A Process-Based Application of State-and-Transition Models: A Case Study of Western Juniper (*Juniperus occidentalis*) Encroachment

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Abstract

A threshold represents a point in space and time at which primary ecological processes degrade beyond the ability to self-repair. In ecosystems with juniper (*Juniperus* L. spp.) encroachment, ecological processes (i.e., infiltration) are impaired as intercanopy plant structure degrades during woodland expansion. The purpose of this research is to characterize influences of increasing juniper on vegetation structure and hydrologic processes in mountain big sagebrush–western juniper (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rydb.] Beetle–*Juniperus occidentalis* Hook.) communities and to identify and predict states and thresholds. Intercanopy plant cover and infiltration rates were sampled in relation to juniper canopy cover. Study plots, arranged in a randomized complete-block design, represented low shrub–high juniper, moderate shrub–moderate juniper, and high shrub–low juniper percentage of canopy cover levels at four primary aspects. In field plots, percentage of plant cover, bare ground, and steady-state infiltration rates were measured. In the laboratory, juniper canopy cover and topographic position were calculated for the same area using high-resolution aerial imagery and digital elevation data. Parametric and multivariate analyses differentiated vegetation states and associated abiotic processes. Hierarchical agglomerative cluster analysis identified significant changes in infiltration rate and plant structure from which threshold occurrence was predicted. Infiltration rates and percentage of bare ground were strongly correlated ($r^2 = 0.94$). Bare ground was highest in low shrub–high juniper cover plots compared to both moderate and high shrub–low juniper cover levels on south-, east-, and west-facing sites. Multivariate tests indicated a distinct shift in plant structure and infiltration rates from moderate to low shrub–high juniper cover, suggesting a transition across an abiotic threshold. On north-facing slopes, bare ground remained low, irrespective of juniper cover. Land managers can use this approach to anticipate and identify thresholds at various landscape positions.

Resumen

Un umbral representa un punto en el espacio y el tiempo en que los procesos ecológicos primarios se degradan más allá de la capacidad de auto-reparación. En los ecosistemas invadidos de enebro (*Juniperus* L. spp.), los procesos ecológicos (es decir, la infiltración) están afectados como la estructura del dosel intermedio de la planta se degrada durante la expansión del bosque. El propósito de esta investigación es caracterizar las influencias del incremento de enebro en la estructura de la vegetación y los procesos hidrológicos en las comunidades de artemisia–enebro occidental (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rydb.] Beetle–*Juniperus occidentalis* Hook.) y para identificar y predecir los estados y los umbrales. La cobertura del dosel intermedio y las tasas de infiltración fueron muestreadas en relación a la cobertura del dosel del enebro. Las parcelas de estudio, organizadas en un diseño completo de bloques al azar, representan el arbusto alto, moderado y bajo–el bajo porcentaje de la cobertura del dosel del enebro en cuatro aspectos principales. El porcentaje de la cubierta vegetal, el suelo desnudo, y las tasas de infiltración en estado de equilibrio se midieron en las parcelas del campo. En el laboratorio, la cubierta de dosel del enebro y la posición topográfica se calcularon para la misma zona usando imágenes aéreas de alta resolución y de datos digitales de elevación. Los análisis paramétricos y multivariados diferenciaron los estados en la vegetación y los procesos abióticos asociados. El análisis jerárquico aglomerativo de grupos identificó cambios significativos en las tasas de infiltración y en la estructura de la planta, a partir de los cuales se predijo la aparición del umbral. La tasas de infiltración y el por ciento de suelo desnudo estuvieron fuertemente correlacionados ($r^2 = 0{,}94$). El suelo desnudo fue más alto en el arbusto bajo–las parcelas de enebro de alta cobertura en comparación con los dos niveles de cobertura moderado y bajo los sitios vistos en el sur, este y oeste. Las pruebas de multivariables indicaron un cambio distinto en la estructura de la planta y en las tasas de infiltración de arbusto moderado a bajo- alta cobertura de enebro, lo que sugiere una transición a través de un umbral abiótico. En las pendientes del norte, el suelo desnudo permaneció independientemente bajo a la cobertura de enebro. Los dueños de tierras pueden utilizar este enfoque para anticipar y determinar los umbrales en las distintas posiciones del paisaje.

Key Words: landscape ecology, phase-shift, state-and-transition, succession, threshold, transition, western juniper

INTRODUCTION

State-and-transition models describe multisuccessional pathways, multiple steady-states, and thresholds of change to explain and predict plant community change (Westoby et al. 1989). Significant contributions have been made toward the

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development of state-and-transition models for rangeland ecosystems (Archer 1989; Davenport et al. 1998; Whisenant 1999; Stringham et al. 2001; Herrick et al. 2002; Bestelmeyer et al. 2003). Stringham et al. (2003) define a *state* as a climate–soil–vegetation domain that encompasses wide variation in species composition, maintained by natural disturbance regimes. Irreversible transitions can occur after one or more of the primary ecological processes (hydrologic, nutrient, and energy cycles) have been altered to the extent that the current state is incapable of self-repair even with the removal of an ecological disturbance or stress. State-and-transition models propose transitions among various community states that are driven or impeded by abiotic and biotic processes. Probabilities of these transitions depend on the relative influence of ecological processes and their supporting structures that maintain the feedback system in a way that either preserves the state or places it on a trajectory toward a new state. Trajectories toward a new state are highly dependent on modifications to structure, process, and resource availability that support an alternative state more than maintenance of the current state. Plant communities that have degraded structure and processes can transition toward a new ecological state that supports a different assemblage of plant species and plant community dynamics than the original community.

Over the past two decades, research has contributed significantly to the development of state-and-transition models in woodland-dominated ecosystems. Archer (1989) developed threshold concepts with woodland establishment in mesquite (*Prosopis* spp.)-dominated ecosystems. In the Archer (1989) model, changes in grazing pressure, fire frequency, and rate of woodland expansion resulted in the irreversible shift of a herbaceous grassland into a shrub-driven domain. The threshold concept for grasslands was further expanded to include both degraded biotic and abiotic structure and processes that limit self-repair with increasing woodland expansion (Milton et al. 1994, Whisenant 1999). With declining vegetation, soil surfaces become exposed to raindrop impacts that form surface crusts and limit infiltration rates resulting in a positive feedback of accelerated degradation (Whisenant 1999).

Juniper (*Juniperus* spp.) and pinyon (*Pinus* spp.) woodlands have expanded throughout the western United States, occupying more than 74 million acres (West 1999). Fuhlendorf et al. (1996) characterized the ecological response of grassland invasion by Ashe's juniper (*Juniperus ashei* J. Buchholz) in Texas. They found that changes in vegetation structure associated with increasing juniper density and cover provided evidence for multiple states and thresholds. Decreased herbaceous biomass with increasing juniper canopy cover reduces cool-season fire potential and frequency and constitutes the crossing of an abiotic threshold. Miller et al. (2006) described thresholds in a western juniper–dominated sagebrush steppe ecosystem stating that multiple biotic, abiotic, and economic thresholds occur with increasing juniper dominance, including the change in fire potential with decreasing fuel loads, loss of native seed pools, exotic species invasion, topsoil loss, and impaired hydrology. However, they affirm that the point in time when these thresholds are crossed has not been identified. Pierson et al. (2007) report elevated sheet erosion and runoff from hill slopes dominated with western juniper because of decreased herbaceous and shrub cover. This, in turn, can lead to a site's inability to sustain or repair degraded hydrologic processes.

The objectives of this study are to identify ecological states and predict thresholds in relationship to both biotic and abiotic structure and process. Structural components include plant density and canopy cover, and the ecological process measured is terminal infiltration rate. Parametric and multivariate analyses are used to describe vegetation states and to determine differences in infiltration rates associated with these vegetation states. Biotic and abiotic threshold occurrence is predicted from these data using hierarchical agglomerative cluster analysis. A process-based state-and-transition model for juniper woodlands is developed from these analyses to describe states and threshold occurrence.

METHODS

Study Site Description

This study was conducted in a western juniper–encroached watershed (approximately 200 ha) located in the Steens Mountain of southeast Oregon (Universal Transverse Mercator, 357 500 E, 4 700 000 N [North American Datum of 1983]; lat 42°26′28″N, long 118°43′57″W). The site is in the High Desert Ecological Province, along the northern extent of the Great Basin Desert (Anderson 1998). Watershed elevation ranges from 1 707 m to 2 073 m, determined from the US Geological Survey (USGS) digital elevation model (DEM) and from 7.5-min topographic maps. Average annual precipitation is approximately 32 cm. Soils are characterized as loamy–skeletal, mixed, frigid lithic Argixerolls, belonging to the Pernty–Rock outcrop complex type, and mixed, superactive, frigid Pachic Haploxerolls, belonging to the Westbutte–Lambring rock outcrop complex type. These soils are formed from colluvium and residuum deposits, weathered from basalt and rhyolite parent material. Soils consist of gravely to cobbly loam or silt loams from the surface to approximately 20-cm to 30-cm depths. These soils typically contain between 20% and 70% rock (stones and cobbles), with the highest content usually located just above bedrock (Natural Resource Conservation Service [NRCS] 2000).

The watershed study area is divided into two ecological sites: South Slopes 12–16 PZ (30.5–40.6-cm precipitation zone; 023XY302OR) and North Slopes 12–16 PZ (023XY310OR), both occurring within the D-23 Major Land Resource Area of the United States (NRCS 2000). Historic vegetation composition on South Slopes was approximately 70% grasses (30–50% bluebunch wheatgrass [*Pseudoroegneria spicata* {Pursh} A. Löve]), 10% forbs, and 20% shrubs (5–10% *Artemisia tridentata* var. *vaseyana* and 2–10% antelope bitterbrush [*Purshia tridentata* {Pursh} DC.]). The North Slopes ecological site occurs on northerly exposures of mountain sideslopes with historic species composition of 10–15% *Artemisia tridentata* var. *vaseyana*, 2–10% *Purshia tridentata*, 2–5% snowberry (*Symphoricarpos rotundifolius* A. Gray), and 40–50% Idaho fescue (*Festuca idahoensis* Elmer). Neither ecological site description (ESD) reported western juniper in the historic plant community. Plant species that are reported for each ESD consisted of the same species that were recorded from field samples collected within the reference community during 2001–2003 (NRCS 2000).

Considering vegetation species listed in the ESDs and from field observations, characteristic plant communities consist of bluebunch wheatgrass, Idaho fescue, mountain big sagebrush, rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G. L. Nesom & Baird), and antelope bitterbrush. Severe overgrazing at the end of the 19th century had a significant effect on many range species throughout the region, including Idaho fescue stands (Griffiths 1902). Although grazing has been significantly less during the 20th century (moderate to light), long-term drought, herbivory, and time have prevented Idaho fescue stands from full recovery.

Study Design and Field Measurement Description

Miller et al. (2006) separate woodland succession into three transitional phases: *phase I*, trees are present, but shrubs and herbaceous species dominate; *phase II*, trees are codominant with shrubs and herbs; and *phase III*, trees are dominant and determine the maximum rates for various fluxes. In this study, a similar approach was used to stratify juniper canopy cover into three classes: *low juniper–high shrub* (LJHS) canopy cover, where shrubs and herbaceous species dominate and drive ecological processes; *moderate juniper–shrub* (MJS) canopy cover, where shrubs and herbs codominate with trees; and *high juniper–low shrub* (HJLS) canopy cover, where trees dominate and regulate ecological processes while shrubs and herbs are significantly reduced from the intercanopy area. HJLS sites exhibited a high intercanopy percentage of bare ground, discernable in the color aerial imagery, whereas MJS sites maintained visible intercanopy shrub cover.

The three cover classes were delineated using georectified, 1:5 000-scale, color, aerial photographs with ERDAS Imagine Geographic Information System software (Leica Geosystems, Gall, Switzerland). The aerial photographs were taken in September 2001 by Valley Air Photos (Caldwell, ID) and delivered as contact prints. These images were then scanned at 1 200 dots per inch and saved in tagged image file format (TIFF). Before classification, a convolution filter (7×7 matrix size) was applied to the images to reduce pixel variation by class type, increasing classification accuracy. Each vegetation class was mapped using a maximum-likelihood supervised classification procedure. A minimum of 50 training areas were used for each class. Training areas were selected primarily from a visual interpretation from the aerial photographs but also from field-based observations. This resulted in an objective-based approach for delineating different class boundaries. Each cover class category was then divided into four aspects (north, south, east, and west) using a USGS 10-m DEM and ERDAS Imagine. Because similar areas to the training sites were selected as potential locations for plots and checked on the ground during the infiltration measurements, a formal accuracy assessment was not necessary.

Within each juniper–shrub and aspect category, study plots were arranged in a randomized complete-block experimental design with four replications per category. This resulted in 44 random 10×10 m plots. After plots had been selected, juniper canopy cover was measured from the aerial photographs around the center of each plot within a 400-m^2 window (Table 1). LJHS areas represent the potential native plant community (matrix) for this watershed, exhibiting comparable vegetation communities described within the ecological site description for both North Slopes 12–16 PZ and South Slopes 12–16 PZ. Because north-facing slopes lacked HJLS sites, this category was not included in the analysis.

Table 1. Average percentage of shrub cover and juniper canopy cover by aspect (± SE), measured from permanent plots for State 1 (low juniper–high shrub), State 2 (middle juniper–shrub), and State 3 (high juniper–low shrub).

Cover	State 1 (%)	State 2 (%)	State 3 (%)
Shrub cover			
East	30.6 ± 3.0	13.2 ± 1.6	2.1 ± 0.8
North	53.7 ± 6.4	28.4 ± 5.5	—
South	35.8 ± 5.7	18.4 ± 4.6	3.0 ± 1.3
West	41.1 ± 2.1	12.7 ± 3.7	2.4 ± 0.6
Juniper cover			
East	0.3 ± 0.3	13.0 ± 3.6	31.6 ± 4.3
North	0.0 ± 0.0	13.3 ± 2.3	—
South	0.8 ± 0.5	14.3 ± 2.4	27.0 ± 2.9
West	1.2 ± 1.1	15.8 ± 3.1	22.7 ± 3.5

Within each plot, perennial plant density (by species) was measured in a 1-m^2 quadrat along six 10-m–long, random transect lines. Sixty quadrats were measured per plot for a total of 240 quadrats (four replications) for each aspect. Intercanopy herbaceous plant canopy cover was measured along five transects within each plot (five of the six transects used for sampling plant density) using the point-intercept method (Elzinga et al. 1998). The first surface feature (i.e., plant species, rock, litter, bare ground, or dead shrub) encountered by the tip of the pin as it was released vertically toward the soil surface was recorded. For each sample, the pin was released a minimum of 50 cm above ground level to reduce error or bias that may occur at shorter distances from the object being sampled. Samples were taken at 15-cm intervals along each transect for a total of 68 samples per line. Percentage of cover was calculated by dividing the number of hits for each feature by the total number of hits per transect line, multiplied by 100. Standard error for each plot was calculated from the standard error value for each transect ($N = 5$).

Terminal infiltration was measured at random locations in the study site using a small-plot rainfall simulator. Simulated rainfall was applied at a 10-cm · h^{-1} rate within a 0.5-m^2 area. Raindrop size was approximately 2.5 mm in diameter, a size comparable to an average natural raindrop (Spaeth et al. 1995). Terminal velocity was approximately 7.0–8.0 m · s^{-1}. Water was sprayed from a nozzle suspended 1.93 m above the soil surface. Terminal rainfall was determined by applying rainfall at a rate necessary to produce runoff, which was considered to be at terminal infiltration rate when the runoff from the plot was consistent across the last couple of time-measurement intervals. Runoff and sediment were collected for each sample interval. Samples were weighed, dried, and then reweighed to provide a measure of total sediment weight by water volume. At each simulation location, the percentage of shrub cover, herbaceous plant cover, and bare ground were measured. Terminal infiltration was compared with the percentage of bare ground to assess the relationship between a surface attribute and an ecological process.

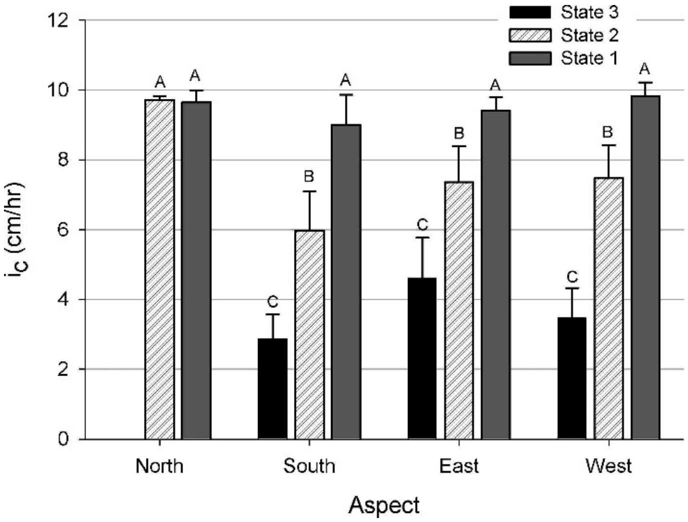

Figure 1. Comparison of infiltration rates between shrub–juniper states and aspect levels. Numerals represent the three ecological states: 1 indicates low juniper–high shrub; 2, middle juniper–shrub; and 3, high juniper–low shrub. Significance was determined from analysis of variance and mean separation using Fisher's Protected LSD test. Different letters above the bars indicate significant difference at $\alpha = 0.05$.

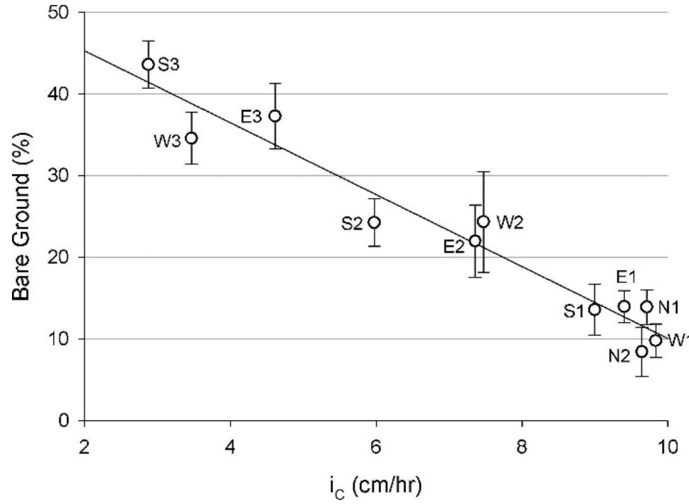

Figure 2. Relationship between average total percentage of bare ground ($\pm$ SE) and average infiltration rate across all shrub–juniper categories and aspects. $Y = -0.2145x + 12.002$, $R^2 = 0.94$. N indicates north; S, south; E, east; and W, west.

Data Analysis

For particular comparisons, the average and variance of shrub, bare ground, and juniper canopy cover were calculated for each plot. Multiple regression was used to assess the relationship between terminal infiltration, percentage of bare ground, and litter production. Differences in percentage of shrub cover, infiltration rates, and percentages of bare ground by juniper–shrub and aspect category were determined using analysis of variance. For significant main effects, post hoc tests of differences between aspect and juniper–shrub level were tested using Fisher's Protected LSD test ($\alpha = 0.05$).

Aspect-level values were grouped into ecologically relevant classes using hierarchical cluster analysis in PC-Ord (McCune and Grace 2002). Data included in the cluster analyses were percentage of shrub cover, juniper cover, and bare ground. Sørensen (Bray Curtis) distance measures and Ward's group linkage methods were used in the analysis. Sørensen distance, measured as a percentage of dissimilarity (PD), is a proportion coefficient that is used to calculate the new intergroup dissimilarities. Ward's method is based on minimizing increases in the error sum of squares. Percentage of information remaining measures the information lost during each step (McCune and Mefford 1999). The formation of distinct groups with high PD indicates significant shifts in ecological structure and, more important, in process. These values can then be used to isolate states and to make predictions of thresholds based on distinct shifts in shrub, juniper, and bare-ground cover.

RESULTS

Ecological processes (measured as steady-state infiltration rates) were sustained in LJHS plots compared with both MJS and HJLS plots on south-, east-, and west-facing slopes (Fig. 1). Similarly, infiltration on MJS plots was greater than on HJLS sites on the same aspects. There was no difference in steady-state infiltration between MJS and LJHS plots on north-facing sites. There was no difference in infiltration rates on LJHS plots among aspect. A linear relationship was observed between infiltration rates and total litter by weight (second-order polynomial $R^2 = 0.86$, $y = 3.21x^2 - 14.5x + 24.6$). LJHS plots had greater litter cover than MJS plots at all aspects, and HJLS plots had the lowest percentage of litter cover. Conversely, bare ground in the interspace increased with increasing juniper canopy cover. On south-, east-, and west-facing sites, percentage of bare ground was highest in HJLS plots and lowest in LJHS plots. No differences were observed in the percentage of bare ground on north-facing sites between LJHS and MJS plots. A strong, negative linear relationship was observed between percentage of bare ground and infiltration ($R^2 = 0.94$, $P < 0.0001$, $y = -0.2145x + 12.0$), suggesting that reliable predictions of intercanopy infiltration can be made with the measure of percentage of bare ground (Fig. 2).

Differences in shrub and juniper canopy cover were observed for all three juniper cover categories. Average percentage of shrub cover was highest in LJHS plots in comparison to all other plots, except on north-facing sites (Fig. 3). Similar to low-cover plots, MJS plots had greater shrub cover than the HJLS plots on south-, east-, and west-facing slopes. HJLS plots had, on average, 27.1% juniper cover, and MJS plots had 14.1% juniper cover. LJHS plots had less than 1% juniper cover.

The hierarchical cluster analysis of averaged values by aspect resulted in a distinct separation between each of the juniper cover categories. These significant breaks may be indicators of predicted state changes of plant communities within the state-and-transition framework. In this analysis, there was a distinct separation of a sagebrush-dominated state (State 1) from a juniper-dominated state (State 2) plots and between State 2 and a juniper-dominated state that has eroded soils and degraded ecological processes (State 3). These separations occurred with 0% information remaining, demonstrating a complete division of the groups in the cluster diagram (Fig. 4).

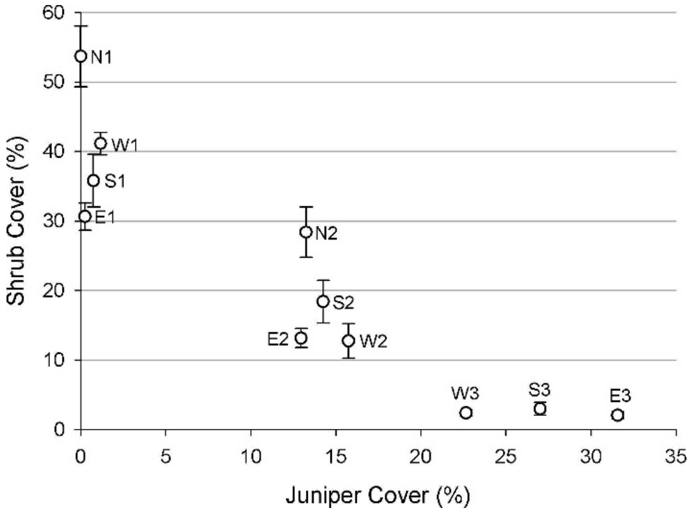

Figure 3. Relationship between shrub foliar cover and juniper canopy cover for all aspect categories and juniper cover levels. Standard error bars represent variability in shrub foliar cover. N indicates north; S, south; E, east; and W, west.

These data were used to develop an empirical model representing each state, transition, and threshold (Fig. 5). The sagebrush steppe (SS) systems without juniper (State 1–phase SS) exhibited both high shrub cover and high bare ground. Juniper-encroached areas (State 1–phase JSS [juniper–sagebrush steppe]) had less shrub cover and lower percent bare ground than State 1 plots. Areas with MJS cover (13.0–15.8%) exhibited an average shrub canopy cover of 18.4% compared with 31.2% in LJHS sites and moderate bare ground (13.9–24.4%). Similarly, areas representing MJS cover (State 2) had an average infiltration rate of 7.6 $cm \cdot h^{-1}$ compared with 9.5 $cm \cdot h^{-1}$ in State 1 plots. Areas with HJLS cover (22.7–31.6%) exhibited an average shrub canopy cover of 2.8%, compared with 31.2% in State 1 plots, and high bare ground (34.6–43.6%). Average infiltration rate in these sites was 3.6 $cm \cdot h^{-1}$ compared with 9.5 $cm \cdot h^{-1}$ in State 1 plots. These data show that total bare ground and infiltration processes had decreased in response to an increase in juniper cover relative to the State 1 plots (Fig. 5). These data also show that the predicted transitions defined in the proposed state-and-transition model are substantiated by empirical results from each of the sampled states. It must be emphasized that this change in infiltration rate is in association with multiple responses to juniper encroachment and not just the juniper–shrub cover categories alone (Petersen and Stringham 2008).

Different from south-, east-, and west-facing slopes that have a mountain big sagebrush–dominated community, north-facing slopes are dominated primarily by either snowberry or a snowberry–mountain big sagebrush mixed community typical of North Slopes 12–16 PZ. With north-facing sites removed from the analysis, the cluster dendrogram revealed a more distinct break occurring between each of the states and phases described in this model on South Slopes 12–16 PZ.

DISCUSSION

These data from this study indicate that the hydrology-based state-and-transition model for western juniper systems can be accurately diagrammed using averaged shrub cover, juniper cover, and bare ground. Additionally, bare ground is an important measure because it is strongly related to infiltration rates, a process that can greatly influence ecosystem structure and function (Gaither and Buckhouse 1983; Wilcox 1994; Petersen and Stringham 2008). The interaction between infiltration rates and shrub and herbaceous plant cover may affect plant community response to fire within a juniper-encroached site. With a decline in shrub and herbaceous plant production, the potential for ladder fuels required to carry a fire through a stand could also decrease. In theory, this could cause a site, which may have had a historic fire-return interval of 30–37 yr for mountain big sagebrush ecosystems (Miller and Rose 1999), to decline to less frequent fire intervals (> 100 yr). As a result, changes in understory cover and infiltration rates may drive communities away from equilibrium along reversible (within state) and irreversible (between states) transitions. This may initiate feedback mechanisms that support a threshold event driving the ecological site to a new state exhibiting a different characteristic structure and function. This study provides criteria for making predictions at an ecological site relative to the current state, community pathway, and thresholds, using the empirical model portrayed in Figure 5. Cluster analysis was found to be a powerful tool for visualizing functional group (grass, forb, shrub, and tree) variation within and between states. Still, interpretation of the clusters must be carefully considered on the basis of the individual attributes contained in the cluster matrix.

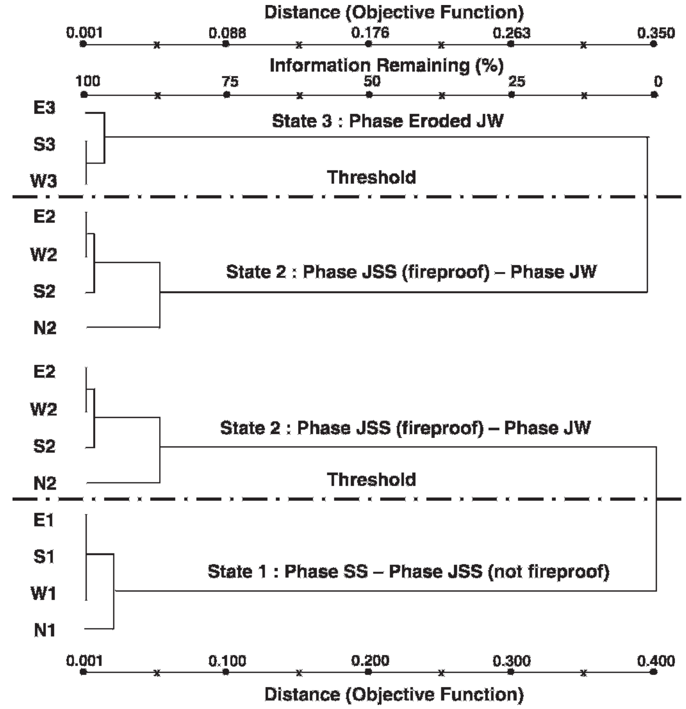

Figure 4. Classification of average plot values for identification of states, phases, and transitions. Analyses were obtained using cluster analysis, with 14.3% chaining above and 18.2% chaining below. N indicates north; S, south; E, east; W, west; JW, juniper woodland; JSS, juniper–sagebrush steppe; and SS, sagebrush steppe.

Stringham et al. (2003) provided examples of a state-and-transition model that are similar to results from this study. They suggested that prolonged stress (i.e., overgrazing,

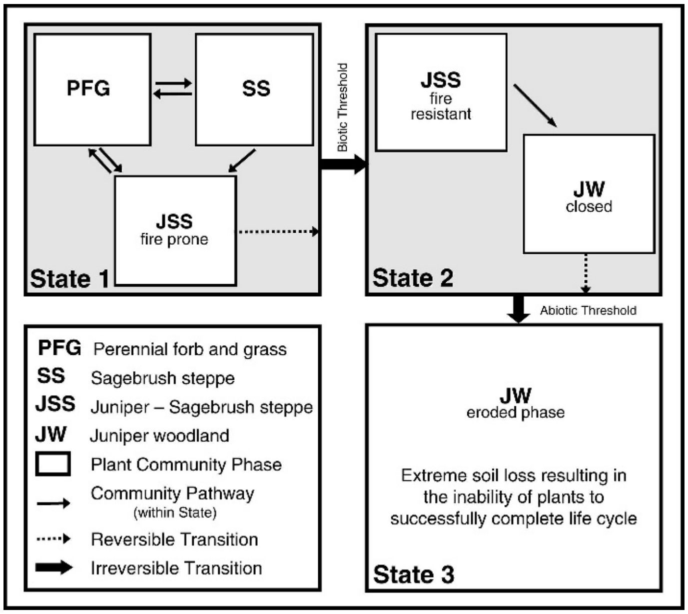

Figure 5. Proposed model of western juniper invasion, incorporating state-and-transition concepts for assessing plant community dynamics.

drought) on an ecosystem can decrease plant cover and production, further impairing the ability of a community to maintain primary ecological processes. A decrease in perennial understory can also increase soil exposure to raindrop impacts, potentially resulting in elevated soil erosion rates (positive feedback response; Pierson et al. 2007; Petersen and Stringham 2008). Additionally, the availability of water to plants throughout the intercanopy zone is dependent on herbaceous and woody plant composition (Breshears and Barnes 1999).

At the Los Alamos National Laboratory, Reid et al. (1999) reported a relationship between juniper encroachment and hydrologic processes (runoff rates, infiltration potential, patch connectivity). They found that bare ground patches had significantly higher sediment production and lower infiltration in intercanopy areas. Similarly, Hester et al. (1997) demonstrate that different cover types (e.g., juniper and intercanopy grass) have different infiltration rates, both with and without fire. Ludwig et al. (1997) demonstrated that a reduction in surface structure (i.e., plant-related patchiness) resulted in accelerated runoff and decreased infiltration rates within Australian rangelands. In our study, intercanopy vegetation was significantly lower in sites with high juniper competition, similarly leading to higher soil surface impacts from raindrops, higher erosion rates, and lower infiltration. According to Ludwig et al. (2005), water and nutrients are redistributed across the landscape from sites with low infiltration rates to areas with high infiltration and are not necessarily lost from the system (Bates et al. 2000). Therefore, the reduction in soil structure and organic carbon in the soil profile is a product of elevated soil erosion (H. Huddleston, personal communication, 2003), materials that are redistributed downslope to sites that function as resource sinks.

Archer (1989) claimed that the introduction or removal of a natural disturbance to a plant community might cause an elevated establishment of woody vegetation that can alter the structure and processes that sustain ecosystem equilibrium. In western juniper woodlands, intercanopy plant community structure is impaired, which results in the degradation of ecological processes, in particular hydrology. The ecological response to declining intercanopy structure and infiltration rates relative to an increase in juniper canopy cover indicates that these ecosystems may cross both biotic (plant controlled) and abiotic (physically controlled) thresholds to alternative states. The abiotic thresholds are characterized by both a reduction in infiltration rates and an increase in erosion levels in juniper-dominated plant communities.

Research has found that as a plant community crosses a threshold into a new state, the initial threshold that is crossed is typically biotic, such as a change in woody plant structure (Westoby et al. 1989; Whisenant 1999). Subsequent thresholds are generally abiotic, such as the change to soil resources that sustain plant communities. In this study, we found that the first threshold in juniper-encroached sites was a change in the biotic component, primarily a decrease in shrub and herbaceous density and cover. This can lead to the inability of these juniper-encroached systems to carry fire. We hypothesize that State 1–phase JSS had an approximate shrub cover of at least 13%, sufficient to sustain fire in these juniper-encroached areas. We hypothesize that sites that had low shrub cover (State 2–phase JSS to phase JW [juniper woodland] with understory shrub cover of approximately 2–3%) were fire resistant. In this scenario, the lack of fire results in the long-term persistence of juniper on the site. With direct competition with juniper, herbaceous vegetation is unable to reestablish to those levels existing before juniper encroachment. Measurements indicate that soil surface exposure increases with a decrease in herbaceous plant cover. Greater soil exposure can potentially experience accelerated erosion rates and decreased soil structure, affecting steady-state infiltration rates (i.e., $3.0 \text{ cm} \cdot \text{h}^{-1}$ in State 3 plots). In this study, State 3 characterized a site that had crossed the abiotic threshold, exhibiting low infiltration ($< 3.0 \text{ cm} \cdot \text{h}^{-1}$) and high sediment production ($1\,007 \text{ g} \cdot \text{m}^{-2}$), unable to self-repair under the current conditions.

The ability of a site to function depends on both ecological structure and processes. When measured individually, these attributes may be inadequate to accurately predict states, transitions, or thresholds for a particular site. However, integrating multiple factors in this analysis (i.e., infiltration, shrub cover, juniper canopy cover, bare ground, litter cover, sediment production, plant cover, rock cover), accuracy can be increased for predicting states and thresholds.

In our model, State 1 exhibits three plant community phases. The perennial, forb-and-grass phase (PFG) shifts into an SS phase as shrub species increase in these communities. The final phase is established as juniper encroaches into either a PFG or SS phase but does not reach full occupation on the site (Figure 5). With greater juniper cover, intercanopy shrub and herbaceous plant density and cover are reduced. We suggest that this reduction in plant growth will also lower wildfire potential. In the absence of a regular fire regime, juniper encroachment (biotic threshold) will continue until the site becomes fully occupied by juniper (JW). These data also show that a lack of surface cover by plants and litter in intercanopy areas will lead to accelerated runoff and erosion (Branson and Owen 1970; Thurow et al. 1988; Thurow 1991; Blackburn et al. 1992; Woo et al. 1997; Davenport et al. 1998; Reid et al. 1999; Petersen and Stringham 2008). Long-term loss of the uppermost soil layer, a reduction in soil structure, and decreased soil organic carbon content can result in the inability of these sites to support a predisturbance plant community (abiotic threshold resulting in an eroded state). However, the lack of recovery potential at an eroded site was not measured in this study, necessitating future investigation and research to support this hypothesis.

MANAGEMENT IMPLICATIONS

The results of this work provide land managers with a tool for predicting ecosystem response, in particular as an indicator of hydrologic processes, to western juniper encroachment using practical, field-based measurements. These results also suggest that managers can more effectively assess the influence that increasing juniper cover has on both biotic and abiotic components of the landscape. Characterizing plant community structure and approximating infiltration rates can be effective measures to identify states and to predict thresholds in juniper-encroached areas. Subsequently, this knowledge can be applied to identify sites and community phases that are at risk of crossing biotic or abiotic thresholds.

LITERATURE CITED

Anderson, E. W., M. M. Borman, and W. C. Krueger. 1998. The ecological provinces of Oregon. Corvallis, OR, USA: Oregon Agricultural Experiment Station. 138 p.

Archer, S. 1989. Have southern Texas savannas been converted to woodland in recent history? *American Naturalist* 134:545–561.

Bates, J. D., R. F. Miller, and T. J. Svejcar. 2000. Understory dynamics in cut and uncut western juniper woodlands. *Journal of Range Management* 53:119–126.

Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.

Blackburn, W. H., F. B. Pierson, C. L. Hanson, T. L. Thurow, and A. L. Hanson. 1992. The spatial and temporal influence of vegetation on surface soil factors in semiarid rangelands. *Transactions of the American Society of Agricultural Engineers* 35:479–486.

Branson, F. A., and J. B. Owen. 1970. Plant cover, runoff and sediment yield relationships on Mancos Shale in western Colorado. *Water Resources Research* 6:783–790.

Breshears, D. D., and F. J. Barnes. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landscape Ecology* 14:465–478.

Davenport, D. W., D. D. Breshears, B. P. Wilcox, and C. D. Allen. 1998. Viewpoint: sustainability of piñon-juniper ecosystems—a unifying perspective of soil erosion thresholds. *Journal of Range Management* 51:231–240.

Elzinga, C. L., D. W. Salzer, and J. W. Welloughby. 1998. Measuring and monitoring plant populations. Denver, CO, USA: US Department of the Interior, Bureau of Land Management, Technical reference 1730-1 BC-650B. p. 178–186.

Fuhlendorf, S. D., F. E. Smeins, and W. E. Grant. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. *Ecological Modeling* 90:245–255.

Gaither, R. E., and J. C. Buckhouse. 1983. Infiltration rates of various vegetation communities within the Blue Mountains of Oregon. *Journal of Range Management* 36:58–60.

Griffiths, D. 1902. Forage conditions of the northern border of the Great Basin. Washington, DC, USA: US Department of Agriculture, Bureau of Plant Industry, Bulletin 15. 60 p.

Herrick, J. E., J. R. Brown, A. J. Tugel, P. L. Shaver, and K. M. Havstad. 2002. Application of soil quality to monitoring and management. *Agronomy Journal* 94:3–11.

Hester, J. W., T. L. Thurow, and C. A. Taylor. 1997. Hydrologic characteristics of vegetation types as affected by prescribed burning. *Journal of Range Management* 50:199–204.

Ludwig, J. A., D. Tongway, D. Freudenberger, J. Noble, and K. Hodgkinson. 1997. Landscape Ecology, function and management. Principles from Australia's Rangelands. Collingwood, Victoria, Australia: CSIRO Publishing. 158 p.

Ludwig, J. A., B. P. Wilcox, D. D. Breshears, D. J. Tongway, and A. C. Imeson. 2005. Vegetation patches and runoff—erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86:288–297.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. Gleneden Beach, OR, USA: MjM Software Design. 300 p.

McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data. Version 4.2. Gleneden Beach, OR, USA: MjM Software Design.

Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2006. Biology, ecology, and management of western juniper. Corvallis, OR, USA: Agricultural Experiment Station, Oregon State University, Technical bulletin 152. 77 p.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management* 52:550–559.

Milton, S. J., W. R. J. Dean, M. A. duPlessis, and W. R. Siegfri. 1994. A conceptual model of arid rangeland degradation. *Bioscience* 44:70–76.

[NRCS] Natural Resource Conservation Service. 2000. Soil survey and ecological site description provided for the watershed study area. Burns, OR, USA: NRCS. 5 p.

Petersen, S. L., and T. K. Stringham. 2008. Infiltration, runoff, and sediment yield in response to western juniper encroachment in southeast Oregon. *Journal of Rangeland Ecology and Management* 61:74–81.

Pierson, F. B., Jr., J. D. Bates, A. J. Svejcar, and S. P. Hardegree. 2007. Long-term changes in runoff and erosion after cutting western juniper. *Rangeland Ecology and Management* 60:285–292.

Reid, K. D., B. P. Wilcox, D. D. Breshears, and L. MacDonald. 1999. Runoff and erosion in a piñon-juniper woodland: influence of vegetation patches. *Soil Science Society of America Journal* 63:1869–1879.

Spaeth, K., M. Weltz, F. Pierson, W. H. Blackburn, D. Fox, D. Merz, P. Shaver, G. Brackley, H. Degarmo, M. Whited, M. Flanagan, K. Hood, and C. Franks. 1995. Small plot rainfall simulation: background and procedures. Washington, DC, USA: US Department of Agriculture–National Resources Conservation Service, Technical note 230-15-12. 31 p.

Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2001. States, transitions, and thresholds: further refinement for rangeland applications. Corvallis, OR, USA: Oregon State University Agricultural Experiment Station, Special report 1024. 15 p.

Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State-and-transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.

Thurow, T. L. 1991. Hydrology and erosion. *In:* R. Heitschmidt and J. Stuth [eds.]. Grazing management: an ecological perspective. Portland, OR, USA: Timber Press, Inc. p. 141–159.

Thurow, T. S., W. H. Blackburn, and C. A. Taylor, Jr. 1988. Infiltration and interrill erosion responses to selected livestock grazing strategies, Edwards Plateau, Texas. *Journal of Range Management* 41:296–302.

West, N. E. 1999. Distribution, composition, and classification of current juniper-pinyon woodlands and savannas across western North America. *In:* S. B. Monsen and R. Stevens [eds.]. 1997. Proceedings: ecology and management of pinyon-juniper communities within the interior west: sustaining and restoring a diverse ecosystem. Ogden, UT, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-9. p. 20–23.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.

Wilcox, B. P. 1994. Runoff and erosion in intercanopy zones of pinyon-juniper woodlands. *Journal of Range Management* 47:285–295.

Whisenant, S. G. 1999. Repairing Damaged Wildlands: biological conservation, restoration, and sustainability. Cambridge, United Kingdom: Cambridge University Press. 312 p.

Woo, M. K., G. Fang, and P. D. diCenzo. 1997. The role of vegetation in the retardation of rill erosion. *Catena* 20:145–159.