Simulating Current Successional Trajectories in Sagebrush Ecosystems With Multiple Disturbances Using a State-and-Transition Modeling Framework

Louisa B. Evers,[1] Richard F. Miller,[2] Paul S. Doescher,[3] Miles Hemstrom,[4] and Ronald P. Neilson[5]

Authors are [1]Fire Ecologist, Bureau of Land Management, Oregon State Office, Portland, OR 97204, USA; [2]Plant and Fire Ecologist Emeritus, Eastern Oregon Agricultural Research Station, Oregon State University, Corvallis, OR 97331, USA; [3]Restoration Ecologist, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA; [4]Research Ecologist (retired), US Forest Service Pacific Northwest Research Station, Portland, OR 97204, USA; and [5]Bioclimatologist (retired), US Forest Service Pacific Northwest Research Station, Corvallis, OR 97331, USA.

Abstract

Disturbances and their interactions play major roles in sagebrush (*Artemisia* spp. L.) community dynamics. Although impacts of some disturbances, most notably fire, have been quantified at the landscape level, some have been ignored and rarely are interactions between disturbances evaluated. We developed conceptual state-and-transition models for each of two broad sagebrush groups—a warm-dry group characterized by Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) communities and a cool-moist group characterized by mountain big sagebrush (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rydb.] Beetle) communities. We used the Vegetation Dynamics Development Tool to explore how the abundance of community phases and states in each conceptual model might be affected by fire, insect outbreak, drought, snow mold, voles, sudden drops in winter temperatures (freeze-kill), livestock grazing, juniper (*Juniperus occidentalis* var. *occidentalis* Hook.) expansion, nonnative annual grasses such as cheatgrass (*Bromus tectorum* L.), and vegetation treatments. Changes in fuel continuity and loading resulted in average fire rotations of 12 yr in the warm-dry sagebrush group and 81 yr in the cool-moist sagebrush group. Model results in the warm-dry sagebrush group indicated postfire seeding success alone was not sufficient to limit the area of cheatgrass domination. The frequency of episodes of very high utilization by domestic livestock during severe drought was a key influence on community phase abundance in our models. In the cool-moist sagebrush group, model results indicated at least 10% of the juniper expansion area should be treated annually to keep juniper in check. Regardless, juniper seedlings and saplings would remain abundant.

Key Words: annual grasses, juniper, livestock grazing, Vegetation Dynamics Development Tool, vegetation treatments

INTRODUCTION

Since the mid-19th century, domestic livestock grazing, introduction of nonnative invasive plants (e.g., cheatgrass [*Bromus tectorum* L.]), changes in wildfire occurrence, conversion of sagebrush-steppe to pinyon–juniper (*Pinus* spp.–*Juniperus* spp.) woodlands (Miller and Wigand 1994), and a history of treatments to eradicate or modify sagebrush (*Artemisia* spp. L.) communities (Pechanec et al. 1944; Frischknecht and Bleak 1957; Cooper and Hyder 1958; Johnson 1958, 1969; Harniss and Murray 1973; Bartolome and Heady 1978; Britton et al. 1981) have produced broad-scale alterations of sagebrush ecosystems throughout the western United States (Bunting et al. 2002; Hemstrom et al. 2002; Connelly et al. 2004; Miller et al. 2011). The loss and alteration of sagebrush community structure and abundance have been associated with declines of sagebrush-obligate species, most notably greater sage-grouse (*Centrocercus urophasianus*; Crawford and Gregg 2001; Connelly et al. 2004; Gregg and Crawford 2009); habitat for other wildlife; and livestock forage.

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Correspondence: Louisa Evers, Bureau of Land Management, Oregon State Office OR-933, 333 SW First Ave, Portland, OR 97204, USA. Email: levers@blm.gov

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The ability to evaluate and predict short and long-term responses of sagebrush communities to natural disturbances, management actions, and their interactions in both time and space using models would allow managers to develop better management plans for the maintenance and restoration of these communities. The state-and-transition paradigm provides conceptual models of potential phases, states, and factors that may cause transitions between phases and states (Bestelmeyer et al. 2003, 2009). The use of state-and-transition models to describe changes in rangeland ecosystems is increasing, but most models are qualitative, simply identifying which disturbances may be responsible for movement between phases within a state and between states (Bestelmeyer et al. 2003; Peterson et al. 2009; Holmes and Miller 2010). A few studies have attempted to quantify the likelihood of movement between phases and states with a single disturbance type, such as the LANDFIRE project (Rollins and Frame 2006), but even fewer have examined multiple disturbances (e.g., Bunting et al. 2002; Hemstrom et al. 2002). Further, most quantitative studies published to date, such as those conducted by Bunting et al. (2002) and Hemstrom et al. (2002), typically relied primarily on expert opinion to estimate disturbance probabilities. Developing quantitative state-and-transition models based on objective data and using multiple disturbances would enhance the ability of land managers to use state-and-transition models to explore how changes in management may interact with natural disturbances and affect the potential long-term trajectory of rangeland ecosystems.

To evaluate potential shifts in different sagebrush community states and phases we used the Vegetation Dynamics Development Tool version 6.0 (VDDT; ESSA Technologies Ltd. 2007) to construct two sagebrush models, consisting of a warm-dry (WD) group and a cool-moist (CM) group of sagebrush communities. In VDDT, the user defines the number of boxes in a pathway, the cover type and structural stage (community phase) of each box, and the age range of each box. 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 each box. 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 each 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 1 yr is added to the age of the cell. If cell age 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. Using a Monte Carlo multiplier file, 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.

We used a combination of climate, soils, and fire occurrence data in combination with literature and expert opinion to assign probabilities of occurrence and the potential impact of different types of disturbances and vegetation responses on sagebrush communities. Our specific objectives were to 1) evaluate sensitivity of the two sagebrush models to different disturbances and responses, 2) quantify the effects of active vegetation management in combination with natural events and responses in retaining reference conditions, and 3) determine how the combination of domestic livestock grazing and vegetation management interacts with natural disturbances and vegetation responses to affect the abundance of different phases and states in sagebrush steppe.

METHODS

Study Area

We selected the Malheur High Plateau Major Land Resource Area (Natural Resources Conservation Service 2006) in southeastern Oregon to evaluate our models because it is an extensive area dominated by sagebrush (Miller et al. 2011) and considered a core area for sage-grouse and other sagebrush-obligate species (Connelly et al. 2004). Federal agencies manage the majority of this resource area with mandates to protect, enhance, and restore habitat for sagebrush-obligate species as well as provide for various uses, such as livestock grazing. Much of the study area lies between 1 190 m and 2 105 m elevation, with Steens Mountain reaching 2 967 m. The area consists of interspersed hills, buttes, isolated mountains, and north–south trending fault-block mountains with little surface water. Most soils are loamy to clayey, well-drained, and shallow to moderately deep on uplands, and poorly to well-drained and very deep in basins. Soil temperature and moisture regimes range from mesic and aridic in the lower elevations ($< 1\,200 \pm 150$ m), to frigid and xeric in the mid-elevations ($1\,200$ to $2\,000 \pm 150$ m), and cryic and xeric in the upper elevations ($> 2\,000$ m). Average annual precipitation varies from 105 mm to 305 mm over most of the area and up to 1 450 mm at its upper elevations (Natural Resources Conservation Service 2006). Winter and spring are the wettest periods and summer is the driest. January is the coolest month, averaging –2°C, and July the warmest, averaging 19°C. Sagebrush-steppe is the dominant vegetation type with western juniper (*Juniperus occidentalis* var. *occidentalis* Hook.) expanding from areas with shallow rocky soils.

Model Assumptions

Ecological Basis. Using ecological site descriptions for the Malheur High Plateau,[1] we sorted sagebrush sites into a CM sagebrush group and a WD sagebrush group based on perennial grass productivity in low, average, and high productivity years (Table 1). Although the accuracy of these descriptors was unknown, they represented the best available information. The ecological sites that fell within each group generally conformed to expectations based on long-term field experience in sagebrush ecosystems in eastern Oregon. We assumed productivity provided a measure of potential recovery rates from disturbance and potential frequency of fire events. Within each group, we constructed VDDT models that included multiple community phases and states where each state represented a suite of community phases that differ in plant composition, structure, and function (Bestelmeyer et al. 2003, 2009). We based our successional states on those reported in a previous compilation (West 1983). We defined reference phases as the historical (pre-Euro-American settlement) community phases and included them in state I of each model. Previous work (not reported here) developed and tested models of the reference conditions that included the timing of deterministic transitions and disturbance types that may have shaped the historical sagebrush ecosystems and served as the basis for this effort (Evers 2010).

We reviewed the literature to determine which disturbances may be important in altering community structure and composition and incorporated them into our models. We selected fire (Connelly et al. 2004), insect outbreaks (Gates 1964; Hall 1965), drought severe enough to kill shrubs (Ellison and Woolfolk 1937; Pechanec et al. 1937), sudden drops in late winter temperatures (freeze-kill; Hanson et al. 1982; Nelson and Tiernan 1983), snow mold (Sturges and Nelson 1986), and vole outbreaks (Frischknecht and Baker 1972) as the appropriate natural disturbances to include. We also included the process of juniper expansion (Connelly et al. 2004; Miller et al. 2005). We then added domestic livestock grazing, postfire seeding, and juniper vegetation treatments (prescribed burning, cutting, and cutting and burning) as management activities. We also included encroachment and dominance of cheatgrass (*Bromus tectorum* L.). Other invasive annual grasses are also becoming problematic in this area, but much less is known about their dynamics. To increase model objectivity, we based as many disturbance probabilities as feasible on the climate

[1]Available at http://esis.sc.egov.usda.gov.

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 values for the different community phases in each sagebrush group. Characteristics are based on ecological site information for the Malheur High Plateau,[1] Winward (1991), and Miller and Eddleman (2000).

	Cool-moist group	Warm-dry group
Modal plant association	*Artemisia tridentata* Nutt. subsp. vaseyana (Rydb.) Beetle; Festuca idahoensis Elmer	*Artemisia tridentata* Nutt. subsp. wyomingensis Beetle & Young; Pseudoroegneria spicata (Pursh) A. Löve; Achnatherum thurberianum (Piper) Barkworth
Precipitation—years producing at least 672 $kg \cdot ha^{-1}$	High and average	High
Dominant soil moisture regime	Xeric	Aridic
Dominant soil temperature regime	Frigid	Mesic
General soil depth	Moderately deep to deep	Shallow to moderately deep
Sagebrush cover by community phase		
Early seral	< 1%	< 1%
Midseral open	1–10%	1–8%
Late seral open	10–30%	8–20%
Late seral closed	> 30%	> 20%

[1]Available at http://esis.sc.egov.usda.gov.

factors indicated as drivers in the literature and used local climate data. Where the literature indicated no obvious climate driver or was ambiguous toward a climate driver, we used expert opinion.

We obtained monthly precipitation and temperature data from 1895 to 2009 for Oregon Climate Division 7[2] and snow data from 1967 to 1996 for the Reynolds Creek Experimental Range (Hanson et al. 2001; Marks et al. 2001). Oregon Climate Division 7 encompasses nearly all of the study area. Although Reynolds Creek Experimental Range lies outside the Malheur High Plateau, it has a similar climate and provided more detailed information on snowpack than was available for Oregon Climate Division 7. We summarized monthly and seasonal mean temperatures and medians for precipitation using a temperature-based definition of winter (monthly average < 1.4°C) and summer (monthly average > 14°C) that better matches plant phenology and hydrological cycles than the typical 3-mo definitions (Neilson et al. 1992). We estimated mean and standard deviation for snowpack duration, snow depth, and snowmelt date for the highest elevation station on the Reynolds Creek Experimental Range. We used these data to estimate the probabilities of many disturbance types included in each sagebrush model (Table 2).

WD Group. The WD group contained two states and 12 community phases (Fig. 1) and included four natural disturbance types and three management activities (Tables 2 and 3). In state I, cheatgrass presence was minimal in reference phases and codominant with native perennials in at-risk phases. In state II, cheatgrass was the dominant understory herbaceous species in threshold phases or the sole dominant plant in the cheatgrass phase. We defined four general reference phases (early seral [ES], midseral open [MSO], late seral open [LSO], and late seral closed [LSC]) and four at-risk phases in state I, and three threshold phases in state II similar to Karl and Sadowksi (2005). The phases we labeled "threshold," for lack of a better term, represented an intermediate stage between state I and the cheatgrass phase of state II. We based deterministic transitions between community phases on the estimated time needed to cross sagebrush canopy cover thresholds. We assumed sagebrush established episodically following wetter than average spring conditions (Johnson and Payne 1968; Boltz 1994) and that the sagebrush population doubled with each establishment episode. Growth rates of individual plants in each age cohort determined how quickly the cover threshold was crossed (McArthur and Welch 1982). The cover thresholds were based on definitions in Karl and Sadowski (2005) and Miller and Eddleman (2000). Using this approach, the ES phase in state I lasted 48 yr and the LSC phase was reached after 78 yr in the absence of disturbance. We assumed cheatgrass was already present throughout the group and that fire (D'Antonio and Vitousek 1992; Bunting et al. 2002) and detrimental levels of livestock grazing (Cottam and Evans 1945; Tausch et al. 1994b; Bradford and Laurenroth 2006; Reid et al. 2008) promoted cheatgrass dominance.

CM Group. The CM group contained three states and nine community phases (Fig. 2) and included seven natural disturbance types and four management activities (Tables 2 and 3). State I had four reference phases (ES, MSO, LSO, and LSC) and two at-risk phases. The two at-risk phases followed the descriptions developed by Miller et al. (2005). In phase I juniper (J1), juniper was present, but a subordinate component of the vegetation. In phase II juniper (J2), juniper was codominant with shrubs and grasses. State II was juniper-dominated and consisted of two phases. In phase III juniper (J3), juniper was dominant, but trees were less than 150 yr old. In the old-growth phase (OG), trees were greater than 150 yr old and at least 75% of the trees exhibited one or more morphological characteristics associated with old trees, such as furrowed bark, rounded tops, and greater than 10% dead crown (Waichler et al. 2001). The OG phase in this model referred to future old juniper woodland that would develop from juniper expansion into the CM group, not to the old-growth juniper woodland that provided the initial seed source

[2]Available at http://www7.ncdc.noaa.gov/CDO/CDODivisionSelect.jsp.

Table 2. Factors used to estimate probabilities of the occurrence and severity of each type of event. Temperature and precipitation values based on Oregon Climate Division 7 descriptive statistics for water years 1885–1886 through 2007–2008 for fire, drought, insect outbreaks, vole outbreaks, freeze-kill, and snow mold, and through 2008–2009 for grazing, postfire seeding, and juniper expansion. Fire occurrence records cover 1980–2006 fire years for Lakeview and Burns Bureau of Land Management districts and Hart Mountain Refuge. Wind frequency based on 10-min 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 1967–1968 through 1996–1997 water years.

Disturbance type	Cycle	Impact	Probability basis	Adjustments to probability basis	Data/literature sources
Stand-replacing fire	Random	Stand-replacement	Combined frequency of spring precipitation $\geq$ 75th percentile and summer precipitation $\leq$ 25th percentile multiplied by frequency of winds ≥ 24 $km \cdot hr^{-1}$ in August (CM group). Combined frequency of spring precipitation $\geq$ 75th percentile and average June temperature $\leq 13°C$ multiplied by frequency of winds > 24 $km \cdot hr^{-1}$ in August (WD group)	Reduced by 25% for sufficient fuel but lack of ignition. Decreased probability in low and average fire years. Increased probability in high and extreme years	Swetnam and Betancourt 1990, 1998; Rorig and Fergusson 1999; Grissino-Mayer and Swetnam 2000; Heyerdahl et al. 2002; Rollins et al. 2002 (probability basis, ignition adjustment); Oregon Climate Division 7 records (precipitation and temperature); remote automated weather station records (wind); fire occurrence records (frequency of low, average, high, and extreme fire years); expert opinion (ignition adjustments)
Mosaic fire	Random	Thinning	Combined frequency of spring precipitation $\geq$ 75th percentile and summer precipitation $\leq$ 25th percentile minus stand-replacing fire frequency (CM group) Combined frequency of spring precipitation $\geq$ 75th percentile and average June temperature $\leq 13°C$ minus stand-replacing fire frequency (WD group)	Reduced by 25% for sufficient fuel but lack ignition and reduced by 25% for effects of grazing Decreased probability in low and average fire years Increased probability in high and extreme years	Same as above (probability basis and ignition adjustment); Oregon Climate Division 7 records (precipitation and temperature); expert opinion (ignition and grazing adjustment)
Stand-replacing fire in cheatgrass	Random	Stand-replacement	1.0 minus combined frequency of total winter precipitation > 80 mm and spring precipitation > 20 $mm \cdot mo^{-1}$	Reduced by 75% to account for sufficient fuel but lack ignition	Britton et al. 1981; Whisenant 1990; Neilson et al. 1992; Rorig and Fergusson 1999 (probability basis and ignition adjustment); Oregon Climate Division 7 records (precipitation and temperature); expert opinion (ignition adjustment)
Drought (severe enough to kill sagebrush)	100–200 yr	Thinning	Literature	None	Cook et al. 2004; Stahle et al. 2007 (cycle and impact)

Table 2. Continued.

Disturbance type	Cycle	Impact	Probability basis	Adjustments to probability basis	Data/literature sources
Insect outbreaks	20–48 yr	Thinning	Literature	Reduced by 50%	Gates 1964; Hall 1965; Speer et al. 2001; Speer and Jenson 2003 (cycle and impact)
Vole outbreaks	45 yr	Thinning	Literature	Reduced by 90% to account for limited area of impact	Murray 1965; Frischknecht and Baker 1972; Parmeter et al. 1987 (cycle and impact); expert opinion (adjustment factor)
Freeze-kill	Random	Thinning	Combined frequency of winter precipitation ≤ 68 mm and January average temperature $\geq 0.89°C$	Reduced by 75% to account for limited area of impact	Hansen et al. 1982; Walser et al. 1990; Hardy et al. 2001; Oregon Climate Division 7 (precipitation and temperature); expert opinion (adjustment factor)
Snow mold	Random	Thinning	Combined frequency of winter > 179 d, snow depth $> 2\,087$ mm, and 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)
Livestock grazing—high utilization	Random	Accelerated movement to next community phase	Combined frequency of winter precipitation > 80 mm plus spring precipitation < 20 $mm \cdot mo^{-1}$	Reduced by 25% to account for assumed grazing system	Neilson et al. 1992; Oregon Climate Division 7 records (precipitation)
Livestock grazing—very high utilization	Random	Transition to another community phase	Combined frequency of winter precipitation < 80 mm plus spring precipitation < 20 $mm \cdot mo^{-1}$	−25% to account for assumed grazing system	Neilson et al. 1992; Oregon Climate Division 7 records (precipitation)
Postfire seeding success	Random	Transition to reference state	Germination: frequency of fall precipitation ≥ 42.7 mm	Establishment: low, frequency of May–June precipitation < 35.36 mm; high, frequency of May–June precipitation > 68.13 mm; average, frequency of May–June precipitation 35.37–68.14 mm	Robichard et al. 2000; Getz and Baker 2007; Keeley and McGinnis 2007; Eiswerth et al. 2009; Oregon Climate Division 7 records (precipitation); expert opinion (adjustment factor)
Juniper expansion	Random	Initiate juniper community phases	Frequency of year with winter precipitation < 80 mm plus spring precipitation > 20 $mm \cdot mo^{-1}$ followed by year with winter precipitation > 80 mm plus spring precipitation > 20 $mm \cdot mo^{-1}$ plus summer precipitation < 28 $mm \cdot mo^{-1}$	None	Miller and Wigand 1994; Romme et al. 2009 (probability basis); Neilson et al. 1992 (biome model); Oregon Climate Division 7 records (precipitation)
Juniper treatments	Random	Thinning (cutting) and stand-replacing (burning)	Expert opinion	None	BLM district fuels specialists

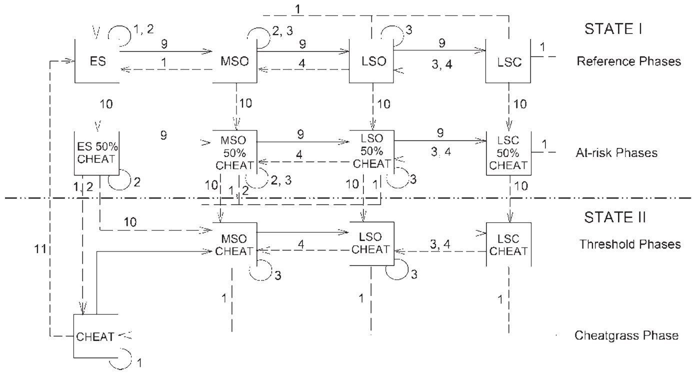

Figure 1. Diagram of the successional pathways for the warm-dry sagebrush group. Solid lines with arrows indicate deterministic pathways in the absence of disturbance, dashed lines with arrows indicate probabilistic pathways due to disturbance, and circles indicate disturbances that reset the relative age within a community phase. Broken lines indicate which community phases belong in which state. Natural disturbances include (1) stand-replacing and (2) mosaic fire, (3) drought severe enough to kill sagebrush, and (4) insect outbreaks. Management activities include livestock grazing at (9) high and (10) very high utilization levels and (11) postfire seeding. Number codes refer to Table 3. Abbreviations: ES, early seral; MSO, midseral open; LSO, late seral open; LSC, late seral closed; and CHEAT, cheatgrass. At-risk phases have understories that are approximately 50% cheatgrass and 50% native bunchgrasses and forbs. Threshold phases have cheatgrass understories.

for juniper expansion. Movement between the reference phases followed the same general process used in the WD group, although specific criteria differed (Evers 2010). Using this process, the ES phase lasted 18 yr and the LSC phase was reached in 31 yr in the absence of disturbance. We based movement between phases with juniper present and in the absence of disturbance on age data for intermediate sites in Johnson and Miller (2006). State III consisted of a single phase (cheatgrass) where cheatgrass was the dominant species.

Disturbances. Each state-and-transition model included disturbances and processes based on information concerning impacts to sagebrush documented in the literature or agreed upon by expert opinion as documented in the literature or based on long-term observations. We used the literature to determine what role climate likely played in the occurrence of certain disturbances and data from Oregon Climate Division 7 and Reynolds Creek Experimental Range to estimate the frequencies of certain climatic events, such as wet springs or deep snowpacks. Observations and models reported in the literature suggested we include fire (Britton et al. 1981; Brown 1982; Bunting et al. 1987; Whisenant 1990; Peters and Bunting 1994), snow mold (Sturges 1986, 1989), freeze-kill (Hanson et al. 1982; Walser et al. 1990; Hardy et al. 2001; DeGaetano and Wilks 2002), vole outbreaks (Mueggler 1967; Frischknecht and Baker 1972; Parmenter et al. 1987), juniper seedling establishment (Miller and Wigand 1994; Romme et al. 2009), the occurrence of detrimental levels of livestock grazing (Craddock and Forsling 1938; Houston 1961; Brotherson and Brotherson 1981; Angell 1997; Adler et al. 2005), and postfire seeding success (Klomp and Hull 1972; Hull 1974; Cox and Anderson 2004; Thompson et al. 2006). These same sources also suggested how climate might have influenced the probability of each event.

Fire. We separated fire events into homogeneous (stand-replacing fire) and heterogeneous burn patterns (mosaic fire) with different probabilities for each type. We reduced the probability of both fire types to account for presence of sufficient fuel but absence of ignitions and further reduced the probability of mosaic fire to account for the effects of livestock grazing on fuel loading and continuity (Table 2). For example, we estimated the probability of any fire in the WD group by identifying the frequency of a wet spring and cool June (presence of sufficient fuel). We multiplied that initial probability by the frequency of high winds in August to estimate the probability of a stand-replacing fire; we estimated the probability of a mosaic fire by subtracting the probability of a stand-replacing fire from the initial fire probability and multiplied the result by 0.75 to account for our assumed effects of grazing on fuel continuity. This assumption also meant that grazing impacts were evenly distributed across the landscape even though they typically were not. We then 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 fire occurrence records; the occurrence of low and average fire years further reduces the probability of either fire whereas the occurrence of a high or extreme year increases the probability. In state II of the WD group, we reduced the resulting probability to account for the presence of sufficient fuel but absence of ignition, and assumed that livestock grazing was minimal. We did not vary the probability of stand-replacing fire, assuming the primary determinant of stand-replacing fire at the individual VDDT cell is weather (L. Evers, unpublished data).

In the WD group, we assumed stand-replacing fire in the reference phases would not result in cheatgrass dominance until age 100 in the LSC community phase (Cline et al. 1977; Young and Evans 1978; Hosten and West 1994; Chambers et al. 2007; Davies et al. 2007; Davies et al. 2008). As sagebrush density increases, native grasses tend to become smaller and shorter, leading to high mortality of both existing plants and any seed when a fire burns (Robertson 1947; Hassan and West 1986; Miller et al. 1986; Bunting et al. 1987; Melgoza and Nowak 1991); we assumed the critical threshold in sagebrush density and cover occurred at approximately age 100. In the at-risk phases, a mosaic fire in the ES and MSO community phases had equal chances of remaining in that state or transitioning into the threshold phases of state II due to interannual variability in the production of both cheatgrass and perennial bunchgrasses, which result from interannual variability in precipitation amount and timing, especially in spring (Cooper and Hyder 1958; Bradley and Wilcox 2009). Stand-replacing fire in the at-risk phases of state I resulted in a transition to state II, cheatgrass phase, after which fire maintained that phase (Knapp 1996; Bradford and Laurenroth 2006; Reid et al. 2008). If a site in the cheatgrass phase escaped fire for at least 20 yr, we assumed sagebrush reestablished and transitioned back to the threshold MSO phase (Young and Evans 1973; Peters and Bunting 1994; Mata-González et al. 2007).

Table 3. General description of event types included in both sagebrush models and their effects. Drought timing and effects are based on Cook et al. (2004) and Stahle et al. (2007). Insect outbreak timing and effects are based on Gates (1964), Hall (1965), Hsaio (1986), Speer et al. (2001), and Speer and Jenson (2003). Freeze-kill effects are based on Hansen et al. (1982), Neilson and Tiernan (1983), Walser et al. (1990), and Hardy et al. (2001). Snow mold effects are based on Sturges (1986, 1989). Vole outbreak timing and effect are based on Murray (1965), Frischknecht and Baker (1972), and Parmenter et al. (1987). Livestock grazing effects based on Craddock and Forsling (1938), Houston (1961), Brotherson and Brotherson (1981), Angell (1997), and Adler et al. (2005). Number codes at the beginning of each event type are keyed to Figures 2 and 3.[1]

Event type	Timing	Effect	Transition to earlier phase?	Area limits?	Groups affected	Community phases affected
1. Stand-replacing fire	Random	Stand replacement	Yes	No	Both	Both groups—all
2. Mosaic fire	Random	Thinning	No	No	Both	WD group—ES, MSO reference and at-risk phases; CM group—ES, MSO, LSO
3. Drought (severe enough to kill sagebrush)	100–200 yr	Thinning	WD group: no—MSO, LSO; yes—LSC. CM group: no	No	Both	WD group—MSO, LSO, LSC in reference, at-risk, and threshold phases; CM group—MSO, LSO, LSC
4. Insect outbreaks	20–48 yr	Thinning	Yes	No	Both	WD group—LSO, LSC in reference, at-risk, and threshold phases; CM group—LSO, LSC
5. Freeze-kill	Random	Thinning	No—MSO; yes—LSO, LSC	Yes—25% of landscape	CM group	MSO, LSO, LSC
6. Snow mold	Random	Thinning	No—MSO; yes—LSO, LSC	Yes—25% of landscape	CM group	MSO, LSO, LSC
7. Vole outbreaks	4–5 yr	Thinning	No—MSO, LSC; yes—LSO	Yes—10% of landscape	CM group	MSO, LSO, LSC
8. Juniper expansion	Random	Initiate juniper community phases	No	No	CM group	LSO, LSC
9. Livestock grazing——high utilization	Random	Accelerated movement to next community phase	No	No	Both	WD group—ES, MSO, and LSO in reference and at-risk phases; CM group—ES, MSO, LSO
10. Livestock grazing——very high utilization	Random	WD group—transition to another community phase CM group—accelerated movement to next community phase	No	No	Both	WD group—ES, MSO, and LSO in reference and at-risk phases; CM group—ES, MSO, LSO
11. Postfire seeding	Random	Transition to reference state	Yes	No	Both	Both groups—cheatgrass phase
12. Juniper treatments	Random	Thinning (cutting) and stand-replacing (burning)	Yes	No	CM group	J1, J2, J3, OG

[1]WD group; warm-dry group; CM group, cool-moist group; ES, early seral; MSO, midseral open; LSO, late seral open; LSC, late seral closed; J1 = phase 1 juniper; J2, phase 2 juniper; J3, phase 3 juniper; OG, old-growth juniper.

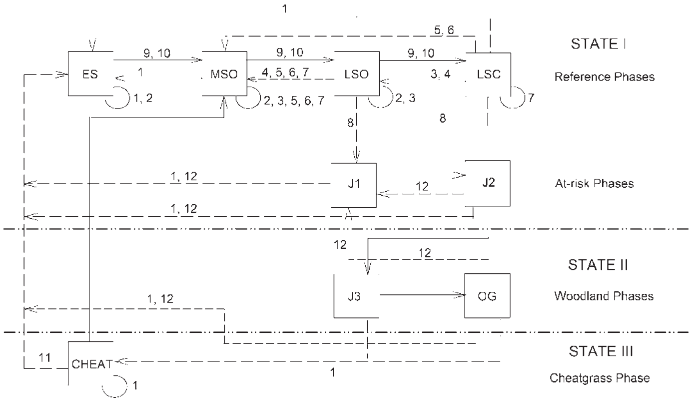

Figure 2. Diagram of the successional pathways for the cool-moist sagebrush group. Solid lines with arrows indicate deterministic pathways in the absence of disturbance, dashed lines with arrows indicate probabilistic pathways due to disturbance, and circles indicate disturbances that reset the relative age within a community phase. Broken lines indicate which community phases belong in which state. Natural disturbances include (1) stand-replacing and (2) mosaic fire, (3) drought severe enough to kill sagebrush, (4) insect outbreaks, (5) freeze-kill, (6) snow mold, and (7) voles. Management activities include (8) juniper expansion, livestock grazing (9, 10), (11) postfire seeding, and (12) juniper treatments — cutting, cutting and burning, and burning. Number codes refer to Table 3. Although juniper expansion could also be considered a natural disturbance, we included it in the management activity group of disturbances since management actions appear to have accelerated the rate of juniper expansion (Miller and Rose 1995, 1999). Abbreviations: ES, early seral; MSO, midseral open; LSO, late seral open; LSC, late seral closed; J1, phase I juniper; J2, phase II juniper; J3, phase III juniper; OG, old-growth juniper; CHEAT, cheatgrass.

In the CM group, mosaic fire in the reference phases of state I reduced sagebrush cover, but did not result in a shift to a different community phase or state. In both states I and II of this group, stand-replacing fire shifted the site into the reference ES phase with one exception. Approximately 2% of the CM group consists of Wyoming big sagebrush communities, which we assumed could react to fire in the same way as the WD group. We represented these communities by including a 2% probability that stand-replacing fire in state II would transition the site into state III, consistent with the WD group model (Fig. 1).

Insect Outbreaks, Drought, Freeze-Kill, Snow Mold, and Voles. Most of the documented damage from aroga moth (*Aroga websteri* Clark) occurred in older sagebrush (Gates 1964; Hsaio 1986) but very little information was available on outbreak frequencies, size, and severity. Pandora moth (*Coloradia pandora* Blake), a ponderosa pine defoliator, appeared to be the most suitable surrogate with many similarities in outbreak characteristics to what is known about the aroga moth (Gates 1964; Hall 1965; McBrien et al. 1983; Hsaio 1986; Speer et al. 2001; Speer and Jenson 2003). Given the lack of evidence on actual aroga moth impacts, we assumed insect outbreak resulted in thinning, rather than stand replacement (Tables 2 and 3). The only documented mortality of sagebrush from drought occurred during the 1930s (Ellison and Woolfolk 1937; Pechanec et al. 1937; Allred 1941), therefore we assumed droughts of similar magnitude were necessary to kill sagebrush at the stand scale (Table 2). In a cyclical disturbance such as an insect outbreak, an outbreak was either present or absent, based on the identified period between outbreaks (Table 3). When an outbreak occurred, the probability of impact was based on the assumed outbreak size, expressed as a percentage of the analysis area, during the buildup and crash phases and during the population peak. Since we assumed the buildup and crash phases of an insect outbreak affected the same proportion and each lasted 2 yr, we used the fourth root of the assumed area of impact to convert the total probability to an annual probability during those phases. We used the square root of the assumed area of impact during the population peak, with population peaks assumed to last up to 2 yr. Earlier testing during construction of the reference condition models, which were the basis of these models, indicated the initial probabilities of impact were too high, so we halved them (Table 2).

Freeze-kill, snow mold, and vole damage were restricted to those areas where deeper snowpacks were characteristic (Tables 2 and 3). We assumed that although vole outbreaks occur every 4 to 5 yr, sagebrush mortality happened only when an outbreak co-occurred with a severe winter. We assumed that such outbreaks were local in nature (Mueggler 1967; Frischknecht and Baker 1972; Parmenter et al. 1987).

Juniper Expansion. Since we could not simulate the actual expansion pattern of juniper, we assumed that all locations in the CM group were equally exposed to juniper seed sources (Chambers et al. 1999; Miller et al. 2005). Most junipers establish under sagebrush (Burkhardt and Tisdale 1976; Eddleman et al. 1994; Miller and Rose 1995; Chambers et al. 1999; Zophy 2006), but we found no studies that established a minimum threshold of shrub cover needed. Therefore, we assumed the J1 phase begins in the LSO and LSC community phases (Table 2). Studies show that once expansion begins, establishment rate is relatively constant (Burkhardt and Tisdale 1976; Chambers et al. 1999; Soulé et al. 2004), so we used the reported juniper tree ages in Johnson and Miller (2006) to determine the shift into subsequent phases.

Livestock Grazing. We assumed the predominant grazing system used was deferred rotation across four pastures, with one pasture rested each year during the main growing period. We considered potential livestock grazing impacts under four levels of utilization related to precipitation: low utilization in high production years, moderate utilization in average production years, high utilization in low production years, and very high utilization in very low production years (Table 2). We estimated the frequency of very high grazing episodes based on the frequency of a very dry winter and spring and multiplying that frequency by 0.75 to account for our assumed grazing system. We assumed livestock grazing under low and moderate utilization levels had no impact, but episodes of high and very high utilization resulted in damage to perennial herbaceous species and favored sagebrush (Holechek et al. 2004; Table 3). In both the CM and WD models, we assumed a high utilization episode accelerated movement toward a transition to a later community phase. A very high utilization episode in the WD group increased cheatgrass abundance (Julander 1945; Pechanec and Stewart 1949; Paulsen and Ares 1961; Billings 1994; Tausch et al. 1994a; Loeser et al. 2007), causing a transition to either an at-risk or threshold phase of the same type (i.e., MSO, LSO, or LSC) although preserving the age of the phase in the transition. A very high utilization episode in the CM group accelerated movement towards a transition to a later community phase at twice the rate of a high utilization episode alone, facilitating rapid movement into the community phases where juniper expansion becomes a possibility (Romme et al. 2009).

Postfire Seeding. In both state-and-transition models, seeding desirable species occurred after a wildfire to reduce or avoid dominance by invasive species (Robichard et al. 2000; Eisworth et al. 2009), but we assumed only a narrow window of opportunity existed to keep cheatgrass from attaining or retaining site dominance (Getz and Baker 2007; Keeley and McGinnis 2007). We chose not to limit postfire seeding on the basis of cost or total number of cells burned in order to explore what level of postfire seeding success was necessary to limit cheatgrass. We assumed the probability of success for seeding in high precipitation years was three times that of an average year, and only one-tenth of an average year during low precipitation years (Table 2). Successful postfire seeding resulted in a transition from the cheatgrass phase to the reference ES community phase in both models despite potential differences in herbaceous species composition.

Juniper Treatments. Prescribed burning, cutting, and cutting plus burning occurred only in the juniper phases of the CM group model. We assumed a collective 10% chance for any type of treatment in a juniper phase, resulting in a 3.3% chance for any specific treatment. Based on conversations with Bureau of Land Management fuels managers, we included prescribed burning in the J1 community phase, all juniper treatments in the J2 phase, and the combination of cutting and burning in the J3 and OG phases. We treated prescribed burning as a stand-replacing fire, shifting the site to the ES community phase. Cutting and prescribed burning had the same outcome as prescribed burning alone, whereas cutting alone shifted the site back to the J1 phase.

Analysis Methods

We constructed a state-and-transition model using VDDT for each sagebrush group to evaluate how juniper expansion, livestock grazing, postfire seeding, and juniper treatments affected the proportions of vegetation phases and states across a landscape. The WD group model contained 3 000 cells and the CM group model contained 2 250 cells in order to allow an equal number of cells in each phase at the beginning of each run and to manage processing time needed for each run. In the version of VDDT used, we could not specify cell size nor did cell size matter in how the program operated. In the model, events in each cell are modeled independently of each other in each simulation year, providing for heterogeneity in outcomes across the area. To evaluate potential impacts, we created a random set of disturbance probability multipliers in a Monte Carlo multiplier file to incorporate variability in both the occurrence and impact of fire, drought, insects, voles, and postfire seeding. For random disturbances, multipliers increased or decreased the probability that the disturbance would occur. For semicyclical disturbances, multipliers affected whether the disturbance would occur or not based on the maximum and minimum interval between occurrences and the minimum and maximum number of years for each occurrence (ESSA Technologies Ltd. 2007). We treated fire, freeze-kill, snow mold, livestock grazing, postfire seeding, juniper expansion, and vegetation treatments as random disturbances and drought, insect outbreaks, and voles as semicyclical disturbances. We ran 50 simulations for 500 yr each and saved the area in each community phase every 10 yr to a file for further analysis. We also extracted the model estimates of the average annual area affected by each disturbance type. The inverse of this percentage estimates the disturbance rotation, or the number of years it would take for the cumulative affected area to equal the analysis area (Romme et al. 2009). To allow ample time for the models to come into dynamic equilibrium, we analyzed model outputs for only the last 250 yr of the 500-yr simulation runs. We compared the estimated fire rotation (inverse of average annual percentage of area affected by fire) in each state-and-transition model to estimated current fire frequencies published in the literature as a form of model validation. Fire rotation is roughly equivalent to a point estimate of the average fire return interval (Romme et al. 2009)

Since we did not have actual data on the amount of area in each community phase in each sagebrush group and were unsure how much difference the initial proportions of each community phase at the beginning of each run would make to final proportions, we compared results between initializing each model with an equal proportion of all community phases and initializing each model with all cells initially assigned to the ES reference phase. We tested model sensitivity to the importance of each management action by first running each model with only the natural disturbances, then by adding each management action type singly (e.g., high utilization or postfire seeding) and in combinations (e.g., high utilization and postfire seeding). We compared the resulting abundance of each community phase and state to the full model, where all disturbance variables were included. Because we were unsure how good our probability estimates were, we varied the probability of high and very high utilization, postfire seeding, juniper expansion, and vegetation treatments between zero and two times the initial probability estimate in the full model and compared the differences in predicted phase abundance. To test our assumption of the impact of livestock grazing on the probability of mosaic fire, we varied the probability of mosaic fire between zero and two times the initial probability and compared both the proportions of phases and states and the estimated fire rotation to the full model. We used the same Monte Carlo sequences for all runs and followed the same procedures as in the initial model runs.

Because the proportions of most community phases were not normally distributed with equal variances, we tested for differences in the abundance of community phases and states between model variants using the Kruskal-Wallis one-way analysis of variance on ranks in SigmaPlot 11.0 (Systat Software 2008). When significant differences were found, we tested for differences between model variants using the Tukey test with a significance level of < 0.05. We examined the importance of 1) the initial proportions of the community phases used at the beginning of each run, 2) the effect of adding management actions to the natural disturbances, and 3) model sensitivity to variations in the probabilities for mosaic fire and management actions.

RESULTS

In both state-and-transition models, predicted output from model runs that began with an equal distribution of community phases and runs that began with the entire area initially assigned to the reference ES community phase were similar (no differences in pairwise comparisons for all community phases in both models). Subsequently, results were based on an equal proportion of all community phases at the beginning of each model run. We evaluated the sensitivity of phases and states to the different disturbance variables by removing, adding, or changing the probability of the disturbance and determining the amount of change in abundance of each phase or state. Very high utilization episodes, postfire seeding, juniper expansion, and juniper treatments produced significantly different proportions of vegetation phases, suggesting high community sensitivity to these types of events. High utilization episodes or livestock grazing in the absence of juniper expansion had little effect, suggesting lower sensitivity. Our simulations produced an estimated fire rotation of approximately 12 yr for the WD group due to dominance of cheatgrass, and 81 yr for the CM group due to the amount of juniper.

WD Sagebrush Group

Adding livestock grazing and postfire seeding to the natural disturbances and removing them from the full model predicted different mixes of community phases ($P < 0.001$ for all community phases). Pairwise comparisons highlighted certain patterns in the abundance of the community phases (Fig. 3A). The WD group was very sensitive to the addition or removal of very high utilization episodes and postfire seeding success. Removing just very high utilization episodes from the full model or adding just postfire seeding success to the natural disturbances resulted in the reference phases of state I occupying over 90% of the landscape (Fig. 3A). Adding just very high utilization episodes to the natural disturbances or removing just postfire seeding success from the full model resulted in cheatgrass-dominated phases (state II) occupying the entire landscape. In contrast, the WD group was relatively insensitive to the addition or removal of high utilization episodes. Removing just high utilization episodes from the full model resulted in state II occupying over 36% of the simulated landscape, which was similar to the full model with all disturbances. Adding just high utilization episodes to the natural disturbances resulted in state II occupying 71% of the simulated landscape, which was similar to the historical model with just natural disturbances. In both cases, reference phases comprised most of the proportion of the landscape that was in state I (Fig. 3A).

Varying the probability of high utilization episodes had little effect on the mix of community phases ($P = 0.494$ for reference LSO phase, 0.869 for state II MSO phase, 0.986 for cheatgrass phase, and < 0.001 for all other phases). Even in those phases in which differences tested as statistically significant, predicted differences were quite small (Fig. 4A) and likely not ecologically significant. In contrast, varying the probabilities of episodes of very high utilization and postfire seeding resulted in clear differences in the abundance of most community phases ($P < 0.001$ for all community phases; Figs. 4B and 4C). However, even doubling the probability of postfire seeding

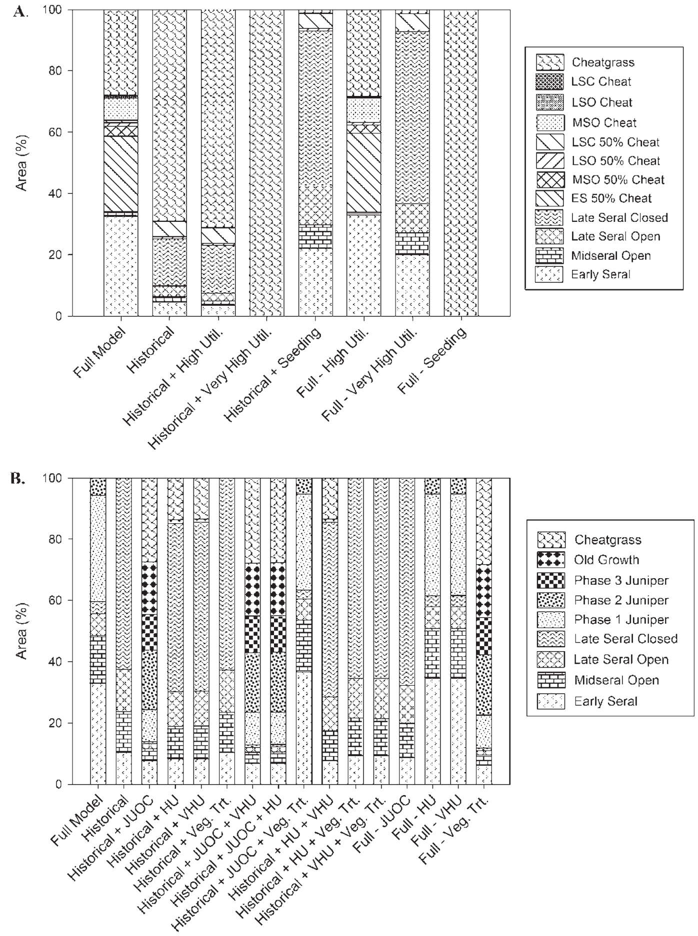

Figure 3. Mix of community phases that result when adding and removing various activities. **A,** The warm-dry sagebrush group includes both natural and management activities (full model), natural disturbances alone (nistorical), and the addition or removal of high utilization livestock grazing episodes (high util.), very high livestock grazing episodes (very high util.) and postfire seeding (seeding). **B,** The cool-moist sagebrush group includes both the full and historical model variants, and the addition or removal of high utilization grazing episodes (HU), very high utilization grazing episodes (VHU), juniper expansion (JUOC), and vegetation treatments (veg. trt.) that includes juniper treatments and postfire seeding. Note that when juniper expansion is not included in the model, veg. trt. refers to postfire seeding only.

success still resulted in community phases with a large proportion of cheatgrass, which was more abundant than in the reference phases and with very little of the reference MSO, LSO, and LSC community phases. Less than 10% of the WD group supported the reference LSO and LSC community phases except when the probability of a very high utilization episode was less than 3% (0.5 very high utilization in Fig. 4B). The reference phases occupied over 90% of the WD group with very high utilization episodes absent, decreasing to only 24% as the probability of very high utilization episodes increased to twice the initial probability in the full model. Varying the probability of mosaic fire also produced minimal differences in the abundance of community phases ($P = 0.051$ for state I reference MSO phase, 0.253 for state I reference LSO phase, 0.002 for state I reference LSC phase, 0.857 for state II MSO

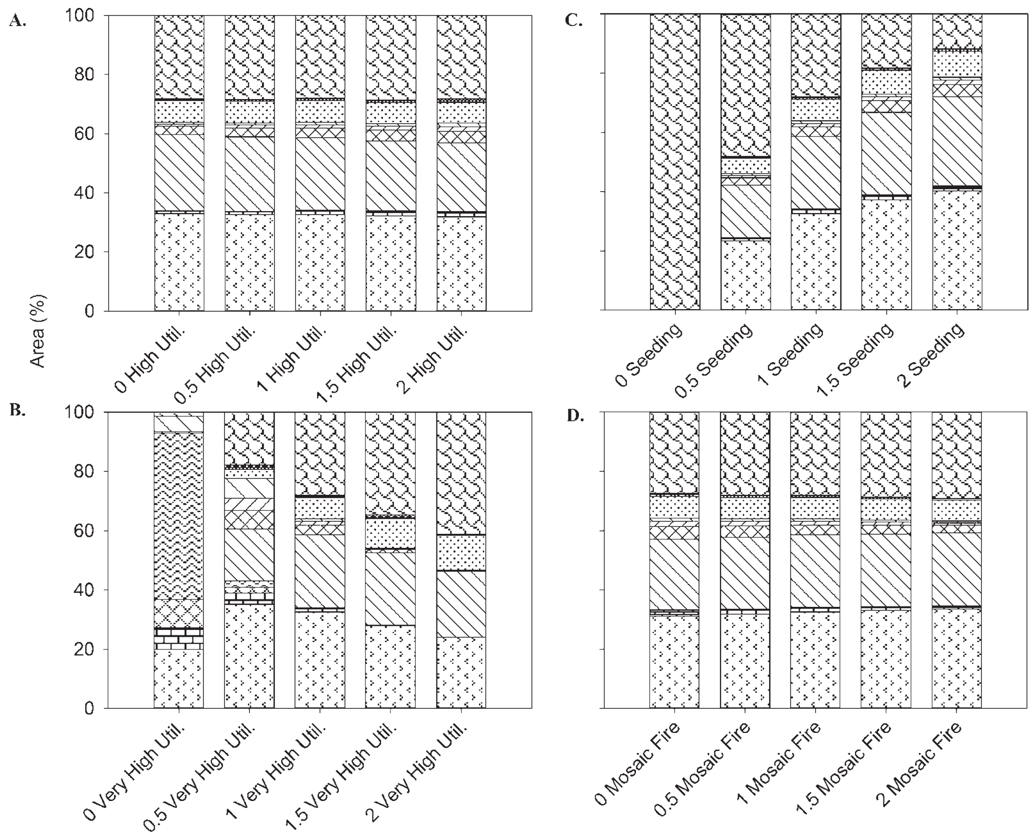

Figure 4. Changes in the mix of community phases resulting from applying different multipliers to the probability of different events in the warm-dry sagebrush model. **A,** Changing the probability of high utilization livestock grazing episodes resulted in very small changes in the mix. **B,** Changing the probability of very high utilization livestock grazing episodes had a pronounced effect. **C,** Changing the probability of postfire seeding success altered the mix of community phases on a similar magnitude as in **B**. **D**, Changing the probability of mosaic fire had only a minor effect on the mix of community phases. See Figure 3A for the legend.

phase, 0.151 for state II LSO phase, 0.015 for state II LSC phase, and < 0.001 for all other phases; Fig. 4D). As with high utilization episodes, even when statistical tests indicated significant differences, actual differences were very small. Varying the probability of mosaic fire had little or no effect on frequency of other disturbances or fire rotation length.

CM Sagebrush Group

Adding juniper expansion, livestock grazing, and vegetation treatments, including postfire seeding, to the natural disturbances and removing them from the full model predicted different mixes of the community phases ($P < 0.001$ for all community phases). As with the WD group, pairwise comparisons highlighted certain patterns in abundance. Four groupings of predicted outcomes resulted (Fig. 3B): 1) the full model plus three scenarios that did not include livestock grazing, 2) those without additional juniper expansion beyond the initial mix of phases, 3) those without vegetation treatments (juniper treatments and postfire seeding), and 4) those lacking both additional juniper expansion and vegetation treatments. The exception was the scenario that included only the historical disturbances, which fell into the second grouping. In all groupings, the addition or removal of high or very high utilization episodes had no apparent effect on the mix of community phases.

In outcome grouping 1, the reference sagebrush phases were dominant, but the early juniper phases and cheatgrass were common. The ES phase was the most common reference phase. When additional juniper expansion was excluded (outcome grouping 2), vegetation treatments (juniper treatments and postfire seeding) eventually eliminated the juniper and cheatgrass phases initially present. When we excluded vegetation treatments (outcome grouping 3), juniper and cheatgrass phases were most abundant and the reference sagebrush phases were only a minor proportion of the cells. The three scenarios that lacked both continued juniper expansion and vegetation treatments (outcome grouping 4) resulted in dominance of the reference sagebrush phases, only minor presence of the early juniper phases, and moderate cheatgrass. In these scenarios, fire was probably responsible for nearly eliminating juniper, but cheatgrass persisted in the absence of postfire seeding.

Altering the probability of juniper expansion also altered the mix of community phases, although pairwise comparisons indicated little or no change occurred in the abundance of the J3, OG, and cheatgrass phases ($P < 0.001$ in all phases except $P = 0.026$ in the cheatgrass phase; Fig. 5A). As the probability of juniper expansion increased, the abundance of the LSC community phase decreased and the abundance of the ES and J1 phases increased by the greatest amount. Altering the probability of either high utilization or very high utilization episodes did not alter the abundance of the LSO, J3, OG, and

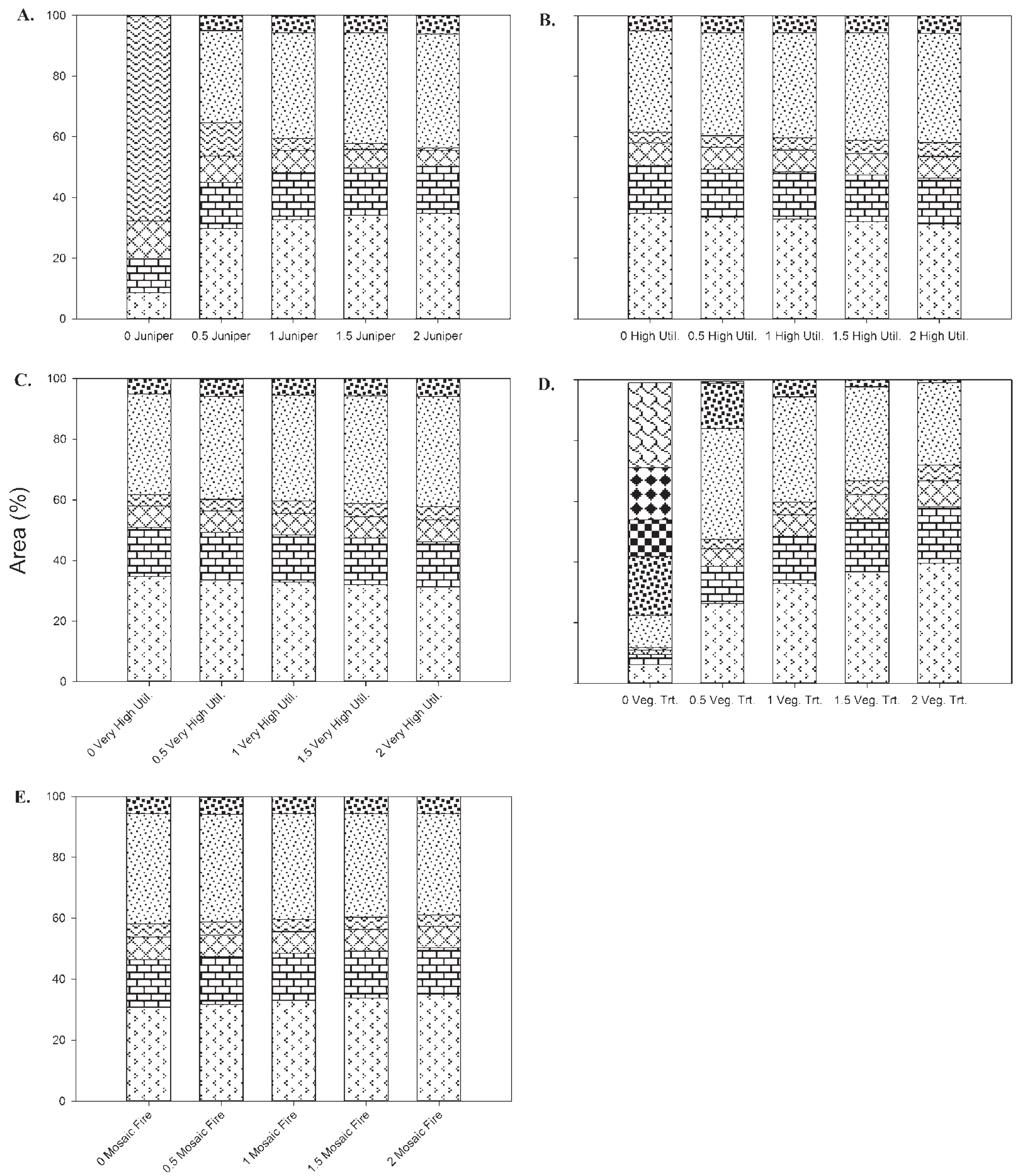

Figure 5. Changes in the mix of community phases resulting from applying different multipliers to the probability of different events in the cool-moist sagebrush model. **A**, Changing the probability of juniper encroachment produced a relatively large effect on the mix of community phases. **B,** Changing the probability of high utilization livestock grazing episodes had only minor effects, as did **C**, changing the probability of very high utilization livestock grazing episodes. **D,** Changing the probability of vegetation treatments, primarily the probability of juniper treatment altered the mix of community phases on a similar magnitude as in **B**. **E,** Changing the probability of mosaic fire had only a minor effect on the mix of community phases. See Figure 3B for the legend.

cheatgrass phases (for high utilization episodes $P=0.518$ for the LSO phase, 0.038 for the J3 phase, 0.041 for the OG phase, 0.199 for the cheatgrass phase; for very high utilization episodes $P=0.042$ for the LSO phase, 0.631 for the J3 phase, 0.026 for the OG phase, and 0.674 for the cheatgrass phase) and resulted in small changes in the other phases ($P < 0.001$ for both disturbance types). Even though the Kruskal-Wallis test indicated some phases did significantly differ, the pairwise comparisons found no differences. Even those changes that were statistically significant were minor and likely were ecologically insignificant (Figs. 5B and 5C). Altering the probability of vegetation treatments had an effect on the mix of community phases on a similar scale as altering the probability of juniper expansion, but in the opposite direction ($P < 0.001$ in all community phases; Fig. 5D). The cheatgrass phase became a significant phase in the absence of postfire seeding. However, when postfire seeding had just half of the success rate specified by the full model, the cheatgrass phase became only a minor component. As with livestock grazing, varying the probability of mosaic fire altered the mix of community phases ($P=0.14$ for the MSO phase, 0.059 for the J3 phase, 0.039 for the OG phase, 0.218 for the cheatgrass phase and < 0.001 for all other phases), but the differences were small and likely not ecologically significant (Fig. 5E). However, altering the probability of mosaic fire did have a more pronounced effect on fire rotation, ranging from 182 yr in the absence of mosaic fire to 50 yr when the probability was doubled (results not shown).

DISCUSSION

We used the literature as a basis for estimating the probabilities of each disturbance type and, in the cases of the cyclical disturbances, the probability of an impact as well. However, a thorough review of relevant literature revealed that work related to disturbance in sagebrush ecosystems is limited, rarely speaking directly to the probability of an event occurring or the magnitude/scale of its impact, and rarely linking the probability of occurrence to climate. In addition, actual probabilities of a given event and the magnitude of its impact vary in space with landscape heterogeneity, such as topography, elevation, and soil characteristics.

Despite these limitations, state-and-transition modeling frameworks such as VDDT allow users to explore the effects of multiple disturbances acting at the same time and help identify research needs. Sensitivity testing also allowed us to understand the degree to which addition, removal, or changes in the probability of a disturbance event or its outcome could alter the distribution of community phases and states. Although our estimates were often based on very limited literature or simply expert opinion, varying probabilities above and below the initial estimates allowed us to determine both the degree of sensitivity and potential magnitude of error if the estimates were incorrect.

The same basic model structure using data from a different climate division or major land resource area could produce outcomes that differ from those for the Malheur High Plateau or alter the relative influence or importance of a disturbance type. Similarly, different types of climate events could be drivers in a different climate division. Nonetheless, we believe the approach outlined in this effort can serve as a basis for developing event probabilities in other major land resource areas and their associated climate divisions. Long-term means and medians can be used as threshold values to explore how trajectories may change between a warmer, drier period and a cooler, moister one or to examine the effects of these periods in sequence. Model probabilities can be based on climate data summarized at different scales, (climate division, single station, or small group of stations), from different sources (instrument records or extrapolated climate data), or predicted climate data from global climate models. State-and-transition modeling frameworks such as VDDT allow users to evaluate vegetation trajectories under different management, natural disturbance, and climate scenarios, although better results are likely where the initial proportion of community phases is known, transitions are well-defined, and the effects of drivers are known.

These results, in combination with previous work (Evers 2010), indicate that juniper encroachment; vegetation treatment, including postfire seeding success; episodes of very high utilization by livestock; fire; and insect outbreaks are particularly important drivers of sagebrush community dynamics on the Malheur High Plateau. The frequency of mosaic fire appears to be subtly important in the CM group, at least with respect to fire rotation. Previous analysis indicated vole outbreaks, snow mold, and freeze-kill were at least moderately important drivers in the CM group and drought severe enough to kill sagebrush is moderately important in the WD group (Evers 2010).

Our model simulations suggest that certain combinations of disturbances are also important, even when some disturbances are not particularly influential on their own. Specifically, episodes of high or very high utilization essentially combine livestock grazing with drought. Our results indicate that these episodes increase the amount of the WD group pushed into functioning-at-risk or alternative states, or increase the speed at which these transitions occur. Other studies reported increased shrub cover and annual species and reduced perennial grass cover, numbers, or productivity under very intensive grazing (Griffiths 1902; Pickford 1932; Shinn 1977; Van Poollen and Lacey 1979; Brotherson and Brotherson 1981), particularly when coupled with drought (Craddock and Forsling 1938; Julander 1945; Loeser et al. 2007; Reisner 2010). Similarly, in the CM group, episodes of high and very high utilization apparently provided greater opportunities for juniper expansion to initiate, by accelerating movement into the later sagebrush community phases. This result is consistent with several studies and reviews that implicate past grazing practices in rapid juniper expansion (Burkhardt and Tisdale 1976; Miller and Wigand 1994; Chambers et al. 1999; Soulé et al. 2003; Romme et al. 2009).

Our models indicated that passive management, such as removal of livestock grazing, would not restore sagebrush communities that were cheatgrass-dominated or juniper-encroached. Postfire seeding was critical for limiting the abundance of cheatgrass-dominated phases in the WD group, but postfire seeding alone was not sufficient to restore reference conditions. Instead, our model indicated that either elimination or reduction in the frequency of very high utilization episodes in addition to relatively high postfire seeding success was necessary. Evans and Young (1978) reported high seeding failure rates where grazing utilization was very high shortly after seeding. In the absence of active restoration efforts cheatgrass can retain site dominance where the native perennial grasses have been lost from the site and seedbank (Young and Evans 1973; Billings 1994; Bollinger and Perryman 2008). Frequent fire, along with the loss of vesicular arbuscular mycorrhizae and high nitrogen availability that often follows a fire and grazing pressure on remaining perennial grasses, favor continued dominance of cheatgrass (Robertson and Pearse 1945; Pyke 1986, 1987; McLendon and Redente 1994; Knapp 1996).

In the absence of juniper treatment, our CM model predicted a landscape dominated by juniper woodland. There are no known natural factors that would limit or halt juniper expansion within the CM group under the current climate (Burkhardt and Tisdale 1969, 1976; Miller and Rose 1995; Knapp and Soulé 1998; Chambers et al. 1999; Soulé et al. 2004). Our model indicated that annually treating 10% of the juniper phases retained a higher proportion of the landscape in state I, although at-risk phases remained abundant. This result was, in part, due to the lack of treatment options for the J1 phase that removed juniper seedlings and saplings but retained enough of the larger sagebrush to increase the proportion of the later reference phases. However, we could not model spatially explicit or easily incorporate legacy aspects of vegetation treatments on the abundance of the juniper community phases. Return to tree dominance can be relatively rapid in small-scale treatments, treatments that leave the juniper seedbank more or less intact, and treatments that leave either seedlings or surviving mature trees (Chambers et al. 1999; Bates et al. 2005).

The modeled fire rotation for the WD Group was similar to other published reports of fire frequencies in the dry sagebrush zone where cheatgrass-dominated areas are widespread (Whisenant 1990; Knapp 1996; Pellant 1996; Knick et al. 2003; Connelly et al. 2004; Bradford and Laurenroth 2006; Reid et al. 2008). However, the fire rotation for the CM group was a bit shorter than current fire frequency estimations based on tree-ring studies at the conifer–sagebrush ecotone (Miller and Rose 1999; Miller et al. 2001; Heyerdahl et al. 2006; Miller and Heyerdahl 2008). Baker (2006) estimated a fire rotation of 70 to 200 yr based on the growth rates of mountain sagebrush and an assumption that late seral community phases dominated, although this estimate does not account for the effects of fine fuel reduction via livestock grazing on fire occurrence and spread. When we reduced the probability of mosaic fire further as part of the sensitivity analysis, the fire rotation for the WD group was unchanged while the fire rotation for the CM group lengthened to 112 yr, more consistent with the frequencies reported in the literature for current conditions. In both groups, further reductions in the probability of mosaic fire had little effect on the abundance of the different community phases and states. Although grazing can influence fire spread, size, and burn pattern (Davies et al. 2010), the actual influence of current grazing practices on the probability of fire is not well known.

Estimating postfire seeding success rates also proved difficult and our models may not adequately represent the influence of continued cheatgrass dominance on seeding success rates. Both Eiswerth et al. (2009) and Boyd and Davies (2010) suggested that postfire seeding success was higher immediately after fire, and lower following subsequent fires in the cheatgrass state. Cheatgrass alters soil physical and chemical properties such that the longer cheatgrass occupies a site, the lower the probability of postfire seeding success (Norton et al. 2004). Yet we lacked the information needed to estimate how the probability of postfire seeding success should change over time. Had we been able to adjust postfire seeding success rate based on the number of past fires in the cheatgrass phase, our modeled outcomes may have been different.

This work was an initial exploration of the use of a state-and-transition modeling framework to quantify how natural and human-related disturbances might affect the trajectory of sagebrush ecosystems under the current climate. VDDT includes more adjustment factors than the ones we elected to use. For example, users can specify a sequence of disturbance events, a sequence of severities for a particular event type, the minimum and maximum number of cells that can be affected by a particular disturbance type in the simulation year, and landscape feedbacks that increase the susceptibility to a given disturbance type. Because so little is known about the dynamics of most natural disturbances we used in our models, we did not include other utilities available in VDDT. Some of these additional functionalities would have been more useful to us if we had some measure of recent past and current distributions of the phases included in each model. That information would have allowed us to further validate our assumptions by including a known sequence of events and year types to compare the predicted distribution of phases with the known distribution. Nonetheless, future work could include some of these additional functionalities, such as how the timing of a particular disturbance type or a particular sequence of disturbance events might affect outcomes.

MANAGEMENT IMPLICATIONS

Our models provided a method for exploring how the combination of management actions and natural disturbances might affect the trajectory of vegetation, particularly when few specifics are known about the current condition. In addition, users can assign management values such as forage production, habitat suitability, and fuel model to each community phase and evaluate how these values, such as habitat needs for sagebrush-obligate species (Holmes and Miller 2010), available forage, and fire risks could change over time under different management strategies or changing climate. Our process for developing many of the probabilities using climate data provides a base model that can be transported to a different major land resource area or scaled downward to a specific location by using climate data for the area of interest. In addition, use of ecological sites as a basis for designating larger groupings of plant communities allows users to examine large landscapes with a manageable number of community phases and states.

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