

RESEARCH ARTICLE

POTENTIAL EFFECTS OF DISTURBANCE TYPES AND ENVIRONMENTAL VARIABILITY ON SAGEBRUSH-STEPPE COMMUNITY DYNAMICS

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ABSTRACT

While fire is widely recognized as an important factor shaping sagebrush (*Artemisia* spp.) ecosystems, little is known about the role other natural events play in these systems. Using a state-and-transition modeling framework in conjunction with the scientific literature and data for climate (temperature, precipitation, and snow), soils (soil surveys and ecological site descriptions), and modern fire occurrence records, we explored how fire and various other natural events might shape sagebrush ecosystems in eastern Oregon, USA, and whether those events could affect fire rotation. Model results suggested other disturbance events were important in shaping all but the most productive sagebrush communities and influenced fire rotation in drier sagebrush communities. Insects and pronghorn browsing may have been as important as fire in shaping sagebrush-steppe landscapes with freeze-kill and snow mold locally important. Our study also demonstrated the use of climate, soils, ecological

RESUMEN

Aunque el papel del fuego está reconocido como un factor importante en ecosistemas dominados por artemisia (*Artemisia* spp.), se conoce poco sobre la influencia de otros eventos naturales sobre estos sistemas. A partir de un marco conceptual de modelos de estado-transición, información de la literatura científica y datos climáticos (temperatura, precipitación y nieve), suelos (descripción de suelos y de la ecología de sitios) y registros modernos de incidencia de incendios, exploramos los posibles efectos de incendios y otros eventos naturales en ecosistemas de artemisia en el este de Oregon, EUA, y sus efectos sobre la rotación de estos incendios. Los resultados del modelo sugieren que otras perturbaciones han tenido efectos importantes en la formación de las comunidades de artemisia—exceptuando las más productivas—que influyen en la rotación del fuego en comunidades más secas. Los insectos y el ramoneo por antílopes pueden haber sido tan importantes como el fuego en la conformación del paisaje en estepas de artemisia, además de factores locales importantes, como heladas e infestaciones del “moho de la nieve.” Nuestro estudio también demostró que el uso de datos climáticos, de suelo y sitio y de

site, and fire occurrence data to derive probabilities of several natural events, providing a more objective approach to estimating reference conditions.

incidencia de incendios puede ser útil para estimar las probabilidades de diversos eventos naturales, suministrando una aproximación más objetiva para determinar condiciones de referencia.

Keywords: *Artemisia arbuscula*, *Artemisia tridentata*, big sagebrush, climate, fire, little sagebrush, Oregon, reference conditions, state-and-transition, USA

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INTRODUCTION

Rarely are multiple disturbances examined to determine how they may interact to shape plant communities. While fire is widely regarded as the key natural disturbance shaping sagebrush (*Artemisia* spp.) ecosystems (Connelly *et al.* 2004, Miller *et al.* 2011), few studies have examined the role of other disturbances or the interactions between these disturbances and fire. Sagebrush ecosystems provide many important economic and social values in the Intermountain West, such as livestock forage, water, recreational opportunities, and wildlife habitat. 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 *et al.* 2011). Human-related disturbances, invasive species, expansion of conifer woodlands, changes in fire regimes, and changes in climate are a complex group of interacting factors that have reduced the area occupied by sagebrush ecosystems by an estimated 14.8 million ha across the western United States (USDI Bureau of Land Management 2004). A better understanding of how other natural events in conjunction with fire might influence the abundance of sagebrush community phases would provide a more sound basis for evaluating the sustainability of current practices and their effects on ecosystem services, such as forage and habitat.

State-and-transition modeling frameworks, such as the Vegetation Dynamics Development

Tool (VDDT) (ESSA Technologies 2007), can be used to examine the influence of natural events on the abundance of different plant community types. Since the current state-and-transition modeling frameworks, such as VDDT, are probabilistic instead of mechanistic, they can operate based on a combination of empirical data and expert opinion when empirical data are lacking. Given that climate is an important top-down driver of the types and frequencies of disturbance events (Breckle 1999, Chapin *et al.* 2002, Holechek *et al.* 2004, Adams 2010), it can be used as a basis for estimating the probability of natural disturbance events within a state-and-transition modeling framework. We used VDDT to explore the following questions concerning sagebrush dynamics: 1) what natural disturbance events in addition to fire might be important influences on the proportions of different sagebrush community phases (seral stages)?, 2) which natural disturbances may have greater influence on sagebrush ecosystem dynamics?, and 3) could other natural disturbances also affect fire frequency?

METHODS

Study Area

We selected the 4-million ha Malheur High Plateau major land resource area (USDA Natural Resources Conservation Service 2006) in southeastern Oregon, USA, as the physical basis for model development. Much of the area lies between 1200 m and 2100 m elevation,

with a few higher mountains. The rolling terrain is interspersed with hills, buttes, isolated mountains, and north-south trending fault-block mountains, and contains little surface water. Soils are primarily loamy to clayey, well-drained and shallow (25 cm to 50 cm) to moderately deep (50 cm to 90 cm) on uplands, and poorly to well-drained and deep to very deep (>90 cm) in valley and basin bottoms. The average annual precipitation ranges from <105 mm in the Alvord Desert to >450 mm on Steens Mountain, but with most of the area receiving 200 mm to 350 mm. Winter and spring are the wettest periods while summer is the driest. January is the coolest month, averaging -2°C , and July the warmest, averaging 19°C .

Model Development

We searched the sagebrush literature to locate studies that discussed sagebrush successional rates and establishment episodes, disturbance events associated with notable sagebrush mortality, and climate factors potentially associated with all of these. We followed additional leads from the references within promising papers. To help identify successional rates, we included studies on the duration of vegetation treatments, such as herbicide use, prescribed fire, and mechanical treatments. Since we were only interested in natural disturbances, we did not include the effects of livestock grazing, invasive plants, or conifer expansion. Although conifer expansion is partially a natural disturbance event with respect to sagebrush, much of the current expansion has been attributed to the effects of past livestock grazing and the resulting impact to fire frequencies, fire suppression, and to increased atmospheric carbon dioxide concentrations (Romme *et al.* 2009). In addition, we obtained ecological site descriptions, soil surveys, climate data, and fire occurrence data to use with the results of the literature review.

Sagebrush groups. In developing the sagebrush groups, we assumed that site productivi-

ty was a strong influence on recovery rates. Since fire was the most-studied natural disturbance in sagebrush-steppe, and because many studies indicated that site productivity is a strong influence on recovery rates following fire (e.g., Harniss and Murray 1973, Boltz 1994, Cook *et al.* 1994, Lesica *et al.* 2007, Bollinger and Perryman 2008), we based our indicator of site productivity on fine fuel production. 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 (Gruell *et al.* 1986, Bunting *et al.* 1987). We used ecological site descriptions for the Malheur High Plateau (<http://esis.sc.egov.usda.gov>) to sort sagebrush communities into four groups based on our identified production threshold for low, average, and high productivity years (Table 1), and on soil surveys to further describe the typical setting for each group.

The Warm-Moist Sagebrush Group (WM Group) occurs mostly in swales, terraces, and near or in riparian areas below 1220 m elevation. The Cool-Moist Sagebrush Group (CM Group) typically occurs on northerly aspects and ridges, but can occur on higher elevation, cooler southerly aspects as well. The Warm-Dry Sagebrush group (WD Group) is found mostly on southerly aspects, well-drained soils, and relatively shallow soils in basin bottoms and terraces typically in the elevation belt below the CM Group. The Shallow-Dry Sagebrush Group (SD Group) resides on soils with low water storage capacity and high evaporation rates that become quite dry by late spring or early summer.

All groups consisted of four community phases: 1) Early Seral (ES), where perennial grasses and forbs dominate although sagebrush seedlings are present; 2) Mid Seral Open (MSO), where perennial grasses and forbs remain dominant but mature sagebrush plants are subdominant; 3) Late Seral Open (LSO), where sagebrush, perennial grass and forbs co-

Table 1. Characteristics of each sagebrush group including modal potential natural plant community, grass production, and sagebrush cover by community phase. The top portion of the table describes modal site characteristics. The bottom portion of the table identifies sagebrush cover thresholds for the different community phases in each sagebrush group. Scientific names for the community species are given in the footnote.

	Warm-Moist Group	Cool-Moist Group	Warm-Dry Group	Shallow-Dry Group
Modal plant association	Basin big sagebrush/ basin wildrye	Mountain big sagebrush/ Idaho fescue	Wyoming big sagebrush/bluebunch wheatgrass- Thurber's needlegrass	Low sagebrush/ Sandberg bluegrass
Years producing at least 672 kg ha ⁻¹	All	High and average production years	High production years	None
Dominant soil moisture regime	Xeric	Xeric	Aridic	Aridic
Dominant soil temperature regime	Mesic	Frigid	Mesic	Mesic to frigid
General soil depth	Deep to very deep	Moderately deep to deep	Shallow to moderately deep	Very shallow to shallow
Percent of area	11 %	16 %	61 %	12 %
-----Sagebrush cover by community phase-----				
Early Seral	<1 %	<1 %	<1 %	<0.25 %
Mid Seral Open	1 % to 10 %	1 % to 10 %	1 % to 8 %	0.25 % to 1 %
Late Seral Open	10 % to 25 %	10 % to 30 %	8 % to 20 %	1 % to 5 %
Late Seral Closed	>25 %	>30 %	>20 %	>5 %

Note: Characteristics are based on ecological site information for the Malheur High Plateau (available at <http://esis.sc.egov.usda.gov>), Winward (1991), and Miller and Eddleman (2000).

Scientific names for community species:

Basin big sagebrush = *Artemisia tridentata* Nutt. ssp. *tridentata* (Scribn. & Merr.) A. Löve

Basin wildrye = *Leymus cinereus* (Scribn. & Merr.) A. Löve

Mountain big sagebrush = *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle

Idaho fescue = *Festuca idahoensis* Elmer

Wyoming big sagebrush = *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young

Bluebunch wheatgrass = *Pseudoroegneria spicata* (Pursh) A. Löve

Thurber's needlegrass = *Achnatherum thurberianum* (Piper) Barkworth

Low sagebrush = *Artemisia arbuscula* Nutt.

Sandberg bluegrass = *Poa secunda* J. Presl

dominate; and 4) Late Seral Closed (LSC), where sagebrush is dominant (Figure 1). A community phase is a distinctive plant community with associated dynamic soil property levels that occur over time (Bestelmeyer *et al.* 2009) within a state or reference community. We used sagebrush cover and the relative proportion of sagebrush and herbaceous vegetation as the primary descriptors for each community phase (Table 1) and ignored sprouting shrubs to simplify model development.

Successional rates. We modeled deterministic movement through the community phases as a function of sagebrush establishment and expansion of sagebrush cover. We used spring and early summer precipitation and temperature records for Oregon Climate Division 7 to estimate the frequencies of sagebrush establishment episodes (Johnson and Payne 1968, Daubenmire 1975, Boltz 1994, Forman *et al.* 2007). Beginning with a single plant, we doubled the number of plants at each establish-

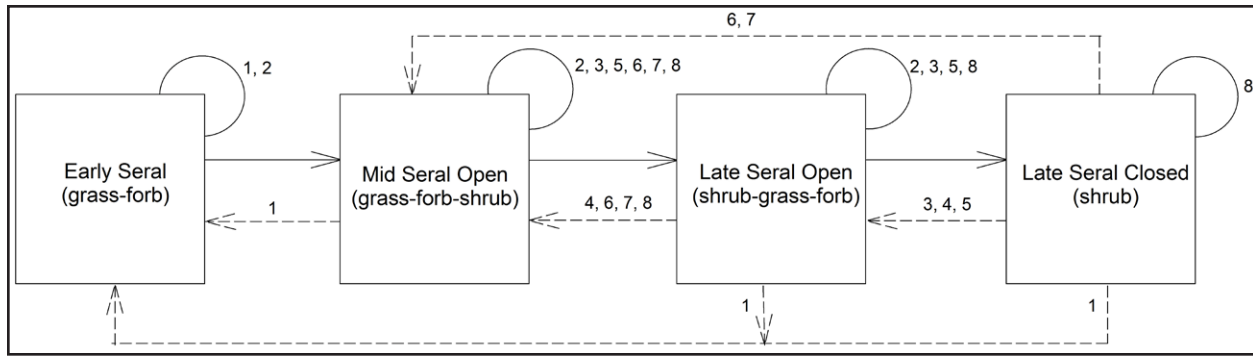


Figure 1. Model structure. Arrows pointing to the right indicate deterministic transitions resulting from succession. Arrows pointing to the left indicate probabilistic transitions to an earlier community phase. Circles indicate probabilistic transitions that remain in the same community phase. Numbers refer to events listed in Table 3.

ment episode. Using crown areas of individual adult sagebrush grown in the wild and in common gardens (Tisdale *et al.* 1965, McArthur and Welch 1982), we estimated potential crown area for individual wild plants; the crown area of basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) represented the WM Group, mountain big sagebrush (*A. tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) represented the CM Group, Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) represented the WD Group, and low sagebrush (*A. arbuscula* Nutt.) represented the SD Group. Assuming that a sagebrush seedling took six years to reach physical maturity (McArthur and Welch 1982),

we then calculated the number of years needed to cross from one community phase to another in each sagebrush group (Johnson 1969, Winward 1991, Miller and Eddleman 2000, Perryman *et al.* 2001, Lesica *et al.* 2007) (Table 2).

Disturbances. In addition to fire (Knick *et al.* 2003, Connelly *et al.* 2004, Knick *et al.* 2005), our review indicated that drought (Ellison and Woolfolk 1937, Pechanec *et al.* 1937, Allred 1941), freezekill (Hanson *et al.* 1982, Walser *et al.* 1990), and snow mold (Nelson and Sturges 1986; Sturges 1986, 1989; Sturges and Nelson 1986); as well as herbivory by pronghorn (*Antilocapra americana* Ord) (Hansen and Clark 1977, MacCracken and Hansen 1981, Howard 1995, Verts and Carraway

Table 2. Estimated establishment and successional rates (years) in the absence of disturbance.

Sagebrush group	Establishment		Years in community phase			
	Probability	Frequency	Early Seral	Mid Seral Open	Late Seral Open	Late Seral Closed
-----years-----						
Warm-Moist	0.75	1.5	0 to 14	15 to 20	21 to 24	≥25
Cool-Moist	0.62	2	0 to 18	19 to 25	26 to 30	≥31
Warm-Dry	0.18	6	0 to 48	49 to 66	67 to 78	≥78
Shallow-Dry	0.15	7	0 to 55	56 to 76	77 to 90	≥91

Note: Establishment parameters based on probabilities of certain climatological conditions in Oregon Climate Division 7. Years in each community phase based on establishment frequency and estimates of canopy closure derived from the literature.

1998), voles (*Microtus* spp.) (Hubbard and McKeever 1961, Mueggler 1967), and aroga moth (*Aroga websteri* Clarke) (Allred 1941, Gates 1964, Hall 1965, Welch 2005) have caused notable sagebrush mortality. Our review of the sagebrush literature helped us to develop estimates of the frequency, severity, and extent of those events, and what climate indicators might be associated with event frequency (Table 3 and Table 4). Based on the nature of the climate association, we modeled fire, pronghorn browsing, freezekill, and snow mold as random events. The only clearly documented drought-related mortality of sagebrush occurred during the 1930s drought (Elli-

son and Woolfolk 1937, Pechanec *et al.* 1937); therefore, we used the estimated frequency of such droughts (Keen 1937, Graumlich 1987, Cook *et al.* 2004), treating it as a cyclical event given the ties of severe drought to various ocean-atmosphere teleconnections (Cayan *et al.* 1998, Knapp *et al.* 2004, Michels *et al.* 2007). The literature for aroga moth was too sparse to characterize the frequency and causes of outbreaks, therefore we used the literature from pandora moth (*Coloradia pandora* Blake) as a surrogate to estimate the frequency and size of outbreaks. Since the literature on forest defoliators indicated that outbreaks have no clear ties to climate (Meyers 1988, Cooke and

Table 3. General description of event types included in all models and their effects. Drought timing and effects based on Cook *et al.* 2004, and Stahle *et al.* 2007. Insect outbreak timing and effects based on Gates 1964, Hall 1965, Hsaio 1986, Speer *et al.* 2001, Speer and Jensen 2003, and N.L. Hampton (Idaho National Lab, unpublished manuscript). Pronghorn browsing effects based on Smith 1949, McArthur *et al.* 1988, Bilbrough and Richards 1993, and Hoffman and Wambolt 1996. Freezekill effects based on Hanson *et al.* 1982, Walser *et al.* 1990, and Hardy *et al.* 2001. Snow mold effects based on Sturges 1986 and 1989. Vole outbreak timing and effects based on Murray 1965, Frischknecht and Baker 1972, and Parmeter *et al.* 1987.

Event type	Timing	Effect	Transition to earlier phase?	Area limits?	Groups affected	Community phases affected
1. Stand-replacing fire	Random	Stand-replacing	Yes	No	All	All
2. Mosaic fire	Random	Thinning	No	No	All	All: WM, CM groups ES, MSO: WD, SD groups
3. Drought	100 yr to 200 yr	Thinning	No: MSO, LSO Yes: LSC	No	All	MSO, LSO, LSC
4. Insect outbreak	20 yr to 48 yr	Thinning	Yes	No	All	LSO, LSC
5. Pronghorn browsing	Random	Thinning	No	Yes: 25% of landscape	WD, SD	MSO, LSO, LSC
6. Freezekill	Random	Thinning	No: MSO Yes: LSO, LSC	Yes: 25% of landscape	CM	MSO, LSO, LSC
7. Snowmold	Random	Thinning	No: MSO Yes: LSO, LSC	Yes: 25% of landscape	CM	MSO, LSO, LSC
8. Vole outbreak	4 yr to 5 yr	Thinning	No: MSO Yes: LSO, LSC	Yes: 10% of landscape	CM	MSO, LSO, LSC

Abbreviations: WM = Warm-Moist Group, CM = Cool-Moist Group, WD = Warm-Dry Group, SD = Shallow-Dry Group, ES = Early Seral Community Phase, MSO = Mid Seral Open community phase, LSO = Late Seral Open community phase, LSC = Late Seral Closed community phase.

Table 4. Factors used to estimate probabilities of the occurrence (random events) or impact (cyclical events) of each type of event. Temperature and precipitation values are based on Oregon Climate Division 7 descriptive statistics for water years 1885 to 1886 through 2007 to 2008. Fire occurrence records cover 1980 to 2006 fire years for Lakeview and Burns Bureau of Land Management districts and Hart Mountain Refuge. Wind frequency is based on 10-minute average wind speeds in August from 12 remote automated weather stations located within the Malheur High Plateau area. Reynolds Creek Experiment Range snow data cover 1967 to 1968 through 1996 to 1997 water years.

Type	Group (P)	Probability Basis	Adjustments	Data/Literature Sources
Stand-replacing fire	WM (0.0085)	Frequency of May monthly temperature $\geq 13^{\circ}\text{C}$ multiplied by frequency of winds $\geq 24\text{ km hr}^{-1}$ in August.	Reduced by 25% to account for sufficient fuel but lack of ignition. Decreased in low and average fire years. Increased in high and extreme years.	Swetnam and Betancourt 1990, 1998, Rorig and Fergusson 1999, Grissino-Mayer and Swetnam 2000, Heyerdahl <i>et al.</i> 2002, Rollins <i>et al.</i> 2002 (probability basis, ignition adjustment) Oregon Climate Division 7 records (precipitation and temperature) Remote Automated Weather Station (RAWS) records (wind) Fire occurrence records (frequency of low, average, high, and extreme fire years) Expert opinion (ignition and grazing adjustments)
	CM (0.0062)	Combined frequency of spring precipitation $\geq 75^{\text{th}}$ percentile and summer precipitation $\leq 25^{\text{th}}$ percentile multiplied by frequency of winds $\geq 24\text{ km hr}^{-1}$ in August.		
	WD (0.0046)	Combined frequency of spring precipitation $\geq 75^{\text{th}}$ percentile and average June temperature $\leq 13^{\circ}\text{C}$ multiplied by frequency of winds $\geq 24\text{ km hr}^{-1}$ in August.		
	SD (0.0046)	Same as WD Group.		
Mosaic fire	WM (0.0645)	Frequency of May monthly temperature $\geq 13^{\circ}\text{C}$ minus stand-replacing fire frequency.	Reduced by 25% to account for sufficient fuel but lack of ignition. Decreased in low and average fire years. Increased in high and extreme years.	Same as above
	CM (0.0497)	Combined frequency of spring precipitation $\geq 75^{\text{th}}$ percentile and summer precipitation $\leq 25^{\text{th}}$ percentile minus stand-replacing fire frequency.		
	WD (0.0352)	Combined frequency of spring precipitation $\geq 75^{\text{th}}$ percentile and average June temperature $\leq 13^{\circ}\text{C}$ minus stand replacing fire frequency.		
	SD (0.0046)	Same as stand-replacing fire in WD Group.		
Drought*	All (0.0375)	Literature	None	Cook <i>et al.</i> 2004, Stahle <i>et al.</i> 2007 (cycle and impact)
Insect Outbreaks	All (0.2943 for buildup and crash) (0.4388 for peak)	Literature	None	Gates 1964, Hall 1965, Speer <i>et al.</i> 2001, Speer and Jenson 2003 (cycle and impact)
Pronghorn herbivory	WD, SD (0.0199)	Combined frequency of winter precipitation $>129.0\text{ mm}$ plus winter average temperature $<-1.07^{\circ}\text{C}$.	Reduced by 75% to account for limited area of impact.	Kindschy <i>et al.</i> 1982, Verts and Carraway 1998, Keating 2002, Yoakum 2006
Freezekill	CM (0.0088)	Combined frequency of winter precipitation $\leq 68\text{ mm}$ plus January average temperature $\geq 0.89^{\circ}\text{C}$.	Reduced by 75% to account for limited area of impact.	Hanson <i>et al.</i> 1982, Walser <i>et al.</i> 1990, Hardy <i>et al.</i> 2001 Oregon Climate Division 7 (precipitation and temperature) Expert opinion (adjustment factor)
Snow mold	CM (0.0177)	Combined frequency of winter >179 days, snow depth $>2087\text{ mm}$, snow melt date later than 25 May.	Reduced by 75% to account for limited area of impact.	Sturges 1986, 1989 Reynolds Creek Experimental Range data (winter length, snow depth, snow melt date) Expert opinion (adjustment factor)
Vole Outbreaks	CM (0.036 for MSO) (0.0785 for LSO) (0.01 for LSC)	Literature	Reduced by 90% to account for limited area of impact.	Murray 1965, Frischknecht and Baker 1972, Parmenter <i>et al.</i> 1987 (cycle and impact) Expert opinion (adjustment factor)

*(severe enough to kill sagebrush)

Roland 2000, Speer *et al.* 2001, Speer and Jenson 2003), we treated arroyo moth outbreaks as cyclical. Lastly, vole population peaks have no clear tie to climate (Murray 1965, Frischknecht and Baker 1972), so we treated vole outbreaks as cyclical events, although we modified event probability by the frequency of deep snowpacks (Mueggler 1967, Frischknecht and Baker 1972, Parmenter *et al.* 1987).

We assigned events, timing, effect including whether the event results in a transition to a different community phase, and any area limitations on the event, to each community phase in each sagebrush group (Table 3). We based each event frequency and adjustment factor on information gleaned from the literature, including what climate factors the literature suggested may be associated with a particular event (Table 4). For example, we estimated the probability of any fire in the WD Group by identifying the frequency of a wet spring and cool June (creating sufficient fuel). We multiplied that initial probability by the frequency of high winds in August to estimate the probability of a stand-replacing fire, and then estimated the probability of a mosaic fire by subtracting the probability of a stand-replacing fire from the initial fire probability. We multiplied both probabilities by 0.75 to account for the presence of sufficient fuel but lack of ignitions (Table 2). Lastly, we included variability in those probabilities based on the frequency of different types of fire years using 1980 to 2006 fire occurrence records for the Burns and Lakeview districts of the Bureau of Land Management and Hart Mountain and Malheur national wildlife refuges; the occurrence of low and average fire years further reduces the probability of a fire while the occurrence of a high or extreme year increases the probability.

Analysis Procedures

Data Sources. We obtained monthly precipitation and temperature data from 1895 to 2009 for Oregon Climate Division 7 (available

at <http://www7.ncdc.noaa.gov/CDO/CDODivisionSelect.jsp>) and snow data from 1967 to 1996 for the Reynolds Creek Experimental Range (Hanson *et al.* 2001, Marks *et al.* 2001). Although Reynolds Creek Experimental Range lies outside the Malheur High Plateau, it has a climate that is similar; this data set provided detailed information on snowpack not available for Oregon Climate Division 7. We summarized monthly and seasonal means (temperature) and medians (precipitation) using a temperature-based definition of winter and summer that better matches plant phenology and hydrological cycles than the typical 3-month definitions (Neilson *et al.* 1992). We estimated the mean and standard deviation for snowpack duration, snow depth, and snowmelt date for the highest elevation station on the experimental range.

Analysis Process. We constructed four state-and-transition models using VDDT version 6.0 (ESSA Technologies 2007). In VDDT, the user defines the number of community phases in a pathway, the cover type and structural stage for each phase, and the age range of each phase. Two types of transitions occur in the software: 1) probabilistic transitions specified by the user, and 2) deterministic transitions specified by the age range in community phase. At the beginning of each simulation, the user specifies what percentage of the simulation cells occurs in each community phase and randomizes the age of each cell within a given community phase. With each time step, VDDT simulates whether a cell is affected by a probabilistic transition. If so, it moves the cell into the community phase or age specified by the transition type. If not, then one year is added to the age of the cell. If cell age then exceeds the age limit of a given community phase, the cell is moved into the next community phase specified in the pathway. Each cell operates independently of all other cells, so the software cannot simulate contagion, such as occurs with fire and insect outbreaks.

The user can incorporate variability in the probability of a transition or establish cycles that control the number of years between a given transition type. To incorporate interannual variability, we created multipliers that increased or decreased the probability of fire and pronghorn browsing. These multipliers were based on the estimated percentage of years in different severity categories (low, average, high, and extreme), and a ratio of hectares affected in each type of year. In the case of fire, we used the fire occurrence records to estimate the severity categories and number of hectares affected in each category. For pronghorn browsing, we created a very simple model of pronghorn population dynamics based on the literature (Kindschy *et al.* 1982, O’Gara and Yoakum 2004, Smyser *et al.* 2006, Yoakum 2006) and estimated the joint probability of a high pronghorn population and severe winter (cold and wet) and assumed pronghorn only used a portion of the landscape during winter. We constrained drought, insect outbreaks, and vole outbreaks to a specified range of years defining the maximum and minimum years between outbreaks and duration of each outbreak (ESSA Technologies 2007). We created 50 randomly-generated sets of multipliers over 500 years each for fire, pronghorn browsing, drought, insect outbreaks, and vole outbreaks, saved these in a multiplier file and used the same multiplier file for all runs.

Each model used 1000 cells of indeterminate size and all models were initialized with an equal proportion of the community phases. We ran 50 simulations for 500 years each, saved the area in each community phase every 10 years, and estimated the average annual area affected by each type of event. To allow ample time for the models to come into dynamic equilibrium, we analyzed model outputs for only the last 250 years of the 500-year simulation runs. We estimated fire rotation by extracting model estimates of the average annual percent of cells affected by fire and taking the inverse value to estimate the number of years

it would take for the cumulative affected area to equal the analysis area (Romme *et al.* 2009).

We evaluated which disturbance events might be important influences on sagebrush dynamics by running the model with each disturbance type by itself and then in various combinations, comparing the predicted abundance of the different community phases to the full model and when fire only was included in the model. We evaluated which disturbance types may have had a greater influence by varying the probability of each event type between 0 and 2 times the initial probability and comparing how much predicted abundance of the different community phases changed. To evaluate the potential impact of the other disturbance types on fire frequency, we compared the estimated fire rotation from the previous two analyses. Because the abundances of most community phases were not normally distributed, we based all analyses on medians rather than means. We tested for significant differences between medians using the Kruskal-Wallis one-way analysis of variance on ranks. When significant differences were found, we ran a Tukey test on all pairwise comparisons with the significance level set at $P < 0.05$.

RESULTS

When all disturbance types were included in all models, the LSC community phase was the most common phase in all groups (Figure 2), with the LSO community phase very close in abundance to the LSC phase in the SD Group. The least common community was the MSO phase in the WM, WD, and SD groups, and the ES phase in the CM Group. All groups were subject to outlier values in at least one community phase, with sudden decreases or increases in abundance followed by a rapid return to values closer to the median.

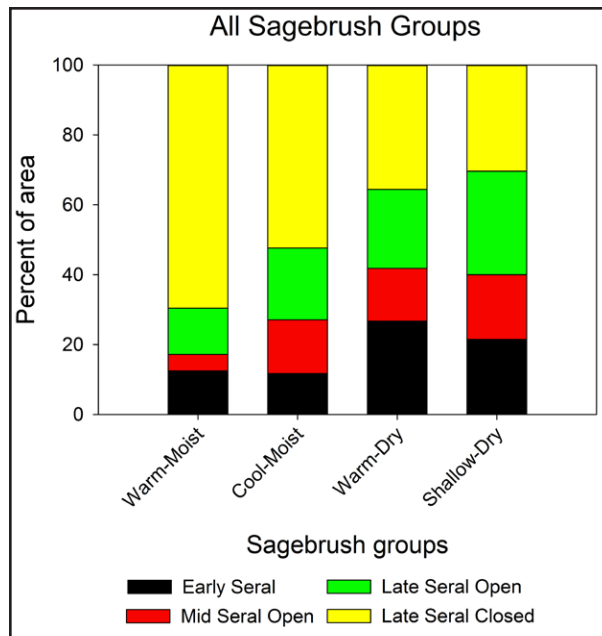


Figure 2. Mix of community phases. The Late Seral Closed (LSC) phase is the most common in all models, although more dominant in the Warm-Moist (WM) and Cool-Moist (CM) groups. The Mid Seral Open (MSO) phase is the least common in the WM, Warm-Dry (WD), and Shallow-Dry (SD) groups while the Early Seral (ES) phase is the least common in the CM Group.

Influence of Disturbance Types Other than Fire

Adding and removing events singly and in combination altered the mix of community phases in all four groups and all four community phases ($P < 0.001$ in all community phases and groups). Since fire was the only disturbance type that created the early seral phase, this phase was absent when fire was excluded from all models. In the WM Group, including drought, insects, or both with fire produced the same mix of community phases as the full model and when only fire was included (Figure 3). The full model and fire-only variant did not differ from each other. The only significant differences occurred when fire was excluded from the model.

Data for the CM Group are not shown due to the large number of combinations examined.

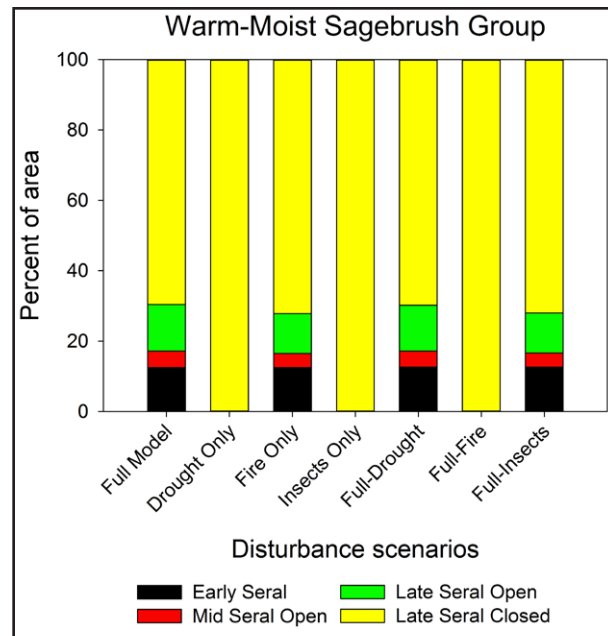


Figure 3. Mix of community phases in the Warm-Moist Sagebrush Group resulting from the addition or subtraction of event types as compared to the full model. Removing fire from the model resulted in complete loss of the Early Seral and Mid Seral Open phases. In all variants, the Late Seral Closed community phase dominated this sagebrush group.

In the CM Group, the abundance of the MSO, LSO, and LSC phases in the full model differed significantly from the fire-only variant ($P < 0.05$). Removing drought or vole outbreaks from the full model produced a mix of community phases most similar to the full model. Combining insect outbreaks and snow mold; drought and fire; and drought, fire, and vole outbreaks produced mixes of community phases most similar to the fire-only variant. In all of the combinations examined, including drought or voles produced minor differences in the mix of community phases relative to when these disturbance types were absent, although vole outbreaks had a slightly greater effect. Variants consisting of drought, insect outbreaks, and vole outbreaks singly or in combination produced the highest proportion of the LSC phase and lowest of the other phases. Adding freeze-kill or snow mold to these other disturbance types, even in the absence of

fire, significantly reduced the abundance of the LSC phase and increased that of the MSO and LSO phases, although these combinations still produced a higher abundance of the LSC phase and lower abundance of the MSO and LSO phases than if fire were included in the model, largely because the ES phase is absent without fire.

The WD and SD groups exhibited similar behavior (Figure 4). As in the CM Group, the

fire-only variant differed significantly from the full model ($P < 0.05$ for the MSO, LSO, and LSC phases). Adding drought to fire produced a mix of community phases most similar to the fire-only variant, and removing drought from the full model produced a mix of community phases most similar to the full model. Excluding drought from any combination did alter the mix of community phases as compared to variants that included drought, but the differences were small even when pairwise comparisons indicated that the difference was significant. Including or excluding pronghorn browsing and insect outbreaks usually produced mixes of community phases that differed significantly from one another ($P < 0.05$).

Potential Importance of All Disturbance Types

In random disturbance types (fire, freeze-kill, snow mold, and pronghorn browsing), varying the base probability in the model had the effect of varying the probability that the event would occur. In cyclical disturbance types (drought, insect outbreaks, and vole outbreaks), varying the base probability in essence varied the probability of mortality, not the probability of the event itself. As would be expected, varying the probability of fire resulted in significant differences in the mix of community phases in all four models (Figure 5); this effect is not discussed further. Similarly, since fire was the only disturbance type to produce the ES phase, there were no differences in the abundance of this phase in all variants examined.

Varying the probability of mortality from drought in the WM Group produced no significant differences in the abundance of any community phase ($P = 0.996, 0.967$, and 0.941 for the MSO, LSO, and LSC phases, respectively). Varying the probability of mortality from insect outbreaks in this group produced only small differences in the abundance of the MSO, LSO, and LSC phases, and only when the probability of mortality was reduced (Fig-

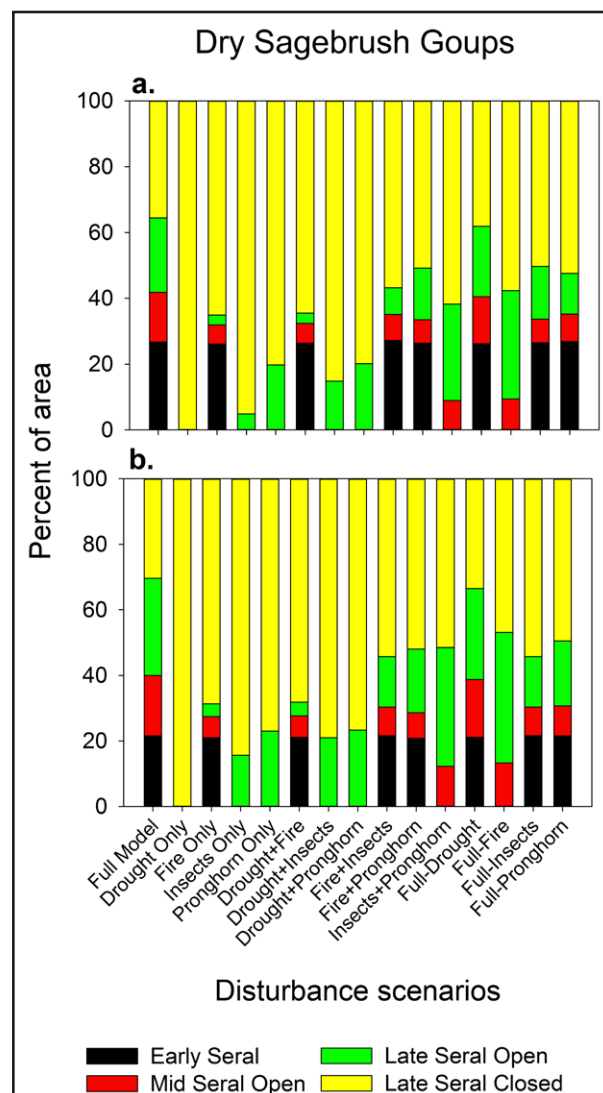


Figure 4. Mix of community phases resulting from the addition and subtraction of event types from the Warm-Dry Sagebrush Group (a) and the Shallow-Dry Sagebrush Group (b). In both groups, the Early Seral phase is present only when fire is included in the model.

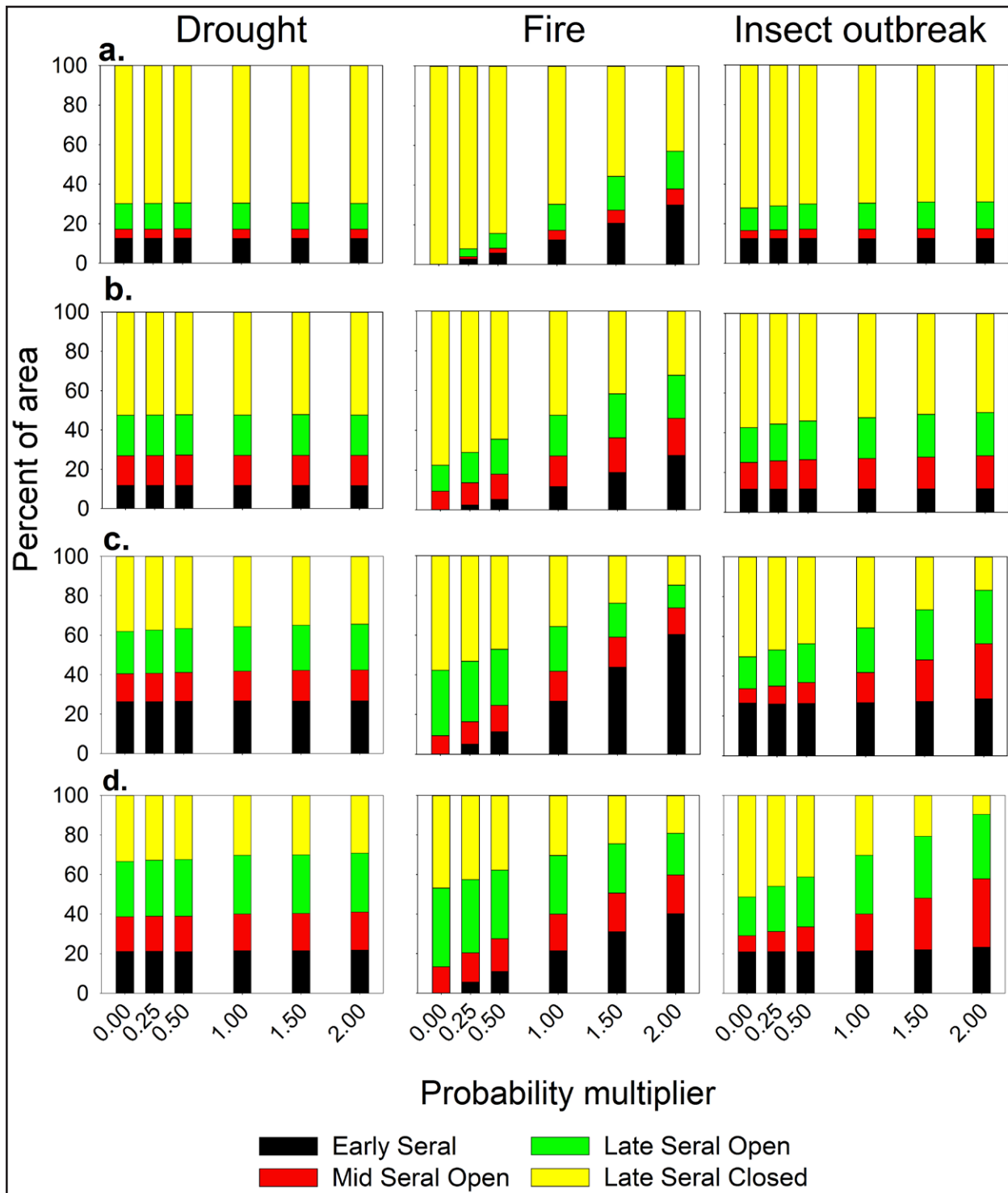


Figure 5. Mix of community phases resulting from varying the probability of drought, fire, and insect outbreaks for the (a) Warm-Moist, (b) Cool-Moist, (c) Warm-Dry, (d) and Shallow-Dry sagebrush groups. Varying the probability of drought had no observable effect on the two moist groups and only a minor effect on the two dry groups. Varying the probability of fire had a large effect on all four groups. Varying the probability of an impact when an insect outbreak occurs had a greater effect on the two dry groups than on the two moist groups with the least effect on the Warm-Moist Sagebrush Group.

ure 5a). Altering the probability of mortality from drought in the CM Group had no effect as well ($P = 0.427$, 0.994 , and 0.965 for the MSO, LSO, and LSC phases, respectively) (Figure 5b). Unlike in the WM Group, varying the probability of mortality from insect outbreaks in the CM Group had a significant effect except at the two highest levels tested (Figure 5b), although this effect was still relatively small.

Altering the probability of freezekill and snow mold in the CM Group produced significant changes in the abundance of the MSO, LSO, and LSC phases (Figure 6a and b). The differences associated with snow mold were more clear for all three phases than for freezekill. Altering the probability of mortality from vole outbreaks also produced significant differences in the abundance of the MSO, LSO, and LSC community phases (Figure 6c), but the differences were smaller and varied by community phase. Differences in the MSO phase were significant at all levels tested, whereas differences in the LSO phase were significant only when the absence of vole-related mortality was compared to a doubling of the likelihood of mortality, and differences in the LSC phase were significant only when the mortality probability increased over that in the base model.

As occurred when disturbance types were added and removed in different combinations, varying probabilities in the WD Group and SD Group produced similar results. Unlike the two moist sagebrush groups, varying the probability of mortality from drought did produce some significant differences in the two dry sagebrush groups (Figure 5c and d). In the MSO and LSC phases, the differences were significant only when increased probabilities were compared to decreased probabilities, and in the LSO phase, they were significant only when absence of drought was compared to a doubled probability of mortality. In both groups, varying the probability of mortality from insect outbreaks (Figure 5c and d) and of pronghorn browsing episodes (Figure 7) pro-

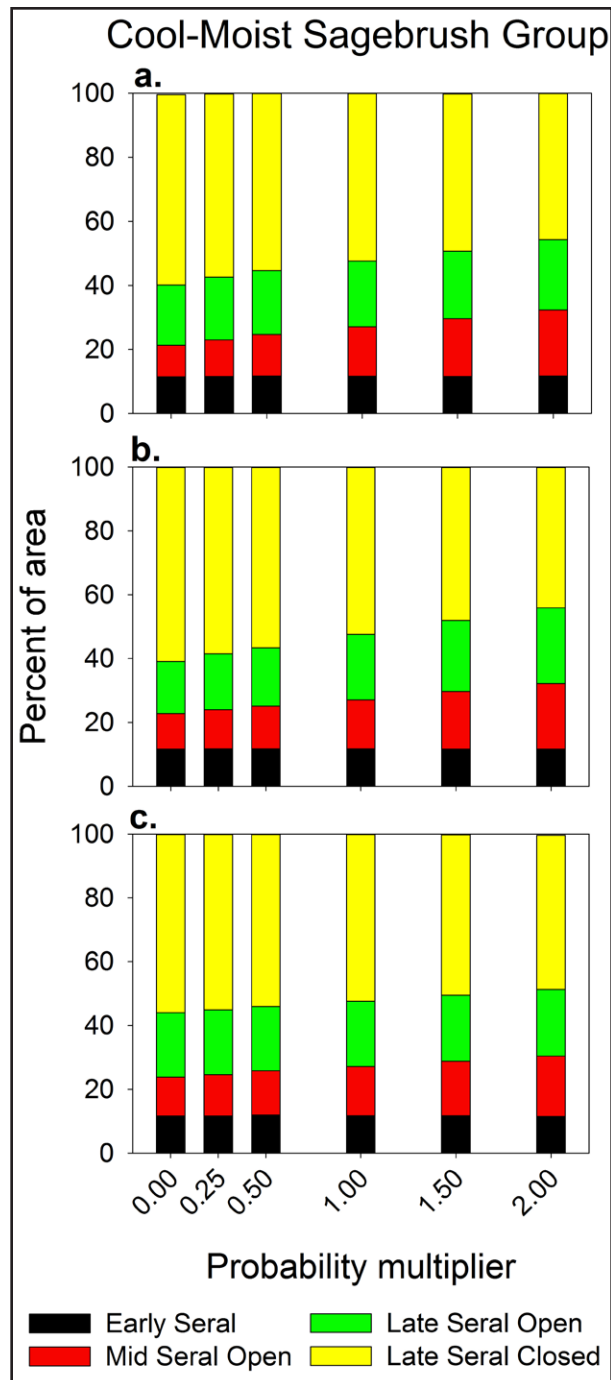


Figure 6. Mix of community phases resulting from varying the probability of (a) freezekill, (b) snow mold, and (c) vole outbreaks in the Cool-Moist Sagebrush Group. Varying the probability of vole outbreaks had only a minor effect on the mix of community phases. As the probability of both freezekill and snow mold increased, abundance of the Late Seral Closed community phase decreased and abundance of the Late Seral and Mid Seral Open phases increased.

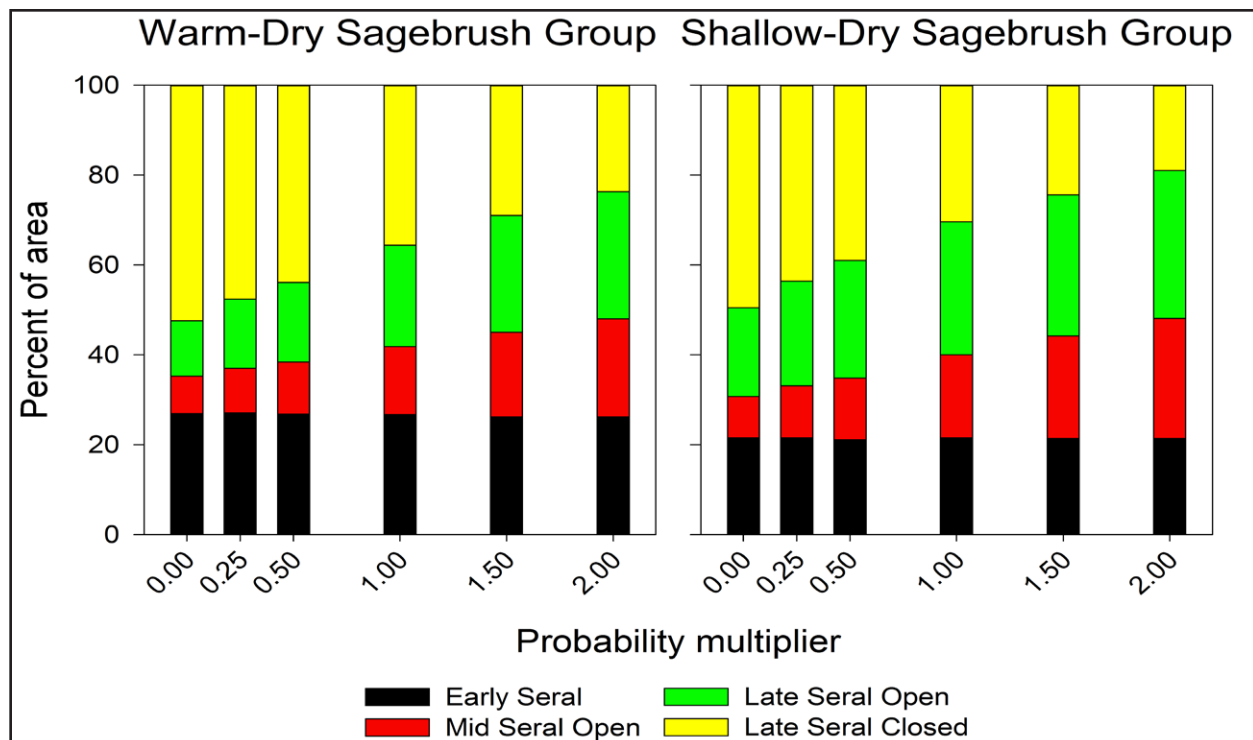


Figure 7. Mix of community phases resulting from varying the probability of severe pronghorn browsing in the two dry sagebrush groups. As the probability of pronghorn browsing effects increases, abundance of the Late Seral Closed phase decreases, and abundance of the Late Seral and Mid-Seral Open phases increases.

duced significant differences in the abundance of community phases with larger differences in the case of pronghorn browsing.

Effects on Predicted Fire Rotation

The full models (all events included) produced fire rotations of 24 yr, 33 yr, 83 yr, and 196 yr for the WM, CM, WD, and SD groups, respectively. In both moist sagebrush groups, neither adding nor removing events other than fire or varying probabilities resulted in any change in the predicted fire rotation, unlike in the two dry sagebrush groups. In the WD Group, the full model produced an estimated fire rotation of 83 yr while the fire-only variant produced an estimated rotation of 99 yr. Removing drought from the full model or adding it to the fire-only variant had little effect on fire rotation. Adding or removing insect outbreaks and pronghorn browsing produced an estimat-

ed fire rotation that was longer than the full model but shorter than the fire-only variant. Varying the probability of drought mortality had a small effect on fire rotation. Varying the probability of mortality from an insect outbreak caused fire rotation to range from 96 yr when insects were absent to 69 yr when the probability was doubled. With pronghorn browsing, fire rotation ranged from 92 yr when pronghorn browsing was absent to 75 yr when the probability was doubled.

Fire rotation in the SD Group exhibited similar behavior as in the WD Group. The full model produced a fire rotation of 196 yr while the fire-only model estimated 213 yr. Adding and removing drought, insect outbreaks, and pronghorn browsing produced a similar effect on fire rotation as in the WD Group, although the effect of adding and removing drought produced a larger change. Adding pronghorn browsing to the fire-only variant and removing

insect outbreaks from the full model produced the same estimated rotation as the fire-only variant. There was no effect on fire rotation when varying the probability of mortality from drought. Varying the probability of mortality from insect outbreak caused fire rotation to range from 213 yr when insect outbreaks were absent to 182 yr when the probability was doubled. Varying the probability of pronghorn browsing caused fire rotation to range from 204 yr when pronghorns were absent to 192 yr when the probability was doubled. The effect of varying the probability of pronghorn browsing was less in the SD Group than in the WD Group and had no effect on fire rotation when the probability decreased.

DISCUSSION

Estimated fire rotations produced by the four models were similar to fire return intervals reported in the literature for the different major subspecies of big sagebrush and for low sagebrush (Burkhardt and Tisdale 1976, Whisenant 1990, Miller and Rose 1999, Miller *et al.* 2001, Knick *et al.* 2005, Baker 2006, Heyerdahl *et al.* 2006, Mensing *et al.* 2006, Miller and Heyerdahl 2008). Tree-ring studies at the sagebrush-conifer ecotone indicate an average fire return interval of 10 yr to 35 yr (Burkhardt and Tisdale 1976, Miller and Rose 1999, Miller *et al.* 2001, Heyerdahl *et al.* 2006, Miller and Heyerdahl 2008). Our estimated fire rotation for the CM Group was near the upper end of these reported intervals. Expert opinion for fire return intervals range from 10 yr to 25 yr on more productive sites, 30 yr to 80 yr on less productive sites, and over 100 yr on very dry, low-productivity sites (Miller and Rose 1999, Knick *et al.* 2005, Miller and Heyerdahl 2008). Our modeled fire rotations all fell within these general categories. However, fire return interval and fire rotation are not the same measures of fire frequency. Fire return interval estimates how often a given spot has burned while fire rotation estimates the num-

ber of years needed to burn an area equivalent in size to the analysis area (Agee 1993, Romme *et al.* 2009). While no clear relationship between the two measures has ever been established, many fire ecologists assume that fire rotation is longer than fire return interval for a given site.

The importance of fire in shaping sagebrush ecosystems is well established (Knick *et al.* 2005, Mensing *et al.* 2006, Miller *et al.* 2011); model results concerning the influence of fire presence, absence, and differing probabilities on the mix of community phases were expected. Our results suggest that fire may indeed be the only significant factor in the most productive sagebrush communities but not in lower productivity sagebrush communities. Our results also suggested two other intriguing linkages between fire and other disturbances and how they affect the mix of community phases: 1) there may be a threshold related to the extent of area a disturbance might affect, above which it has an influence on both fire rotation and the mix of community phases, and below which it does not; and 2) the relative frequency of another disturbance relative to the frequency of fire may also be an important consideration.

With respect to the first possible linkage, we assumed vole outbreaks affected only 10% of the landscape in the Cool-Moist Group and our results indicated that vole outbreaks had only a small impact. Conversely, we assumed that freeze-kill, snow mold, and pronghorn browsing affected 25% of the landscape in models that included them, and each of these did influence fire rotation and the mix of community phases. If this threshold actually exists, it may lie somewhere between 10% and 25% of the landscape. With respect to the second possible linkage, we set the drought frequency to vary between 100 yr and 200 yr (Table 3) and, once the probability of mortality was factored in, had an estimated rotation of greater than 475 yr in all models. Drought had little or no influence on the mix of community

phases and no influence on fire rotation in the two moist sagebrush groups, which had estimated average fire rotations of less than 35 yr. In contrast, drought had a more noticeable effect in the Warm-Dry Group where the estimated fire rotation was 83 yr, and a somewhat larger influence in the Shallow-Dry Group where the estimated fire rotation was 196 yr.

Insect outbreaks may be more important than previously recognized, particularly in the drier sagebrush groups, affecting the mix of community phases in all four sagebrush groups and modifying fire rotation in the two dry groups. The link between insect outbreaks and subsequent fires is well established in forest ecosystems. By opening tree canopies, insect outbreaks alter fuel amount and arrangement, and within-stand environmental conditions, facilitating the start and spread of fires (Furniss and Carolin 1977, Wright and Bailey 1982, Agee 1993), although there may be several years between an outbreak and a fire and not all forest stands affected by an insect outbreak necessarily burn. Insect outbreaks in sagebrush may operate in a similar manner by opening canopies (Hsiao and Temte 1976; Hsiao 1986; N.L. Hampton, unpublished manuscript) and shifting site resources to grasses and forbs. The subsequent increase in grasses and fine fuel continuity should facilitate the start and spread of fires in sagebrush ecosystems.

The apparent importance of pronghorn browsing in the Warm-Dry and Shallow-Dry sagebrush groups was a surprise, having a greater effect on the mix of community phases and fire rotation than we expected. As with insect outbreaks, pronghorn browsing when animal populations were high and winters were severe would shift site resources to grass, increasing fuel amount and continuity, and subsequent fire risks. However, we are less confident that this particular interaction is as strong as the model suggests. Although pronghorn populations were much higher before 1850 (Elliott 1910, O’Gara and Yoakum 2004), they were also lower than populations east of the

continental divide where the impact of high pronghorn populations during severe winters has been documented (O’Gara and Yoakum 2004). Thus, we are less certain that population peaks would have had the same effect on the Malheur High Plateau as on the western Great Plains. If we overestimated the probability of pronghorn browsing, then the Late Seral Closed community phase might have been more abundant and the Mid Seral and Late Seral Open phases less abundant in both dry sagebrush groups.

We are puzzled by the lack of effect on fire rotation in the two moister sagebrush groups in our models. We allowed for mosaic fire in the Late Seral Open and Late Seral Closed community phases in the WM and CM groups but not in the WD and SD groups. This difference in model design could have removed a source of variability, particularly given that the two late seral community phases comprised more than half the area of all four models (Figure 2). Alternatively, this result may also indicate that how fires burn could be as important as whether they burn. According to fire occurrence records for Burns and Lakeview BLM districts and Malheur and Hart Mountain national wildlife refuges (1980 to 2011), only 2% of fires exceeded 2023 ha, yet these fires accounted for 73% of the total hectares burned. Use of fire by Native Americans was well documented in the Great Basin (Gruell 1985, Robbins 1999, Griffen 2002, Stewart 2002), although the number of fires and area affected were not. 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 before 1850 as in modern fire records (Swetnam and Betancourt 1998, Hessl *et al.* 2004, Heyerdahl *et al.* 2008). In the times before 1850, a year in which a great many hectares burned, fires may have consisted of a large number of small- to medium-sized events, given the ratio of human- to lightning-caused fires

suggested by Stewart (2002) and the low number of lightning strikes that actually start fires in rangeland ecosystems (Latham and Williams 2001). Since 1980, such years consisted of a few very large fires, believed to be largely due to changes in fuel structure resulting from a combination of past grazing, aggressive fire suppression, and a variety of other human-caused changes (Connelly *et al.* 2004, Knick *et al.* 2005, Heyerdahl *et al.* 2006). The resulting landscape patterns would have been very different before 1850 than since 1980 even if the frequencies of the different types of fire years were similar.

These models allowed us to explore the relationships between fire and other types of natural events: how they may have collectively shaped the abundance of different community phases and whether other disturbance types could affect fire rotation. Our results suggest that fire is the only significant shaper of the most productive sagebrush communities but that the importance of other disturbance types increases as site productivity declines. There may also be thresholds associated with how much area is affected by a given disturbance type if disturbance effects are significant above the area threshold but insignificant below it. The relative significance of a disturbance type other than fire may also depend on how much

longer its frequency is compared to fire frequency. Future testing could explore these potential linkages further. For example, we varied the probability of sagebrush mortality associated with drought, but we did not vary the drought cycle itself to explore whether the importance of drought might increase if it occurred more often. The relative importance of mosaic fire as compared to stand-replacing fire could be tested by excluding one versus the other and varying the probabilities of each fire type separately. Bringing these models into a geospatial state-and-transition modeling framework could alter some of these results since we could not model the contagion principles so important to how fires and insect outbreaks actually work. We assumed fire was the only stand-replacing event since the literature only weakly hinted that any other disturbance type could be stand-replacing. Scientific documentation of natural events other than fire is limited, rarely addresses the probability of the event or the magnitude of its impact, and rarely links the probability of occurrence or impact to climate. However, an aroga moth outbreak in 2012 in the northern Great Basin suggests that insect outbreaks might also be stand-replacing under certain conditions in the Warm-Dry Sagebrush Group. If so, the importance of insect outbreaks could increase further.

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