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Indicators of ecosystem function identify alternate states in the sagebrush steppe

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Abstract. Models of ecosystem change that incorporate nonlinear dynamics and thresholds, such as state-and-transition models (STMs), are increasingly popular tools for land management decision-making. However, few models are based on systematic collection and documentation of ecological data, and of these, most rely solely on structural indicators (species composition) to identify states and transitions. As STMs are adopted as an assessment framework throughout the United States, finding effective and efficient ways to create data-driven models that integrate ecosystem function and structure is vital. This study aims to (1) evaluate the utility of functional indicators (indicators of rangeland health, IRH) as proxies for more difficult ecosystem function measurements and (2) create a data-driven STM for the sagebrush steppe of Colorado, USA, that incorporates both ecosystem structure and function. We sampled soils, plant communities, and IRH at 41 plots with similar clayey soils but different site histories to identify potential states and infer the effects of management practices and disturbances on transitions. We found that many IRH were correlated with quantitative measures of functional indicators, suggesting that the IRH can be used to approximate ecosystem function. In addition to a reference state that functions as expected for this soil type, we identified four biotically and functionally distinct potential states, consistent with the theoretical concept of alternate states. Three potential states were related to management practices (chemical and mechanical shrub treatments and seeding history) while one was related only to ecosystem processes (erosion). IRH and potential states were also related to environmental variation (slope, soil texture), suggesting that there are environmental factors within areas with similar soils that affect ecosystem dynamics and should be noted within STMs. Our approach generated an objective, data-driven model of ecosystem dynamics for rangeland management. Our findings suggest that the IRH approximate ecosystem processes and can distinguish between alternate states and communities and identify transitions when building data-driven STMs. Functional indicators are a simple, efficient way to create data-driven models that are consistent with alternate state theory. Managers can use them to improve current model-building methods and thus apply state-and-transition models more broadly for land management decision-making.

Key words: decision-making tool; ecological site; grazing management; indicators of rangeland health; northwestern Colorado, USA; state-and-transition model (STM); threshold; vegetation dynamics.

Introduction

State-and-transition models (STMs), conceptual models of vegetation change based on alternate state theory, are increasingly applied as tools for land management decision-making (Westoby et al. 1989, Bestelmeyer et al. 2003, Suding and Hobbs 2009*b*). An advantage of the STM framework is that it embraces ecosystem complexity by portraying threshold changes between alternate states along multiple axes, including management and natural disturbance (Briske et al. 2003). These models of vegetation change describe dynamics in a variety of ecosystems, particularly semiarid rangelands with a short history of grazing like the sagebrush steppe of western North America (Cingolani et al. 2005). The U.S. Department of Agriculture Natural Resources Conservation Service (USDA NRCS) together with partners is currently developing thousands of these models for use in land management across the United States, and STMs are being developed and used in Mongolia, Africa, Australia, and elsewhere (Sasaki et al. 2008, Hobbs and Suding 2009). However, models are often developed based on expert knowledge with little published quantitative ecological data (Suding and Hobbs 2009*b*). Recent efforts have focused on creating models based on ecological data collection (Bestelmeyer et al. 2009, Martin and Kirkman 2009, Petersen et al. 2009). This paper presents one way to integrate ecosystem structure and function when constructing data-driven STMs.

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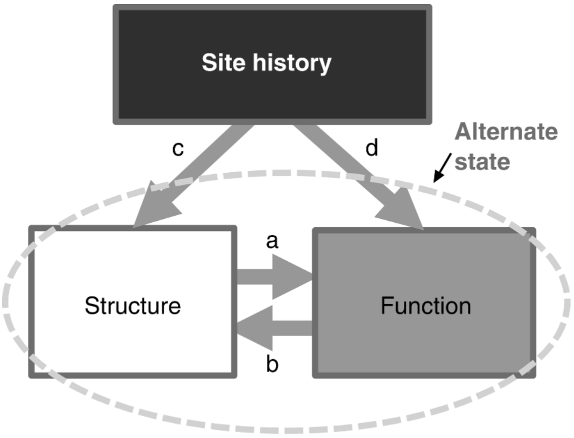

FIG. 1. Hypothesized relationships between site history and ecosystem structure and function, approximated by plant species composition and indicators of rangeland health (IRH) from private and public rangelands in and around Elkhead watershed, northwestern Colorado, USA. Structure and function influence each other (arrows a and b) through negative or positive feedbacks. Site history (including management and disturbance history) directly impacts structure (arrow c) and function (arrow d). Environment is included with site history in analyses to ensure that we do not attribute variations to management that are also related to environmental factors.

Ecosystem function is important in alternate state theory, but often is not addressed in STM construction. There are three steps to creating a model: (1) identifying potential alternate states, (2) identifying transitions between states, and (3) identifying management practices and disturbances that make states vulnerable to and trigger transitions (Briske et al. 2003). A state is "a suite of temporally-related plant communities and associated dynamic soil properties that produce persistent, characteristic structural and functional ecosystem attributes" (Bestelmeyer et al. 2009). Many efforts to create data-driven STMs use plant species composition to define states (Allen-Diaz and Bartolome 1998, Oliva et al. 1998, Jackson and Bartolome 2002, West and Yorks 2002). Identifying states using multivariate analyses, rather than a priori based on expert knowledge, can help free this process from subjectivity or bias (Allen-Diaz and Bartolome 1998). However, defining states only by species composition overlooks functional attributes that distinguish states from each other (Stringham et al. 2003, Bestelmeyer et al. 2009). Sites that differ in species composition but not function are likely to be different communities that can undergo continuous change from one to the other rather than distinct states (Stringham et al. 2003). Recent efforts connect ecological processes to states and transitions through experiments and observation of structural and functional attributes (Stringham et al. 2001, Chartier and Rostagno 2006, Petersen et al. 2009, Zweig and Kitchens 2009). These studies generally focus on one or two transitions between states because ecosystem function is difficult to measure. In contrast, this study aims to create an STM that includes many important drivers of transitions, as is needed for rangeland management.

New methods for rapidly assessing ecosystem function are available that can overcome practical constraints and allow functions to be linked with plant species composition in constructing data-driven STMs. The indicators of rangeland health (IRH) are used to assess the integrity of rangeland ecosystem processes by evaluating structural attributes related to those processes in terms of their deviation from reference conditions (Pellant et al. 2005). Based on qualitative ratings of 17 indicators, observers evaluate each of three rangeland health attributes: soil and site stability, hydrologic function, and biotic integrity. For example, *bare ground* is an indicator of soil and site stability, and it considers the size and connectedness of bare ground patches within a site. This qualitative, fast survey technique is meant as an assessment tool and not to monitor change over time because it is not necessarily repeatable, but taking quantitative measurements related to indicators can ensure consistency (Pellant et al. 2005). Miller (2008) and Herrick et al. (2010) applied the IRH assessment process and found that it yielded valuable information about how ecosystem functions varied across large areas (Escalante National Monument, Utah and the USA, respectively).

To identify transitions and ways to manage them, the relationships between management and potential alternate states must be identified (Fig. 1). Transitions occur when a threshold is crossed, or "ecological processes responsible for maintaining the . . . state degrade beyond the point of self-repair" (Stringham et al. 2003). They are caused by successional processes, ecological disturbances, and management actions, alone or in combination (Briske et al. 2005). Structure and function affect each other as well, with negative feedbacks sustaining a state and positive feedbacks causing transitions between states (Briske et al. 2005). For example, an experimental manipulation of soil erosion showed that the transition to an eroded state included multiple interacting structural and functional thresholds, including reductions in litter and vegetation cover, increases in water runoff and erosion, changes in soil structure, and a shift to shrub dominance (Chartier and Rostagno 2006). Management can alter both structure and function. The conceptual model that guides our data analysis (Fig. 1) incorporates these relationships. Temporally replicated rangeland vegetation studies show that transitions sometimes occur without proximate changes in management (Allen-Diaz and Bartolome 1998, Jackson and Bartolome 2002).

In this study, we (1) evaluate the utility of the IRH as a proxy for ecosystem function and (2) create a data-driven STM that incorporates both ecosystem structure and function for the Claypan ecological site in northwestern Colorado, USA (Major Land Resource Area 48A, Southern Rocky Mountains; USDA NRCS 2006; see Plate 1). We sampled plots with similar soils and climate but different management histories to infer the effects of management on these areas. We used multivariate statistics to define potential states based on plant species composition and as a starting point for further analyses (Fernandez-Gimenez et al. 2009). Based on these potential states, we posed three questions that relate to our objectives and to the conceptual relationships among structure, function, and management (Fig. 1). First, how are the qualitative IRH related to quantitative measures that approximate the same processes? If the qualitative IRH as we applied them are good measures of ecosystem processes, we hypothesize that they will be correlated with quantitative measurements of related attributes. Second, do potential states that differ in plant species composition differ in IRH as well? In other words, is structure related to function (Fig. 1a, b)? Finally, how are IRH and species composition related to site history and environmental variables (Fig. 1c, d)? In answering these questions, we outline a data-driven approach to constructing STMs.

Materials and Methods

We sampled soils and vegetation in plots with different site histories to infer the effects of management practices and disturbances on plots with similar environmental characteristics and to construct a state-and-transition model. Space-for-time substitution is necessary in studies that aim to describe long-term ecosystem responses to disturbance when long-term data are lacking (Jenny 1941). Ewers and Pendall (2008) found high replicability in vegetation responses to disturbance across three sagebrush sites, supporting this design.

Site selection

Data were collected on private and public rangelands in and around the Elkhead watershed of northwestern Colorado (40°38.5′ N, 107°12.5′ W). Fifteen private landowners, the Bureau of Land Management (BLM), and the U.S. Forest Service (USFS) permitted us to sample on their land (~60% of all land in the watershed). A detailed inventory of site management history was conducted through landowner interviews (Knapp and Fernandez-Gimenez 2009) and review of agency (NRCS, BLM, USFS) records. Sampling focused on the Claypan ecological site. An ecological site is a type of land with similar soil characteristics, climate, and vegetation, and land within the same ecological site is hypothesized to respond similarly to management practices and disturbances (USDA NRCS 2003). Areas that represent all existing combinations of management practices were identified: historical grazing intensity, a qualitative estimate of typical stocking rate based on interviews with 26 local land managers (Knapp 2008); seeding history; and shrub management practices including aerial spraying, mechanical treatment, or none. Random plot locations were stratified by management history and located at least 200 m apart.

Soil, plant species, and indicator data were collected within 20 × 50 m plots. We sampled 41 plots for vegetation in 2007 and 2008 and soils and IRH in 2009.

Soils

Soil data were collected for two purposes: (1) to validate that sampled plots matched the Claypan ecological site and exclude plots that did not, and (2) to help evaluate soil-related IRH. Soil descriptions following NRCS protocols (Schoeneberger et al. 2002) were based on a soil pit or auger hole $\geq$50 cm deep in the center of each plot. The same observer recorded texture, structure, color, root density, and carbonates in each layer. The ecological site was verified by matching each soil description with the Claypan ecological site soil description, characterized by a thin clay loam or clay A horizon and a fine-textured subsoil that restricts water movement and availability. Soil clay content in the top 10 cm was calculated from average field textures weighted by horizon thickness.

Plant species composition

We measured plant cover by species to differentiate potential states. We used the line-point intercept method, sampling at 1-m intervals along five 50-m transects spaced 5 m apart in the plot (250 points per plot; Bonham 1989). We recorded foliar and basal cover.

Indicators of ecological processes

To link potential states defined by species composition to ecological processes, we assessed the indicators of rangeland health (IRH, listed in italics to distinguish from other variables; Pellant et al. 2005). We rated 16 of the 17 indicators on their degree of departure from reference conditions, defined as the degree to which an indicator is outside the normal range of variation for that ecological site under a natural disturbance regime (none-slight, slight-moderate, moderate, moderate-extreme, extreme-total). We followed the guidelines in Pellant et al. (2005) with several modifications. Thirteen IRH were evaluated qualitatively in the field by two experienced observers. The observers assigned levels of deviation from reference conditions for each IRH using a reference sheet for the Claypan ecological site that we developed based on the Generic Reference Sheet (Pellant et al. 2005). Our reference sheet defined reference conditions for each IRH (the none-slight rating) based on our experience working on the ecological site, and defined deviations from reference conditions using the Generic Reference Sheet. It also included variation that would be expected due to environmental conditions (e.g., water flow patterns on steeper slopes should be longer) as recommended in the IRH handbook (Pellant et al. 2005). Moderate and greater deviations from reference conditions were collapsed into one category (moderate) for analysis. We omitted *plant community composition relative to infiltration and runoff* because the field team felt it was too subjective.

In addition to 13 qualitative IRH, we evaluated three IRH based on quantitative measures that we converted to deviations from reference conditions according to the categorical IRH scale based on the category descriptions in the Generic Reference Sheet. We took this approach because the qualitative evaluation of these IRH relies directly on quantitative data we also collected. *Functional/structural groups* was calculated from the number of native perennial functional groups (shrubs, N-fixing perennial forbs, non-N-fixing perennial forbs, short and mid-height cool-season bunchgrasses, and cool-season rhizomatous grasses) that exceeded 2% of production based on dry mass rank (Coulloudon et al. 1999). *Functional/structural groups* was rated according to number of functional groups as follows: ≥ 5, none-slight; 4, slight-moderate; <4, moderate. *Soil surface resistance to erosion* was derived from soil aggregate stability, measured using a field method that is highly correlated with laboratory measurements and inter-rill erosion (Blackburn and Pierson 1994, Herrick et al. 2001). Nine randomly located paired shrub canopy and shrub interspace aggregate samples were rated from one (unstable) to six (stable). The indicator was derived from average aggregate stability according to the descriptions for each rating in the Generic Reference Sheet (Pellant et al. 2005): >4.5, none-slight; <4.5, slight-to-moderate; <3.5 or $>50\%$ shrub interspaces with aggregate stability <4, moderate. *Plant production* was derived from production estimates made using a double sampling method (Pechanec and Pickford 1937), where production was visually estimated in 15 0.1 m^2 circular subplots and clipped in a subset of three of them. Estimates were corrected by a ratio estimator of dry to estimated masses (Reich et al. 1993), and further adjusted for percentage utilization at each plot by the grazed class method (Schmutz et al. 1963, Coulloudon et al. 1999). We did not use percentage of expected production to calculate *plant production* because of uncertainty about whether the estimates in the site descriptions represented total or herbaceous production. Instead, *plant production* was rated as follows based on the Z scores of herbaceous production values within each sampling year: >0, none-slight; <0, slight-to-moderate; <-1, moderate.

To determine whether the qualitative IRH are useful as indicators of process and were objectively evaluated, we made related quantitative measurements known to be linked to processes (Pellant et al. 2005). Basal plant cover is related to *water flow patterns*, percentage litter cover is related to *litter amount*, and percentage bare ground is related to *bare ground*. Line-point intercept, described previously, generated these measures. Basal plant cover is related to water flow path length and the ability of the system to recover after disturbance (Gutierrez and Hernandez 1996). Percentage litter cover and percentage bare ground are correlated with runoff and susceptibility to water erosion (Smith and Wischmeier 1962, Blackburn and Pierson 1994). Size and percent cover of basal gaps between plants are thought to be correlated with *water flow patterns*, *litter movement*, and *plant community composition in relation to infiltration and runoff*. We measured gaps using the gap intercept method along two 50-m transects in each plot, recording basal gaps >20 cm (Herrick et al. 2005). Annual forbs were ignored because they are variable, but we counted annual grasses as stopping a gap because of the functional importance of *Bromus tectorum* (cheatgrass) in this system (e.g., Baker 2007).

Site history and environment

Transitions between states within an ecological site are thought to be triggered by management practices and ecological disturbances, here referred to collectively as site history. Environmental factors may make certain transitions more likely in some areas within an ecological site relative to others. Categorical site history variables were determined by communicating with land managers and included: historical grazing intensity (below medium vs. medium-high to high), chemical shrub treatment (spraying), mechanical shrub treatment, and seeding with grasses. We were only able to sample two plots that had been seeded with grasses, so this practice was not included in statistical analyses but was evaluated qualitatively. We also recorded evidence of rodent activity (pocket gophers and voles) and measured distance from water, a proxy for grazing intensity (e.g., Bailey et al. 1996). In addition to soils, we recorded environmental variables in the field including slope and aspect. Aspect was transformed into a continuous variable with higher values for more productive northeastern slopes and low values for southwestern slopes (Beers et al. 1966).

Data analysis

For multivariate analyses, plant cover values were square-root transformed to allow less abundant species that are important ecologically to influence the analysis. Rare species that occur in fewer than 5% of plots and annual forbs were omitted to reduce noise in the data (McCune and Grace 2002).

Potential states for the Claypan ecological site were defined by plant species composition using hierarchical agglomerative cluster analysis (flexible beta linkage method, beta $= -0.25$; 44 species). The cluster dendrogram was pruned at the number of groups with the most significant indicator species (Dufrene and Legendre 1997), the number of groups that is most representative of ecological differences (McCune and Grace 2002). Year (2007 vs. 2008) split one potential state (the alkali sagebrush/western wheat shrubland) into two groups, but we combined them because they were similar in species composition. We evaluated whether potential states differed in species composition using multi-response permutation procedure (MRPP), a test of the hypothesis of no difference between groups of objects based on random permutations of matrices (Berry et al. 1983).

TABLE 1. Correlations between the qualitative indicators of rangeland health (IRH ratings) and quantitative measures of related ecosystem properties from private and public rangelands in and around Elkhead watershed, northwestern Colorado, USA.

Indicator of rangeland health Quantitative measure	Correlation coefficient (Pearson's R)	P
Water flow patterns		
Basal gaps (%)		
>20 cm	0.56	<0.001
20–50 cm	NS	
50–100 cm	0.63	<0.001
101–200 cm	0.47	<0.01
Mean basal gap size	0.53	<0.001
Bare ground (%)	NS	
Bare ground		
Basal gaps (%)		
>20 cm	0.69	<0.001
20–50 cm	0.44	<0.01
50–100 cm	0.67	<0.001
100–200 cm	0.56	<0.001
Mean basal gap size	0.31	<0.05
Bare ground (%)	NS	
Litter movement		
Basal gaps (%)		
>20 cm	0.56	<0.001
20–50 cm	0.36	<0.05
50–100 cm	0.55	<0.001
100–200 cm	0.43	<0.01
Plant mortality and decadence		
Proportion of live-to-dead canopy cover	NS	
Litter amount (+ too much, − too little)		
Litter basal cover	NS	
Invasive plants		
Invasive plant foliar cover	0.69	<0.001

Notes: NS is not significant. There are no quantitative indicators for *reproductive capability of perennial plants*. We did not measure any quantitative indicators for *pedestals and terracettes*, *gullies*, *compaction*, or *soil surface loss or degradation*.

The following statistical analyses evaluated the utility of IRH for approximating ecosystem functions and determined the relationships among structure, function, and site history, answering the three research questions. Correlations quantified relationships between qualitative IRH and quantitative measures. We tested for IRH differences between potential states (Fig. 1a) using MRPP. We explored which IRH predict membership in each potential state defined by plant species composition (Fig. 1b) relative to all other states using logistic regression. IRH were excluded from analysis when they did not vary across a potential state. Significant effects were identified using backward selection with an alpha of 0.10 to ensure that all meaningful variables remain in the model and given our relatively small sample size. Finally, we used logistic regression to discover which site history and environmental variables could predict states and IRH (Fig. 1c, d). We included environmental variables in this analysis to confirm that we did not attribute a difference to management that was also related to underlying variations in environmental variables within the Claypan ecological site. Site history and environmental variables were excluded when they did not vary across a potential state. *Wind-scoured, blow-out, and/or depositional areas* was left out of all analyses because it never deviated from reference conditions.

Cluster analysis and MRPP were performed using PCOrd (McCune and Mefford 1999). Correlation analyses were performed using R (R Core Development Team 2008). Logistic regression was performed using SAS (SAS Institute 2002–2008).

RESULTS

IRH and quantitative measures

Many IRH are correlated with quantitative measures that approximate similar site properties (Pellant et al. 2005; Table 1). The IRH are integrative and take many structural attributes into account, so while many of the measured quantitative indicators were likely used in evaluating the qualitative IRH, they are not completely dependent on these quantitative measures. *Water flow patterns*, *bare ground*, and *litter movement* indicators were significantly correlated with the percent basal gap

TABLE 2. Descriptive names for potential states of the Claypan ecological site, as identified by cluster analysis, with indicator species and mean species richness.

Potential state	N	Indicator species	Mean species richness
Alkali sagebrush shrubland with diverse understory (Diverse)	3	*Melica bulbosa*, *Helianthella uniflora*, *Perideridia gairdnerii*, *Cirsium eatonii*, *Elymus elymoides*, *Achnatherum lettermanii*, *Symphoricarpos rotundifolius*, *Artemisia tridentata* ssp. *vaseyana*	38.3
Alkali sagebrush/bluegrass shrubland (Bluegrass)	5	*Poa secunda*	34.8
Native Grassland	10	*Koelaria macrantha*, *Phlox longifolia*	28.3
Alkali sagebrush/western wheatgrass shrubland (Wheatgrass)	11	*Pascopyrum smithii*; *Amelanchier utahensis*, *Astragalus wetherillii*, *Delphinium nuttallianum*, *Lomatium grayi*, *Microseris nutans*	29.3
Three-tip sagebrush shrubland (Three-tip)	4	*Artemisia tripartita*, *Poa interior*, *Achillea millefolia*	32.0
Alkali sagebrush shrubland with sparse understory (Sparse)	6	*Artemisia arbuscula* ssp. *longiloba*, *Gutierriezia microcephala*, *Orthocarpus luteus*	34.7
Planted Grassland	2	*Elymus lanceolata*, *Bromus inermis*, *Pseudoroegnaria spicata*	24.0

Notes: Potential states were identified using hierarchical cluster analysis on plant cover by species for 41 plots (44 species). Indicator species were significant according to indicator species analysis at $P < 0.05$. Species names are from the USDA PLANTS database (USDA NRCS 2010).

cover >20 cm measured by the gap intercept method. *Invasive plants* was correlated with foliar cover of invasive plants.

IRH and potential states

Cluster analysis of species composition by plot identified seven potential states, named here but called by the short names in parentheses in the rest of the text: alkali sagebrush shrubland with diverse understory (Diverse), alkali sagebrush/bluegrass shrubland (Bluegrass), alkali sagebrush/western wheatgrass shrubland (Wheatgrass), three-tip sagebrush shrubland (Three-tip), native grassland (Native Grassland), alkali sagebrush/sparse understory (Sparse), and planted grassland (Planted Grassland; Table 2). MRPP revealed that all potential states had different plant species composition except Diverse, Bluegrass, and Planted Grasslands (Bonferroni-corrected alpha = 0.003).

Potential states defined by plant species composition are associated with differences in IRH (MRPP, $P < 0.05$). IRH differed among several potential states when compared pairwise with Bonferroni correction, a conservative test (Table 3). Sparse, Wheatgrass, Planted Grassland, and Native Grassland potential states each differ in at least one IRH from at least two other states. Three-tip and Bluegrass differ from one other state.

Logistic regression showed which processes, as described by IRH, predict which states. To avoid multicollinearity among predictor variables, we reduced the number of IRH in this analysis to 12 uncorrelated ones (correlation coefficient $r < 0.5$). *Pedestals and terracettes* and *bare ground* were excluded because they were related to *water flow patterns* ($r = 0.66, 0.56$); *gullies* IRH was excluded because it was correlated with *litter movement* ($r = 0.72$).

TABLE 3. Probabilities that differences in indicators of rangeland health ratings between potential states for the Claypan ecological site are due to chance, based on multi-response permutation procedure (MRPP).

Potential state	Diverse	Bluegrass	Wheatgrass	Three-tip	Sparse	Native grassland
Bluegrass	NS					
Wheatgrass	NS	0.0133				
Three-tip	NS	NS	**0.0005**			
Sparse	NS	**0.0029**	**0.0000**	NS		
Native Grassland	NS	NS	0.0085	0.0199	**0.0001**	
Planted	**0.0000**	0.0124	0.0067	0.0166	0.0069	**0.0019**

Note: P values in bold are significant after Bonferroni correction (Bonferroni-corrected alpha = 0.003). "NS" indicates not significant.

TABLE 4. Significant relationships between processes (IRH ratings: none-to-slight, slight-to-moderate, and moderate or higher) and potential states according to logistic regression.

State	Indicators of rangeland health (IRH)	P	Odds ratio
Sparse	*water flow patterns*	0.03	9.8
Native Grasslands	*litter movement*	0.02	12.9
	invasive plants	0.09	0.1
	soil surface loss or degradation	0.06	0.2
Wheatgrass	*water flow patterns*	0.01	0.1
	soil surface resistance to erosion	0.09	0.4

Notes: Indicators (IRH) were selected using backward selection at $P < 0.10$. Odds ratios > 1 show that IRH deviations from reference conditions increase the odds of being in a particular state. Diverse, Three-tip, and Planted Grassland states had too few observations for this analysis. Bluegrass had no significant relationships with IRH.

Many potential states were predictable based on levels of IRH (Table 4). *Water flow patterns* are characteristic of the Sparse potential state. Lack of deviation from reference conditions in *water flow patterns* and *soil surface resistance to erosion* was characteristic of the Wheatgrass potential state. Native Grasslands deviated from reference conditions in *litter movement* but had little *soil surface loss or degradation* or *invasive plants*.

Three potential states had too few occurrences (<5) to be predicted by IRH using logistic regression: Diverse, Three-tip, and Planted Grassland. However, some patterns merit qualitative assessment. Three of four Three-tip plots deviated from reference conditions in *water flow patterns, bare ground, soil surface loss or degradation,* and *soil surface resistance to erosion*. Both Planted Grassland plots deviated from reference conditions in *functional/structural groups* and *invasive plants*. Diverse plots did not consistently deviate in any IRH.

Site history, environment, IRH, and potential states

Site history and environmental variables predicted potential states according to logistic regression (Table 5), and several qualitative relationships are also worth noting. Aerial spraying predicted occurrence of the Native Grasslands potential state. Northeast aspect predicted occurrence of the Three-tip potential state, and two of four Three-tip plots were mechanically treated. Southwest aspect predicted occurrence of Wheatgrass. Steeper slope and less clayey soil texture predicted the Sparse potential state. No site history or

TABLE 5. Significant relationships between site history and environmental processes and (A) indicators of rangeland health (IRH ratings: none–slight, slight–moderate, and moderate or higher) and (B) potential states, according to logistic regression.

IRH or potential state	Site history and environmental variables	P	Odds ratio
Indicators of rangeland health			
Water flow patterns	transformed aspect	<0.01	2.7
	slope	0.08	1.1
Bare ground	clay	0.07	0.9
Rills	rodent activity	0.01	8.6
Soil surface loss or degradation	spraying	<0.01	0.1
	mechanical treatment	0.10	6.7
Plant mortality and decadence	grazing intensity (med. high-high vs. low-med.)	0.04	0.2
	clay	0.06	1.1
Soil surface resistance to erosion	transformed aspect	0.04	3
	clay	0.02	0.9
Invasive plants	distance from water	0.09	0.9
Potential state			
Native Grasslands	spraying	<0.001	27.0
Sparse	slope	0.06	1.7
	clay	0.02	0.8
Three-tip	transformed aspect	0.04	7.5
Wheatgrass	transformed aspect	0.06	0.26

Notes: Variables included were significant at $P < 0.10$ according to backward selection. Odds ratios greater than 1 show that management practices or increasing values of environmental variables increase the odds of IRH deviation from reference conditions and state occurrence. *Pedestals and terracettes*, *litter amount*, *litter movement*, and *plant production* IRH and Diverse, Bluegrass and Wheatgrass potential states had no significant relationships. *Gullies*, *compaction*, and *reproductive capability of perennial plants* IRH and Planted Grassland potential state had too few observations for this analysis.

PLATE 1. Alternate states of the Claypan ecological site in and around the Elkhead watershed, northwestern Colorado, USA. States were identified based on differences in ecosystem structure (species composition) and function (indicators of rangeland health). On the left, the alkali sagebrush shrubland with a diverse understory functions as expected for this climate and soil type. On the right, the alkali sagebrush shrubland with a sparse understory is characterized by water erosion. Photo credits: E. Kachergis.

environmental variables predicted occurrence of the Diverse or Bluegrass potential states. Both Planted Grassland plots were former wheat fields that had been planted with mostly nonnative grasses, although sample size was too small for statistical analysis.

Site history and environmental variables both predicted deviations from IRH reference conditions according to logistic regression (Table 5). Mechanical treatment predicted deviations from reference conditions in *soil surface loss or degradation,* while spraying predicted lack of *soil surface loss or degradation. Invasive plants* increased with decreasing distance from water, a proxy for grazing pressure. Lower historical grazing intensity predicted occurrence of *plant mortality and decadence*. Rodent activity predicted *rills*. Numerous environmental variables were related to levels of IRH, including surface soil texture, slope, and aspect.

DISCUSSION

Qualitative IRH are related to quantitative indicators

Correlations between IRH and quantitative measures of site attributes that are related to processes suggest that the IRH can be applied consistently and objectively and used to approximate function. In particular, the percent cover of basal gaps was correlated with several indicators of overland flow erosion. *Litter amount* and *plant mortality and decadence* were not correlated with quantitative measures, possibly because IRH were assessed in a different year than plant and litter cover. Also, assessment of these qualitative IRH incorporates additional site properties such as litter depth and observations of decadence. An advantage of the IRH is that they are integrative, taking into account multiple site properties for each indicator. In these cases, the IRH may approximate functions better than associated quantitative measures.

Some potential states are functionally distinct

Ecosystem structure and function are related. Many states differ in levels of at least one indicator and indicators predict the occurrence of several states (Fig. 2), consistent with our conceptual model (Fig. 1). Native Grassland and Sparse potential states were significantly related to IRH deviations from reference conditions. While sample size was too small for statistical testing, Planted Grassland and Three-tip potential states also were consistently related to deviations from reference conditions. Each of these states differed uniquely in IRH from all other states. Because they differ in both structure (plant composition based on foliar cover) and function (IRH), these four potential states likely represent alternate states of the Claypan ecological site as defined by Bestelmeyer et al. (2009).

In contrast, other potential states are not related to IRH, suggesting that these states differ in species composition but not function. The literature suggests that biotic thresholds are often crossed before abiotic thresholds (Archer 1989, Briske et al. 2005). Potential states that differ in species composition may have crossed biotic thresholds, but only if the potential states differ in abiotic processes do they actually represent alternate states. It is likely that the two potential states that were not functionally distinct, Diverse and Bluegrass, do not represent alternate states but communities that shift readily between each other (Stringham et al. 2003). Because IRH on these and the Wheatgrass potential state matched reference conditions, these potential states likely are part of a native alkali sagebrush shrubland reference state, or set of plant communities where ecological processes are operating within their historical range of variation under a natural disturbance regime for the Claypan ecological site (Bestelmeyer et al. 2009).

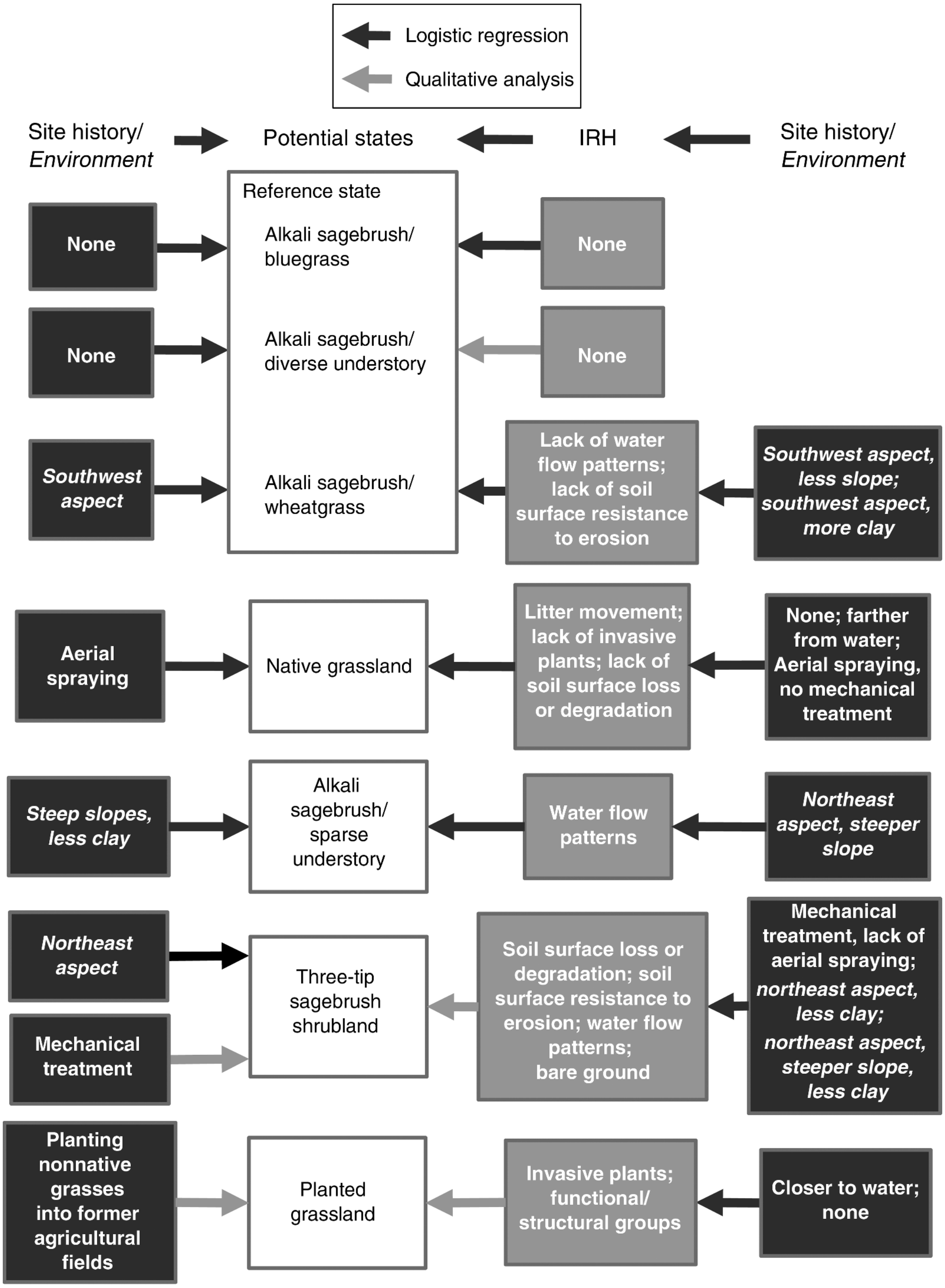

FIG. 2. Flow chart showing data-driven relationships between potential alternate states of the Claypan ecological site in northwestern Colorado, USA, and processes (IRH ratings), site history, and environmental factors. Dark arrows show statistically significant relationships ($P < 0.10$) according to logistic regression (Tables 4 and 5), while lighter arrows show relationships based on qualitative analysis. We found that structure, function, and site history were related, as expected in our conceptual model (Fig. 1). However, relationships were often not exclusive, implying that links are not as tight as expected in theory.

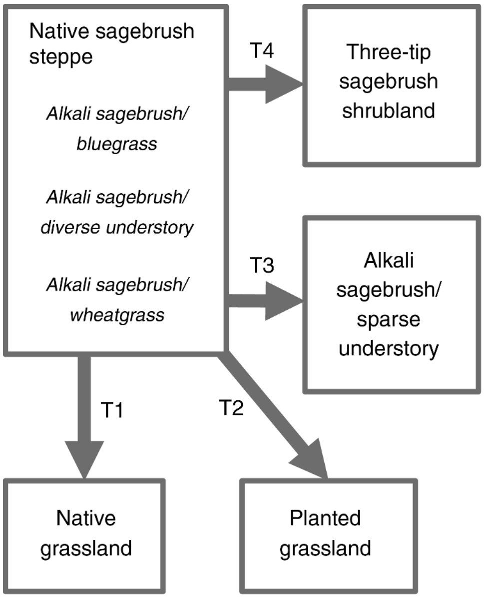

FIG. 3. Data-driven state-and-transition model for the Claypan ecological site in northwestern Colorado. The gray boxes represent alternate states with unique processes as measured by the indicators of rangeland health ratings (Table 4). Causes of transitions between states according to relationships with site history and process (Fig. 2) are marked with gray arrows. When environmental factors are important for state occurrence (Fig. 2) they are also noted. Key: T1, aerial spraying with herbicide; T2, planting nonnative grasses; T3, erosion by water, occurs on steep slopes; T4, mechanical treatment, also associated with northeast aspects.

Site history and environmental factors affect structure and function

Specific management practices are associated with three potential states (Fig. 2), likely triggering transitions to those states: spraying with Native Grasslands and (qualitatively) mechanical treatment with Three-tip and planting grasses into former agricultural fields with Planted Grasslands. These relationships between management and structure support the idea that land with similar climate, soils, and topography (e.g., an ecological site) responds similarly to management, a hypothesis that is implicit in the way STMs are discussed and used (USDA NRCS 2003). However, environmental variables also predicted occurrence of three states, showing that natural variation is a driver of ecosystem structure even within the Claypan ecological site. The Sparse potential state occurred on steeper slopes with less clayey soil texture, but was not related to any management practices that we measured. Steep slopes probably make these areas more vulnerable to crossing an erosion threshold when grazed (Fynn and O'Connor 2000), but further work is needed to show this relationship. STMs should note environmental factors like slope when they are important for ecosystem dynamics.

Management and states are related, but they do not have a one-to-one relationship except in the case of Planted Grasslands. For example, eight of 10 plots in the Native Grasslands state were aerially sprayed with herbicide, and three sprayed plots were not in this state. Combined with the importance of environmental variation, these findings suggest that management should not be used to define states a priori when constructing STMs.

Site history and environment both predicted deviation from IRH reference function (Fig. 2). Rodent activity, mechanical treatment, spraying, historical grazing intensity, and distance from water, a proxy for grazing intensity, are related to IRH levels. Environmental variation predicted deviation from IRH reference function despite the fact that we took it into account when evaluating many of the IRH. This suggests that deviation from reference conditions is more likely given certain site characteristics (e.g., accelerated erosion is more likely on steep slopes). This reinforces the need to include environmental variation in the description for each indicator on the Reference Sheet, as recommended in the IRH handbook (Pellant et al. 2005).

Our initial conceptual model of the effects of management on structure and function implies direct links among them (Fig. 1). However, our findings suggest more complex relationships between management and ecosystem structure and function, which are also modified by environmental factors like slope (Fig. 2). Relationships between particular potential states, levels of IRH, and management practices were often not exclusive. It is possible that management, structure, and function are not as tightly linked as implied by the alternate state theory-based conceptual model (Fig. 1). Also, we were unable to capture some of the important drivers of change and interaction effects within the scope of this study. Experimental approaches (Martin and Kirkman 2009, Firn et al. 2010) and local and expert knowledge (Knapp et al. 2011) are needed to complement observational studies like this one and reveal specific interactions between site history, structure, and function. In the meantime, STMs should include transition probabilities to communicate uncertainty in predicting transitions between states.

A novel approach for building data-driven STMs

The IRH were reliable and useful for approximating processes on the Claypan ecological site and constructing an objective, data-driven STM (Fig. 3) that is consistent with alternate state theory and with long-term observations by ranchers and other land managers in the area (Knapp et al. 2011). Communities within the reference state were identified by their lack of deviation from reference functions. Alternate states were differentiated from communities when functions were uniquely associated with them. Management factors and processes that predicted alternate states may cause transitions between them. While this model is based on ecological data, drawing this model was a qualitative process that also relies on knowledge from other sources such as assumptions based on ecological theory and past research. Particularly when relying on single point in time ecological sampling using a space-for-time design, we recommend involving local and expert knowledge holders in addition to ecological data collection for building STMs (Knapp et al. 2011). Experiential knowledge can provide a broader spatial and temporal context for understanding ecological changes identified through multivariate analysis of field data. This model is intended to be updated as more is learned (Westoby et al. 1989).

While our approach ensures that the model is consistent with alternate state theory, it does not test the underlying assumption that this system exhibits alternate states. Some authors caution against building models without testing these assumptions (Suding and Hobbs 2009*a*), but they also acknowledge the near-impossibility of testing them in the absence of long-term data. With evidence growing that models based on alternate state theory provide a useful framework for land management in a variety of systems and contexts (Suding et al. 2004, Martin and Kirkman 2009, Firn et al. 2010), thousands of these models are being created for land management in the United States (e.g., USDA NRCS 2003). The IRH are a relatively fast, simple addition to current model-building methods. Our approach could be used to make the empirical approach to building STMs more consistent with alternate state theory, and thus improve future models.

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