community phases. All thinning events operated only in the MSO, LSO, and LSC community phases. Insect outbreaks occurred only in the LSO and LSC phases in all models. Fire was the only event in the ES phase in all models.

RESULTS

Contrary to our expectations and based on average annual percentage of area affected, fire appeared to have less influence than other disturbance types, except drought (table 2). Estimated fire rotations were 24, 33, 83, and 196 years for the WM, CM, WD, and SD Groups, respectively. Most disturbance types occurred more frequently than fire. In each model, some sort of disturbance occurred rather frequently across the landscape as a whole. Frequencies ranged from every four years in the CM Group to every 26 years in the SD Group.

The LSC community phase was the most common phase in all groups under simulated historical conditions (figure 3). The least common phase was the MSO phase in the WM, WD, and SD Groups and the ES phase in the CM Group. All groups were sensitive to changes in the probability of fire and insects. The WM and CM Groups were insensitive to changes in the probability of drought, while the WD and SD Groups were sensitive. The CM Group also was moderately sensitive to changes in the probabilities of insect and vole outbreaks, and sensitive to changes in the probabilities of snow mold and freezekill, affecting the abundance of the MSO and LSC community phases more than the LSO phase in all cases except snow mold. Both the WD and SD Groups were sensitive to changes in the probability of pronghorn browsing. In general, increasing the probability of a disturbance tended to decrease the abundance of the later community phases and increase the abundance of the earlier community phases while reducing the probability had the opposite effect.

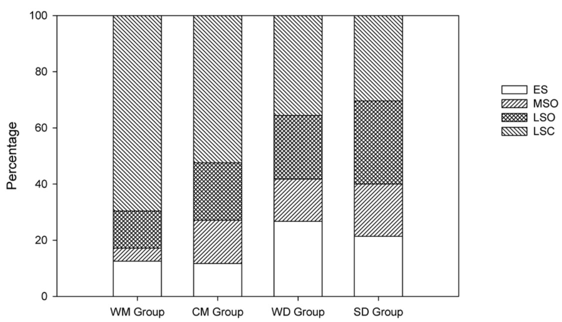

Figure 3. Mix of community phases. The late seral closed (LSC) phase is the most common in all models, although more dominant in the warm, moist (WM) and cool, moist (CM) models. The midseral open (MSO) phase is the least common in the WM, warm, dry (WD), and shallow, dry (SD) groups while the early seral (ES) phase is the least common in the CM group.

Altering the frequency of the different types of fire years had a large impact on fire rotation and the mix of community phases, particularly in the abundance of the ES phase, in all four groups. Natural fire rotation lengthened 2.7 times in the WM and CM Groups and 3.5 times in the WD and SD Groups. The resulting fire rotations were well outside the fire frequencies or rotation reported in the literature (Baker 2006; Burkhardt and Tisdale 1976; Heyerdahl et al. 2006; Knick et al. 2005; Mensing et al. 2006; Miller et al. 2001; Miller and Heyerdahl 2008; Miller and Rose 1999; Whisenant 1990).

The simulated historical landscape provided breeding habitat on 86 percent of the area, compared to the 80 percent recommended (Connelly et al. 2004), but only about one-quarter of that was high quality habitat. Brood-rearing habitat occurred on 64 percent of the landscape, with twice as much early brood-rearing habitat as late brood-rearing (figure 4). Most of the brood-rearing habitat was moderate quality. Wintering habitat was found on 53 percent of the simulated historical landscape with over half in the WD Group. We did not include early brood-rearing provided by the SD Group in these results as chicks use the edges of this habitat more than the interior (Alridge 2000, 2005; Goodrich 2005) and we did not model patch shape or edge characteristics. Similarly, we did not include the SD Group in the wintering habitat total as that group provides habitat only in low snow years.

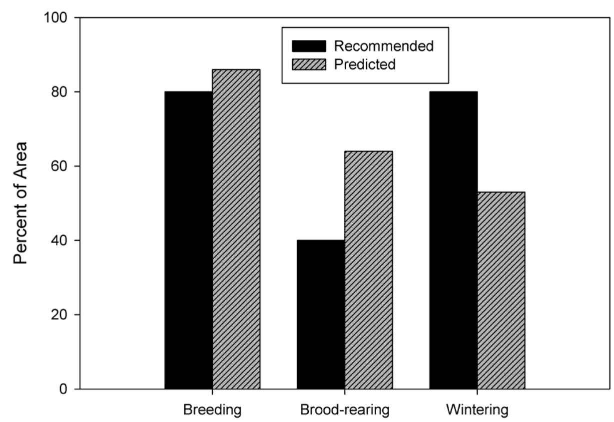

Figure 4. Amount of moderate and high quality seasonal sage-grouse habitat. Landscape amounts are based on the proportions of each group as determined from soil surveys in the Malheur High Plateau major land resource area. Not all groups provide all types of seasonal habitat.

DISCUSSION

Our results suggest that the various thinning agents, which are not as obvious as fire and not monitored for frequency, variability, or impacts, may have been more important than fire in affecting sage-grouse habitat historically. The current perception of the importance of fire on sage-grouse seasonal habitat may be based more on the current predominance of very large, homogeneous fires and current problems with annual grasses that can follow such fires. Historically, insect outbreaks in particular may have been of equal importance as fire in shaping the abundance and quality of seasonal sage-grouse habitat. Insect outbreaks tend to affect a many-fold larger area when they occur (Gates 1964; Hall 1965) than the most severe fire season on record and may have occurred more frequently than fire in the WD and SD groups. These two groups comprise the majority of potential sage-grouse habitat in the study area.

We suspect that disturbance probabilities for some factors, such as fire, should vary by community phase, which could also influence the interactions between disturbances. For example, abundance and continuity of grasses and the relative proportion of live and dead woody fuel in sagebrush crowns likely varies between the different community phases in each model. This variation should affect the likelihood that fire could successfully ignite and spread. However, we lack sufficient information on that variation to adjust the probability of fire accordingly. Similarly, the amount of sagebrush cover would likely result in differing probabilities of insect outbreaks between community phases. We were able to estimate different probabilities by community phase only for voles, based on the winter diet of voles and relative proportion of sagebrush to grass in the CM Group (Mueggler 1967; Parmenter et al. 1987; Sturges 1993). In that model, it appeared the frequency of insect outbreaks altered the frequency of vole outbreaks by altering the abundance of the LSO community phase–the phase in which a vole outbreak is most likely to have an effect. If we were able to make similar distinctions in disturbance probabilities by community phase, then more interactions between disturbances might have occurred.

We speculate that modern burned-hectare totals per fire season in our study area may not be much different from those prior to 1850. Use of fire by Native Americans is well documented even in the Great Basin (Griffen 2002; Gruell 1985; Robbins 1999; Stewart 2002). Tree-ring studies of fire extent in pre-1850 forests indicate that regional fire years (years where fire is widespread throughout a large area, the equivalent of extreme fire years today) occurred at about the same frequency prior to 1850 as in modern fire records (Hessl et al. 2004; Heyerdahl et al. 2008; Swetnam and Betancourt 1998). One possible difference between the 500 years before 1850 and the time since 1980 is average fire size, as compared to total hectares burned per year. Before 1850, a year where a great many hectares burned may have consisted of a large number of small to medium-sized fires. Since 1980, such years typically consist of a few very large fires, believed to be largely due to changes in fuel structure resulting from a variety of human-caused changes (Connelly et al. 2004; Heyerdahl et al. 2006; Knick et al. 2005). The landscape patterns and resulting sage-grouse habitat quality and availability would have been very different before 1850 than since 1980 even if the frequencies of the different types of fire years were similar.

We assumed if the fire frequencies in the literature and fire rotations from the models were relatively close, the model results were a reasonable representation of the reference period, predicting the mix of community phases and sage-grouse seasonal habitat. Therefore, we compared the estimated fire rotation in our final models against tree-ring based estimates and published expert opinion estimates of fire frequency. Tree-ring studies at the sagebrush-conifer ecotone indicate an average fire return interval of 10 to 35 years (Burkhardt and Tisdale 1976; Heyerdahl et al. 2006; Miller et al. 2001; Miller and Heyerdahl 2008; Miller and Rose 1999). Expert opinion for fire return intervals range from 10 to 25 years on more productive sites, 30 to 80 on less productive sites, and over 100 years on very dry, low-productivity sites (Knick et al. 2005; Miller and Heyerdahl 2008; Miller and Rose 1999). The modeled fire rotations all fall within these general categories. Thus, the indirect evidence suggests the mix of community phases is reasonable.

The simulated historical quantity of sage-grouse seasonal habitats appears to be similar to that recommended by sage-grouse biologists, with the exception of wintering habitat (Connelly et al. 2004; Connelly et al. 2000). Our models predicted that the MHP provided 6 percent more breeding habitat, about 50 percent more brood-rearing habitat, but around 34 percent less wintering habitat that sage-grouse biologists recommend (Connelly et al. 2000). Although sage-grouse will winter in the SD Group in many locations, the majority of wintering populations in Oregon have been observed in sites dominated by big sagebrush (Connelly et al. 2004), placing them in either the WD or CM Groups. Assuming our model design was appropriate, the results suggest either the lower availability of wintering habitat might have been population bottleneck, or that sage-grouse did not need quite as much wintering habitat as biologists recommended.

CONCLUSIONS

This project demonstrates methods to examine potential sagebrush ecosystem dynamics and habitat for historical conditions using a state-and-transition modeling framework. It also demonstrates how climate data can be used to develop objective disturbance probabilities. Our study also provides objective criteria that could be used to evaluate expert opinion and the logical arguments that underpin such opinion. It also points out the importance of understanding the frequency and intensity of disturbance variables incorporated into such models.

The modeled fire rotations were within the range reported largely based on expert opinion in areas where surrogates for fire history are not available. Fire may not have been the most important disturbance factor shaping historical landscape patterns and habitat availability, just the most visible and easily studied factor. The frequency of the different types of fire season is an important, but possibly overlooked factor in how fire might have shaped historical habitat availability.

Sage-grouse breeding and brood-rearing habitat availability may have been greater than that recommended by sage-grouse biologists, but wintering habitat may have been less in the historical landscape. If so, these shortage categories along with a predominance of less than optimal habitat may indicate population bottlenecks that could have limited sage-grouse population potential. Disturbances that promote later community phases increase the abundance of nesting and wintering habitat. Disturbances that favor early phases increase lekking and pre-laying hen habitat, while disturbances that favor middle community phases increase brood-rearing habitat. Higher quality sage-grouse habitat across the landscape requires a mix of all community phases distributed among the four sagebrush groups.

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