

DISSERTATION

AN ALTERNATE STATE APPROACH TO RANGE MANAGEMENT
IN THE SAGEBRUSH STEPPE

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ABSTRACT

AN ALTERNATE STATE APPROACH TO RANGE MANAGEMENT IN THE SAGEBRUSH STEPPE

Describing and predicting sudden shifts between alternate states in ecosystems is a frontier in ecology with important implications for natural resource management and human well-being. The range profession has recently adopted an approach to land management decision-making based on alternate state theory. The Natural Resource Conservation Service and partners are creating state and transition models (STMs), conceptual models that describe shifts in ecosystems, for many types of land throughout the US. Motivated by this national STM-building effort, this dissertation has two practical objectives: 1) to create data-driven STMs that describe sagebrush steppe ecosystem response to management, and 2) to develop guidelines for STM creation. A third objective grew out of the need to create theoretically accurate STMs: to determine whether spatial and temporal patterns of vegetation in northwest Colorado sagebrush steppe are consistent with predictions of alternate state theory. The first chapter introduces this work with a review of alternate state theory and how it is applied in constructing STMs. I conducted an observational study of sagebrush steppe response to management practices and ecological

disturbances on two soil types in the lower Elkhead watershed. The second chapter examines plant species composition as an indicator of alternate states, a test of the current approach to building STMs. The third chapter investigates whether areas with different structure also differ in function, as predicted by alternate state theory. The fourth chapter compares trait-based group composition to species composition as an indicator of alternate states. From these chapters, I conclude that there are large, management-relevant differences in species composition within environmentally similar areas and that many of these differences are related to site history, as would be expected if these represent alternate states. The Indicators of Rangeland Health show that some states defined by species composition are associated with unique processes that may serve as positive feedback mechanisms which maintain alternate states. Relationships between species composition, processes and environmental gradients suggest that environmental variation may make some transitions between states more likely and should be acknowledged in STMs. Multiple-trait based group composition identifies many of the same potential states and transitions as species composition, but is also sensitive to some different management practices. The Indicators of Rangeland Health and plant traits are simple additions to current STM-building methods that can improve and expedite STM creation. In the final chapter, I describe long-term sagebrush steppe dynamics based on 50 years of monitoring data from the upper Elkhead watershed and evaluate evidence for alternate states. Gradual changes in composition after spraying and the steady increase of a non-native grass suggest

that this high-elevation sagebrush steppe ecosystem does not experience sudden shifts between alternate states. I conclude that the alternate state approach to range management shows promise for describing management-relevant ecosystem dynamics and organizing current knowledge. Given the equivocal evidence supporting predictions of alternate state theory for Elkhead watershed sagebrush steppe, further research should determine which aspects of alternate state theory must be confirmed to create useful STMs. In addition, long-term monitoring, modeling, and experiments are needed to validate and update models as we learn more about the sagebrush steppe.

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Chapter 1. Introduction and Literature Review

INTRODUCTION

Ecological research has shown that ecosystems undergo major shifts in response to unpredictable environmental stresses (Scheffer et al. 2001). These shifts impact ecosystem health as well as the health of the people who depend on the goods and services that ecosystems provide (Millenium Ecosystem Assessment 2005). Although the timing of stresses to ecosystems is unpredictable, their occurrence is inevitable. The challenge is to maintain the interlinked health of ecosystems and people in the face of unpredictable stresses and ecosystem shifts.

Rangelands cover over 300 million hectares in the US and provide many important ecosystem services including provisioning of food and clean water (Havstad et al. 2007). However, semi-arid rangelands are also particularly vulnerable to catastrophic ecosystem shifts because their low and episodic resource availability limits their ability to respond to stresses (Bestelmeyer et al. 2006; Chartier and Rostagno 2006; Cingolani et al. 2005; Kefi et al. 2007). For example, in a desert grassland, drought or overgrazing can trigger grass die-off and result in erosion and soil loss; this can cause a shift to a persistent shrub-

dominated state that will not recover without intensive management (Peters and Herrick 2006). These dynamics can be explained by alternate state theory, a promising framework for describing ecosystem change (Scheffer and Carpenter 2003). Similar dynamics have been observed in semi-arid rangelands around the world including Australia, Africa and South America (Chartier and Rostagno 2006; Friedel 1991; Ludwig et al. 2005b). The application of alternate state theory to land management decision-making could aid society in avoiding unwanted ecosystem shifts and restoring ecosystem functions to degraded landscapes (Scheffer and Carpenter 2003; Suding et al. 2004).

Given accumulating evidence of sudden shifts between alternate states, the Natural Resources Conservation Service (NRCS) and partners have adopted an approach to range management based on alternate state theory (USDA NRCS 2003). State-and-transition models (STMs) are conceptual models that describe the possible configurations of biota and processes in an ecosystem and the shifts between these (Westoby et al. 1989). With an STM in hand, a manager can identify the state their land is in, anticipate the transitions that could be caused by different management actions, and weigh the opportunities and risks posed by each option. STMs provide a more realistic view of rangeland ecosystem change than older, succession-based models because they incorporate non-linear dynamics and multiple axes of change in addition to continuous changes (Briske et al. 2005). These models also provide a way of integrating and storing a set of hypotheses about ecosystem behavior from multiple sources, including local, expert, and scientific knowledge (e.g. Knapp et

al. 2011). The NRCS is currently creating STMs throughout the US that apply alternate state theory to ecosystems. There is a need for efficient ways to create data-driven STMs that are consistent with theory and that can be updated as we learn more.

Motivated by this national STM-building effort, this dissertation has two practical objectives: 1) to create data-driven STMs that describe sagebrush steppe ecosystem response to management, and 2) to develop guidelines for STM creation. A third objective grew out of the need to create theoretically accurate STMs: to determine whether spatial and temporal patterns of vegetation in northwest Colorado sagebrush steppe are consistent with predictions of alternate state theory. In this introduction, I review alternate state theory and types of evidence for alternate states, describe STMs and their utility for range management, and review some of the outstanding theoretical questions and practical considerations for creating models. In the following chapters I will focus in more detail on evidence for alternate states based on spatial variation and long-term data in the sagebrush steppe, and the use of species composition, ecosystem process indicators and plant traits for understanding sagebrush steppe dynamics and building STMs.

ALTERNATE STATE THEORY

Sudden shifts in ecosystems can be explained by alternate state theory. A state is a recognizable, persistent combination of interacting ecosystem components,

with characteristic species and processes. A state is stable if it tends to return to equilibrium when disturbed (Folke et al. 2004). A state can be thought of conceptually as a “basin of attraction”, or a ball in a cup that tends to return to the lowest point (Figure 1.1; Scheffer and Carpenter 2003). There is growing evidence that multiple alternate stable states exist in many ecosystems.

Alternate state theory arose from efforts to model the relationship between ecosystems and changes in abiotic environmental factors. Some ecosystems respond gradually to gradual changes in external conditions (Figure 1.2a; Scheffer and Carpenter 2003). Other ecosystems change rapidly when external conditions approach a critical point (Figure 1.2b). In both cases, only one state is possible given current conditions, and returning to equilibrium after disturbance is only a matter of time (Scheffer and Carpenter 2003). The concept of smooth change dates back to Clements’ theory that plant succession towards a climax state was only interrupted by external disturbances that took the ecosystem “back” to an earlier state (Clements 1916). In a third case, an ecosystem can switch to an alternate state once it crosses a critical threshold in environmental conditions (Figure 1.2c). This threshold is equivalent to bifurcation in mathematical system models, or a point at which small changes in conditions result in large changes in system behavior and equilibria (Kuznetsov 1995). Note that over a certain range of conditions, two different ecosystem states are possible (Figure 1.2c). Thresholds, or points at which a small change in process results in a large change in state variables, can be triggered by a switch in controlling variables.

The question of whether alternate states exist in particular ecosystems is important because alternate state dynamics have major implications for ecosystem management and sustaining ecosystem services. A one-state system implies that the effects of disturbance are temporary, and with sufficient time the system will return to the only equilibrium possible (Scheffer and Carpenter 2003). Most vegetation classifications in the past have relied on succession-based models such as the range condition model (Dyksterhuis 1949) that assume a one-state system for areas with a given set of environmental conditions. These models recommend simply removing the disturbance that caused the shift in order to restore ecosystems. A multi-state system, however, requires additional energy inputs to disrupt the processes maintaining each state and shift from one state to another (Figure 1.1, 2c). This view recognizes that different disturbances have different effects, and that more intensive management involving multiple disturbances is sometimes required to cause desirable shifts in ecosystems.

Evidence for alternate states identifies spatial and temporal patterns in ecological systems that are similar to the patterns predicted by alternate state theory (e.g. Figure 1.2). Evidence has been found using experiments, observational studies, modeling, and local or expert knowledge. However, evidence for alternate states can almost never be conclusive, especially when observational evidence is used (Scheffer 2009; Suding and Hobbs 2009a). Alternate states are best identified using a combination of approaches. The

discussion below draws on Scheffer (2009), but I focus on semi-arid rangelands and/or herbivory where the literature is available.

Many predictions of alternate state theory can be tested using experiments. Theory predicts that different initial states lead to different final states, a phenomenon known as path dependency. For example, experiments with floating and submerged plants growing in buckets of water have shown that at different initial plant numbers, there is a different outcome of which plant eventually becomes dominant (Scheffer 2009). Likewise, an herbivory threshold was shown when similar deer densities drove a small population of a forage plant towards extinction whereas a larger plant population was unaffected (Augustine et al. 1998). Such studies require replicates that start their development from a slightly different state and changes that can be tracked through time. Second, disturbance can trigger a shift to another state. For example, Martin and Kirkman (2009) found that removing hardwoods and re-introducing fire to wetlands in the southeastern US promoted a shift to a native herbaceous-dominated state after five years. This prediction is often easier to test than varying initial conditions, but it also requires enough time to observe the shift. Finally, a system could exhibit hysteresis in response to forward and backward changes in conditions (e.g. Figure 1.1c). Hysteresis occurs when the shift back to the original state occurs at different levels of an environmental condition than the shift to the alternate state. For example, Firn et al. (2010) studied sites dominated by a non-native grass known to reach dominance in the presence of grazing. They found that removal of grazing did not result in reduction of this grass; in contrast,

fertilization combined with continued grazing resulted in an increase in the palatability of the grass and reduced its dominance. While experiments provide the strongest evidence for alternate states, they are difficult to conduct in systems that change slowly, like semi-arid shrublands.

Observational studies can identify spatial and temporal patterns that are consistent with the predictions of alternate state theory. In a time series of a system variable, sudden jumps can be used to identify alternate states. For example, lakes in Wisconsin suddenly increase in phosphorous concentrations when anoxic conditions caused by algae blooms cause a release of phosphorous from soil into water (Carpenter et al. 2001). This triggers a shift to an alternate, eutrophic state. This example also passes another test for the existence of alternate states: changes in state follow the shape of the catastrophe fold (Figure 1.2c), or the system responds to changes in a conditioning factor according to two different functions when the system is in different states. For example, a eutrophic lake shifts back to a non-eutrophic state at a lower concentration of soil phosphorous than the concentration that triggered the initial eutrophication. Similarly, browsing by elk in Yellowstone National Park historically reduced willow and (indirectly) beaver populations; since willows established in hydrologic conditions favored by beaver ponds, reduction of elk browsing is unlikely to trigger a transition back to a willow-beaver state (Wolf et al. 2007).

In addition to changes over time, sharp spatial boundaries and multi-modality of state variable frequency distributions can be evidence of alternate

states. Many have used differences in ecosystem characteristics such as plant species composition in different locations to identify potential alternate states (e.g. Allen-Diaz and Bartolome 1998). For example, arid lands often exhibit “banded vegetation”, with patches of vegetation interrupted by areas of bare ground. Arrangement of vegetation patches is critical to the capture of water and nutrients in the landscape (Ludwig et al. 2005b). Cellular models that approximate these vegetation patterns and resource processes have suggested several spatial indicators of change from a vegetated to a bare state, including patch size and arrangement (Kefi et al. 2007).

Identification of feedback mechanisms, in the field or using mathematical models, can also support the existence of alternate states. Negative feedbacks, or processes that have a self-arresting effect on changes within the system, stabilize alternative states in ecosystems. Positive feedbacks, in contrast, are self-reinforcing changes that tend to drive a system out of an alternate stable state. Using a simple mathematical model, Noy-Meir (1975) demonstrated that overexploitation could drive alternate states in a commercial grazing system: when herbivore stocking rates are maintained at high levels, and as plant production decreases, the herbivores consume more and more of each plant because there is less and less available food, reducing production further. This positive feedback between herbivore consumption and reduced plant production can result in a shift to a low-production state, where essentially the only plants left are those that are protected from grazing (e.g. under a shrub). Similar feedbacks have been demonstrated using observational studies that establish

changes in structure and processes of ecosystems. For example, in southern New Mexico, changes in soil stability associated with mesquite encroachment have triggered a switch from grassland to mesquite shrubland (Schlesinger et al. 1990). In the sagebrush steppe, cheatgrass invasion has changed the fire regime, resulting in a positive feedback loop with more frequent fires and thus continuing cheatgrass dominance (Whisenant 1990). The threshold is crossed when structural changes trigger irreversible functional changes, as when cheatgrass density reaches a threshold beyond which the fire regime is altered. The existence of feedbacks alone, however, isn't always enough to trigger a switch to another alternate state (Scheffer 2009). Modeling and local knowledge are generally the best approaches for determining the stability of alternate states over the long-term, because long-term field data are rare.

While the theoretical implications of alternate state theory are vast, several authors have suggested that relevance to management may be a more useful way to differentiate alternate states than a theoretical basis (Rodriguez Iglesias and Kothmann 1997; Westoby et al. 1989). Evidence for alternate states can almost never be conclusive (Scheffer 2009; Suding and Hobbs 2009a). In addition, such evidence may not be necessary for the approach to be useful for management: economic analyses have shown that if threshold behavior is possible in a system, the rational action is to manage the system to avoid them (Ludwig et al. 2005a). The high costs associated with thresholds suggest the more prudent management and research agenda is to assume that ecosystems do have alternate states and to work to prove that they do not (Scheffer 2009).

STATE-AND-TRANSITION MODELS (STMs): AN APPLICATION OF ALTERNATE STATE THEORY FOR RANGELAND MANAGEMENT

State and transition models (STMs) are decision-making tools that describe rangeland ecosystem change. STMs describe potential alternate vegetation states on a rangeland site, identify possible transitions between those states, and assist range managers with recognizing opportunities to manage for favorable transitions and hazards to avoid unfavorable transitions (Westoby et al. 1989). The model takes the form of a box-and-arrow diagram (Figure 3). The boxes, or states, “represent a suite of plant community phases occurring on similar soils that interact with the environment to produce persistent functional and structural attributes and a characteristic range of variability” (Briske et al. 2008). Within a state, smaller boxes represent plant community phases, which can shift continuously among each other. Arrows between states represent transitions between states, which can be triggered by disturbances, management practices, weather, or a combination of factors. As in alternate stable state theory, continuous and reversible processes of change are dominant within states, while discontinuous and irreversible processes cause transitions between states (Briske et al. 2005). Thus, STMs can accurately describe dynamics in a variety of systems. This is a major reason that they have replaced models for ecosystem management based on linear succession (e.g. the range condition model; Dyksterhuis 1949). State and transition models have been created for a variety of ecosystems worldwide (Allen-Diaz and Bartolome 1998; George et al.

1992; Hobbs and Suding 2009; Jackson and Bartolome 2002; Stringham et al. 2001; Westoby et al. 1989).

STMs provide a framework for communicating current understanding of system behavior and organizing and integrating different types of ecological knowledge. The main use of STMs is as a decision-making tool containing a set of hypotheses about how a system works. With an STM in hand, a manager can identify the state his or her land is in, see the transitions that could be caused by different management actions and unpredictable disturbances, and weigh the opportunities and risks posed by different options (Bestelmeyer et al. 2003; Westoby et al. 1989). The risks are especially important because alternate state dynamics imply that sudden changes may occur that would be impossible or extremely costly to reverse. STMs also can accelerate learning because they store our current understanding of the dynamics of particular ecosystems. Mental models underlie all of our interactions with the world (Jones et al. 2011). Making mental models explicit as STMs can generate shared understanding among diverse actors, including the scientists and land managers involved in range management (Abel et al. 1998), and form a basis for future communication (Heemskerk et al. 2003). The information contained in an STM can then be updated as more is learned about the system, or as the system itself changes. This “explicit learning” process enhances the capacity of managers to respond to environmental stresses such as drought and adapt to novel stresses such as climate change (Roux et al. 2006).

STMs have been adopted by the Natural Resource Conservation Service (NRCS) and partners as the primary tool for assessing rangeland ecological status and interpreting monitoring data (USDA NRCS 1996). Thousands of models are currently being created for ecosystems throughout the US. Each STM is developed for a particular type of land with similar climate, soils, and potential native plant community that is thought to respond similarly to management, known as an ecological site (USDA NRCS 2003). While many STMs have been created using expert knowledge, there is increasing interest in creating STMs based on ecological data (e.g. Petersen et al. 2009) and by combining data sources (e.g. Knapp et al. 2011).

Because of the tension between management relevance and theoretical accuracy as well as the difficulty of proving alternate states' existence, STM development by the NRCS and others varies in how strictly it follows alternate state theory. In the original paper on the subject, Westoby, Walker, and Noy-Meir (1989) stated that “we are proposing [the STM] because it is a practicable way to organize information for management, not because it follows from theoretical models about dynamics”—thus, they “consider management rather than theoretical criteria should be used in deciding what states to recognize.” Many subsequent scientific papers have suggested that theoretically consistent models are more useful for management and argued for stronger links between STM development and alternate state theory (Bestelmeyer et al. 2009; Briske et al. 2008; Stringham et al. 2003). NRCS technical guidance on creating STMs

similarly emphasizes development of theoretically consistent models (USDA NRCS 2003).

Two specific points where STMs can diverge from alternate state theory are the stability of alternate states and the existence of thresholds between states. Both are central to distinguishing alternate states from communities in STMs (Briske et al. 2008, Bestelmeyer et al. 2009), but are also very difficult to establish in the theoretical sense (Scheffer 2009). Stability depends heavily on the scale being considered (Rodriguez Iglesias and Kothmann 1997), including spatial and temporal grain and extent, because systems often exhibit different stability characteristics at different scales (Turner et al. 1993). In addition, it is widely recognized that transient states can last decades and are important for management (Westoby et al. 1989, Suding and Hobbs 2009). For these reasons, stability of alternate states in STMs has been defined in practical rather than theoretical terms: by an inability to recover in timeframes that are important to management (e.g. Laycock 1991), or without restoration of key processes (Stringham et al. 2003) via some sort of active management (Bestelmeyer et al. 2009). In contrast, the existence of thresholds is required to distinguish states according to NRCS technical documents (USDA NRCS 2003). This is despite the fact that it is difficult to verify thresholds without long-term experiments and/or models, which exist only for a few ecological sites in the US. As applied in STMs, demonstration of threshold dynamics often hinges on the expert knowledge of local land managers combined with information gathered on similar

sites. However, study of thresholds is an active, fruitful area of current ecological research which has been partially motivated by the national STM-building effort.

The sagebrush steppe literature contains a wealth of information about ecosystem response to management which can inform STM development.

Below, I review the literature on potential alternate states of the sagebrush steppe. I focus on mountain big sagebrush and dwarf sagebrush plant communities because these are the communities I studied in the field. While I wrote this review independently, West and Young (2000) produced a similar list of the plant communities and causes of transitions between them in the sagebrush steppe.

Sagebrush with Diverse Understory (Reference State)

Although early ecologists argued that the sagebrush steppe region was dominated by grasses before the introduction of domestic grazing (Weaver and Clements 1938), and some early studies of graveyards and relict areas seemed to confirm this (Stoddart 1941; Wright and Wright 1948), evidence shows that sagebrush is a natural part of the ecosystem (Ellison 1960; Harniss and Murray 1973). Pre-settlement sagebrush steppe likely consisted of a fairly open stand of sagebrush shrubs, with a diverse and productive perennial grass and forb understory (Blaisdell 1953; Ellison 1960; Laycock 1991).

Domestic livestock grazing can be consistent with maintaining a diverse sagebrush state. Moderate grazing in mid to late summer and fall, after plants have mostly completed their growth and reproduction, can maintain the grass

and forb understory (Bork et al. 1998; Laycock and Conrad 1981; Mueggler 1950). Late spring and early summer grazing, when grasses and forbs are at their peak growth, is more detrimental, resulting in a decrease in the grass and forb understory and an increase in sagebrush (Blaisdell and Pechanec 1949; Crawford et al. 2004). Exclusion of domestic and wild ungulate grazing can also result in reduced herbaceous production, higher sagebrush cover, and reduced species richness and diversity (Manier and Hobbs 2007).

Fire is a characteristic disturbance of this state. Pre-settlement, mountain big sagebrush/snowberry rangelands had a historic fire return interval of 12-15 years, and mountain big sagebrush/Idaho fescue had a historic fire return interval of 15-25 years (Crawford et al. 2004). Sagebrush cover returns within a range of 10-50 years (Ziegenhagen and Miller 2009) but most often between 30-35 years (Harniss and Murray 1973; Wambolt et al. 2001; Watts and Wambolt 1996). Fire also increases perennial grass and forb cover and production within 2-3 years of treatment (Mueggler and Blaisdell 1958; Wambolt et al. 2001), especially for mountain big sagebrush communities (Crawford et al. 2004). This effect does not last beyond 12-15 years (Anderson and Holte 1981; Blaisdell 1953; Wambolt et al. 2001) and perennial grass and forb production decreases as sagebrush increases (Anderson and Inouye 2001; Harniss and Murray 1973). The fire return interval for black sagebrush, a similar species to alkali sagebrush, is 100-200 years (Crawford et al. 2004).

Cheatgrass

Cheatgrass has taken over thousands of acres of lands formerly dominated by sagebrush (Crawford et al. 2004; Weaver and Clements 1938; Whisenant 1990; Young et al. 1972). Cheatgrass invasion is thought to occur because of a variety of factors, including climate, nitrogen enrichment, and overgrazing. However, it gains dominance in the community because the fine fuels it generates burn frequently and sagebrush does not have time to re-establish (Jones and Monaco 2009; Whisenant 1990). This positive feedback sustains a cheatgrass-dominated alternate state. This state most often occurs in the warmer, drier Wyoming big sagebrush ranges and rarely in the higher, cooler mountain big sagebrush and low sagebrush ranges (Crawford et al. 2004).

Dense Sagebrush Shrubland

Dense, even-aged stands of large mountain big sagebrush are well-documented in sagebrush rangelands (Blaisdell 1953; Laycock 1994; Young et al. 1972). Mountain big sagebrush has the potential to increase in density more than other sagebrush species (Winward 2004). Often, dense stands are associated with decreased abundance and production of perennial grass and forbs (Blaisdell 1953; Manier and Hobbs 2007; Young et al. 1972) and decreased availability of forage to grazers because of physical protection by sagebrush. Dense sagebrush stands are capable of persisting for long periods even when grazing has been removed (Anderson and Holte 1981; Robertson 1947; West et al. 1984). This fits the prediction of alternate state theory that the system responds

differently to a controlling factor when it is in different states (Scheffer 2009). For this reason, dense even-aged mountain big sagebrush stands are thought to be an alternate stable state (Laycock 1991).

This state is triggered by two interacting factors: 1) overgrazing and resulting competitive superiority of sagebrush over grasses and forbs (Ellison 1960) and 2) exclusion of fire disturbance (Blaisdell 1953; Crawford et al. 2004). Removal of domestic grazing will not necessarily promote recovery of understory grasses and shrubs, although they do recover in some cases (when refugia of grasses and forbs are present; Anderson and Inouye 2001). Fire or another form of shrub control may be necessary to reduce sagebrush dominance and trigger a transition away from this state.

Eroding Sagebrush Shrubland

Excessive soil erosion in the sagebrush steppe can create soil conditions that prevent plant establishment and cause a shift to an alternate, eroding state. Many commonly-occurring disturbances cause erosion to increase, including long warm dry spells (Miller et al. 1994), moderate to severe fire (Pierson et al. 2002b; Pierson et al. 2008), and overgrazing (Blackburn and Pierson 1994). These disturbances increase erosion by removing plants and litter from a site and increasing the amount of bare ground; plants and litter slow water movement off of a site and improve infiltration, reducing runoff and erosion (Blackburn and Pierson 1994; Pierson et al. 2002a). While erosion tends to decrease as plant cover increases and litter accumulates, if these do not recover, an erosion

threshold may be crossed where the eroded soil surface does not allow plant establishment (Friedel 1991). An alternate state driven by water erosion has been described in Patagonian rangelands (Chartier and Rostagno 2006).

Planted Grassland

Many formerly cultivated lands in the sagebrush steppe have been planted with perennial grasses. Cultivation has many long-term effects on soil that likely alter site processes, including loss of soil organic matter (Burke et al. 1995), loss of the silt fraction due to repeated plowing and erosion (Burke et al. 1995), and formation of a “plow layer” that inhibits water infiltration (Schaetzl and Anderson 2005). After abandonment, agricultural lands in the sagebrush region are often colonized by annual weeds including cheatgrass, but native sagebrush steppe vegetation will replace these “over long time frames” (Ellison 1960). Under the Conservation Reserve Program (CRP), which provides technical and financial assistance to landowners for conservation of soil and other natural resources, these lands are planted to non-native perennial grasses (e.g. smooth brome, crested wheatgrass) that tend to form dense stands with few native grasses and forbs (Christian and Wilson 1999). Local land managers have indicated that it may take eighty years or more for the native sagebrush vegetation to return.

Native Grassland

Like fire, spraying herbicides that kill sagebrush releases grasses and forbs from competition and promotes a transition from dense sagebrush to native sagebrush

steppe. Initial spraying efforts used 2,4-D (2,4-dichlorophenoxy acetic acid), which killed sagebrush and often resulted in big increases in herbage production (Crawford et al. 2004; Mueggler and Blaisdell 1958). The fact that 2,4-D affects many additional plant species and may have reduced plant diversity has limited its use (Blaisdell and Mueggler 1956; Crawford et al. 2004). Tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea) was introduced in 1973 and affects only sagebrush at low application rates (Crawford et al. 2004; Whitson and Alley 1984). Application decreases sagebrush cover and can increase grass and forb production 50-500% and 15-140% even over 10-17 years (Crawford et al. 2004; Halstvedt 1994; Olson and Whitson 2002; Whitson and Alley 1984; Whitson et al. 1988; data from Halstvedt 1994). Application also does not affect long-term species richness (Olson and Whitson 2002). Success of spraying in promoting growth of perennial grasses is dependent on how many grasses are left in the understory, and spraying sometimes results in dominance of invasive annuals (Young et al. 1972). Sagebrush control also depends on soil properties: clay soils are known to bind Tebuthiuron and affect its effectiveness and residence time in the soil (Olson and Whitson 2002).

The chemically managed grasslands that result from spraying can last decades and are important to grazing management, causing many to think of sprayed areas as an alternate state (Knapp and Fernandez-Gimenez 2009b). The persistence of these grasslands is probably related to the size of sprayed areas. Sagebrush seed disperses within three meters of a plant, seed only remains viable for 2-3 years, and establishment events are rare and dependent

on favorable environmental conditions (Ziegenhagen and Miller 2009), suggesting that dispersal limitation of sagebrush is a likely cause for the persistence of this state. In the past, mostly large (>250 acre) contiguous areas were sprayed, although recent efforts have employed more irregular patterns.

BUILDING STMs: THEORETICAL QUESTIONS AND PRACTICAL CONSIDERATIONS

Because STM creation is ongoing throughout the US, now is a crucial time to test and refine methods of model building. Motivated by this national STM-building effort, this dissertation has two practical objectives: 1) to create data-driven STMs that describe sagebrush steppe ecosystem response to management, and 2) to develop guidelines for STM creation. A third objective grew out of the need to create theoretically accurate STMs: to determine whether spatial and temporal patterns of vegetation in northwest Colorado sagebrush steppe are consistent with predictions of alternate state theory. I focus on finding efficient ways to create data-driven STMs that are consistent with theory, rather than proving the theory, because the evidence required to prove that different communities truly represent alternate states requires many more resources than are usually available.

I addressed these objectives using an observational study and an analysis of long-term vegetation data from private and public rangelands in the Elkhead watershed of northwest Colorado (40° 38.5' N, 107° 12.5' W). For the

observational study, I 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 several state-and-transition models. 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). A similar approach is being taken by the NRCS in building STMs throughout the US. The observational study provides the basis for Chapters 2-4. In Chapter 5, I use long-term data to examine evidence of alternate states (Knapp and Fernandez-Gimenez 2009b; Knapp et al. 2011). Long-term data were available only on public lands which were higher in elevation and ecologically dissimilar (higher precipitation, different species) from the rest of the watershed, so they could not be used to directly test the STMs developed in earlier chapters.

Below I briefly introduce the theoretical and practical questions that motivate each chapter, and outline how they are addressed. Each chapter is formatted as a paper, with paragraph and bibliography formats corresponding to the journal targeted for publication. Chapters are written in the third person to reflect co-authorship.

Chapter 2. Differences in Plant Species Composition as Evidence of Alternate States in the Sagebrush Steppe

Alternate state theory suggests that ecosystem dynamics are driven by strong interactions among biotic and abiotic components (Briske et al. 2006). A key

prediction is that recognizable configurations of biotic and abiotic factors should repeat across the landscape, corresponding to alternate states (Scheffer and Carpenter 2003). Plant species composition is related to many ecosystem functions (e.g. infiltration; Huenneke et al. 2002; Ludwig et al. 2005b; Rietkerk et al. 2004) and thus is often used as an indicator of alternate states (Allen-Diaz and Bartolome 1998). However, plant species composition is also related to heterogeneity in soils and other abiotic characteristics due to physiological constraints imposed by different environments (Bestelmeyer et al. 2006; Gleason 1926; Whittaker 1967). Thus, differences in species composition in plots sampled at different locations cannot be interpreted as alternate states until environmental heterogeneity is ruled out.

Evidence suggests that arid and semi-arid landscapes are hierarchical: patterns arise from heterogeneity in abiotic factors at broader scales and from dynamics driven by biotic and abiotic interactions at smaller scales (O'Neill et al. 1986; Peters et al. 2006). The STM-building strategy being adopted by the NRCS and partners employs this hierarchical view. Landscape-scale patterns related to soil heterogeneity, known as ecological sites, overlie and constrain localized self-organization within environmentally similar areas (Bestelmeyer et al. 2006; McAuliffe 1994; Peters et al. 2006). Areas with different species composition within the same (theoretically uniform) ecological site correspond to alternate states.

The second chapter tests the hierarchical approach to landscapes currently applied in constructing STMs. Drawing on the assumptions of this

approach, I predict that environmental factors drive differences in species composition between ecological sites (Hypothesis A) but that, within ecological sites, species composition is related to disturbances and management factors that trigger transitions to alternate states (Hypothesis B). Alternatively, if Hypothesis A is false, then the abiotic factors on which these ecological sites are based are not good criteria for stratifying the landscape; if Hypothesis B is false, then environmental context is an important driver of species composition even within environmentally similar ecological sites and differences represent environmentally driven vegetation types rather than alternate states. I test these hypotheses by comparing species composition between and within two sagebrush steppe ecological sites on plots that have been managed differently. Based on this approach, I construct and compare two data-driven STMs.

Chapter 3. Indicators of Ecosystem Function Identify Alternate States in the Sagebrush Steppe

A major contribution of alternate state theory and the STM to ecosystem management is their emphasis on key processes that maintain desirable ecosystem states or cause transitions to undesirable states. However, most data-driven STMs rely only on structural indicators (species composition) to identify states and transitions. This approach overlooks functional attributes that distinguish states from each other (Bestelmeyer et al. 2009; Stringham et al. 2003). 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 alternate states (Stringham et al. 2003). Several recent efforts connect ecological processes to states and transitions through experiments and observation of structural and functional attributes (Chartier and Rostagno 2006; Petersen et al. 2009; Stringham et al. 2001; Zweig and Kitchens 2009), but most STMs are built using observational studies with space-for-time substitution. Experiments tend to focus on one or two states and transitions, whereas observational studies are able to encompass more of the important drivers of ecosystem change. As STMs are adopted as an assessment framework throughout the US, finding effective and efficient ways to create data-driven models that integrate ecosystem function with structure is vital.

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) 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). 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 and the USA).

The third chapter aims to 1) evaluate the utility of functional indicators (IRH) as a proxy 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. This chapter explores the

relationships between potential states, IRH, site history factors and environmental variables on plots within the Claypan ecological site. The primary questions are: how do IRH relate to quantitative measures that approximate the same processes? Do potential states that differ in plant species composition differ in IRH as well--in other words, is structure related to function? Finally, how are IRH and species composition related to site history and environmental variables? In answering these questions, I outline a data-driven approach to constructing STMs that includes ecosystem function in addition to structure.

Chapter 4. Comparing species and trait-based approaches for describing sagebrush steppe response to range management

A good indicator of alternate states should be sensitive to changes in state and the disturbances that trigger them. Plant species composition is related to environmental variation in addition to disturbance history, complicating its use as an indicator of alternate states. Plant traits are another promising way to understand and model ecosystem dynamics. A large and growing body of work links disturbances and environmental changes to changes in abundance of plant traits at the community level (e.g. Cornwell et al. 2008; Diaz et al. 2004). Using composition of plant traits in place of species composition (or combinations of species and traits) to build STMs may be useful because trait-based groups may have a stronger and more mechanistic link to management and be better indicators of change in state.

The fourth chapter compares plant species and trait-based group composition to understand ecosystem response to disturbance in the sagebrush steppe, testing the prediction that trait group composition is more related to disturbance and less related to environmental variation than is species composition. This chapter again draws on species composition data from plots with different management histories on two ecological sites. Three relatively simple trait group classification schemes were defined *a priori*, drawing on previous studies of response to disturbance in sagebrush steppe to come up with trait groups that are well established in this system. I identified plots with similar species and trait group composition using hierarchical cluster analysis. First, I evaluate whether the two approaches identify the same overall differences in vegetation. Next, I ask how potential alternate states based on trait group composition are related to site history (management and disturbance) and environmental variation. Finally, I recommend what level of specificity in trait group definition is necessary to identify alternate states on these sagebrush steppe ecological sites.

Chapter 5. Long Term Vegetation Change in California Park: Evidence for Alternate States?

Determining whether alternate states exist in particular ecosystems is important because alternate state dynamics have major implications for ecosystem management and sustaining ecosystem services. Long-term records of plant community change in the sagebrush steppe offer a unique opportunity to explore

evidence for alternate states in semi-arid rangelands. Heavy grazing in the second half of the 19th century represented an intense and novel perturbation to the ecosystem (Mack and Thompson 1982; West and Young 2000), resulting in an increase in shrubs and a decrease in understory herbaceous plants that may have constituted a shift to an alternate state. Additional disturbances over the last century, including spraying with broad-leaf herbicides and species introductions, may have triggered further shifts.

The fifth chapter describes long-term (50-60 yr) changes in plant species composition in California Park and examines evidence for alternate states in a high-elevation sagebrush system. I use loop frequency (Parker Three-step) data to describe changes in composition, and draw on photos and other supplementary information to confirm loop frequency findings. I predicted that long-term changes would be similar to those predicted by STMs from nearby private lands (Kachergis et al. in press; Knapp and Fernandez-Gimenez 2009b; Knapp et al. 2011) and other areas of the sagebrush steppe (West and Young 2000). In addition, I hypothesized that changes in composition would match the characteristics of alternate state dynamics: they would occur as jumps in the time series, they would be related to disturbance (grazing, spraying and drought history), and they wouldn't resume their original values once disturbance was removed. This case study provides valuable insights into the long-term dynamics of sagebrush rangelands that are recovering from historic overgrazing.

CONCLUSION

STMs are a promising tool for rangeland management decision-making. There is much evidence for the existence of alternate states in semi-arid ecosystems and the sagebrush steppe in particular. A review of the literature revealed five potential alternate states related to non-native plants that alter fire regimes, herbivory that alters biotic interactions between sagebrush and the understory, erosion that prevents plant understory growth and establishment, historic cultivation and subsequent planting of grasses which alters both biotic and abiotic conditions, and spraying herbicides. Experimental evidence is difficult to come by in this slowly-changing system with few long-term experimental sites. However, local knowledge confirms that these differences are important for management, regardless of whether they are “true” alternate states as proposed by theory. Indeed, economic analyses suggest that if thresholds are suspected to exist in a system, the rational decision is to try to avoid them (Ludwig et al. 2005a). Their relevance to management suggests that the burden of proof ought to be shifted towards proving that thresholds do not exist (Scheffer 2009). As the alternate state approach to range management is applied across the US, it is crucial to find efficient methods to build STMs that can then be updated as more is learned. The following four chapters explore the application of alternate state theory in building data-driven STMs that describe sagebrush steppe dynamics.

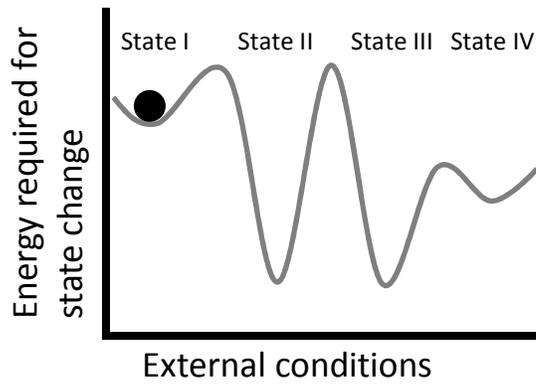


Figure 1.1. Conceptual diagram of potential alternate states in an ecosystem under different external conditions (modified from Scheffer et al. 2001 and George et al. 1992). The ball represents the current state of the system, and different “cups” show potential alternate states or domains of attraction.

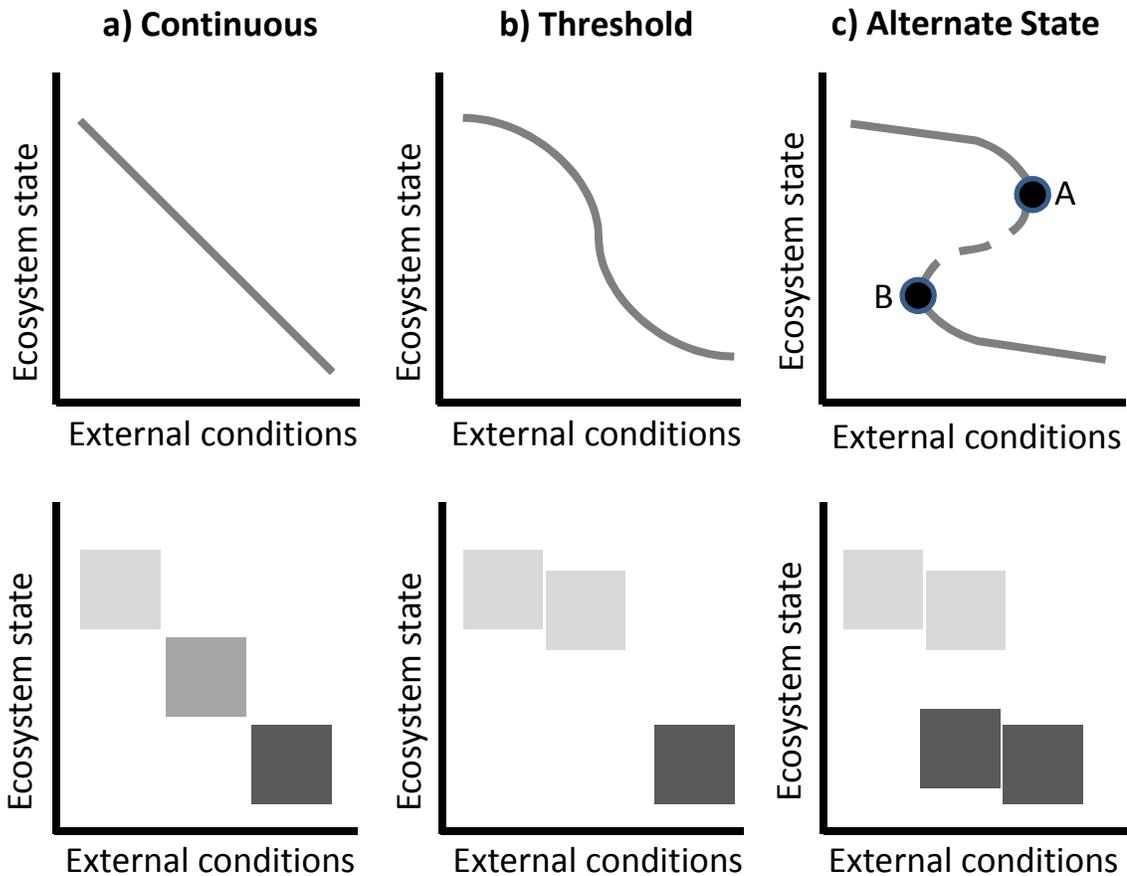


Figure 1.2. Contrasting ecosystem state responses to changes in external conditions (adapted from Scheffer and Carpenter 2003 and Suding and Hobbs 2009b). Ecosystem state is a unique combination of biota and processes operating within a normal range of variability, but is represented by a relatively quickly-changing state variable in this diagram (e.g. plant cover). External conditions are either independent of the system or so slowly-changing as to be almost independent. Specific examples of external conditions include ecosystem management (e.g. grazing) or environmental processes (e.g. nutrient accumulation), in which case these model make contrasting predictions about state change over time. Environmental gradients (e.g. soil texture) can also be external conditions, in which case these models make contrasting predictions about state changes across space. a) Smooth, gradual response to external conditions. b) Approaching a certain level in external conditions, there is a large change in ecosystem state with only a small change in external conditions. c) Beyond the critical levels in environmental conditions (A, B), a state change occurs due to a shift in the underlying processes that maintain the state. The shift back occurs at a different level of external conditions than the shift to the state occurred at, a phenomenon known as hysteresis.

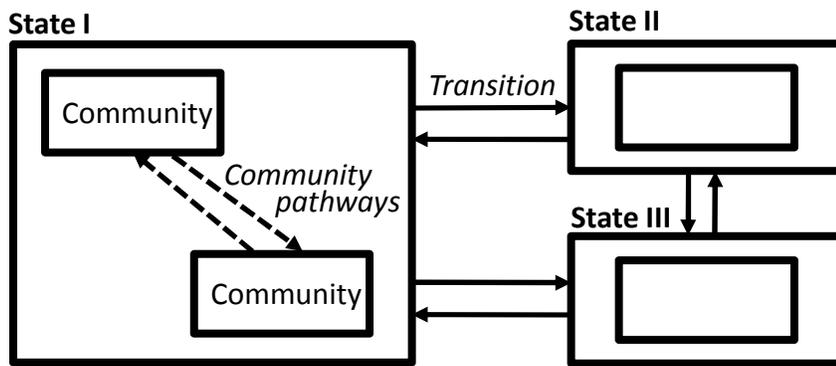


Figure 1.3. Conceptual diagram of a state and transition model (adapted from Stringham et al. 2001 and Bestelmeyer et al. 2003). See text for explanations of states, transitions, communities, and community pathways.

Chapter 2.
**Differences in Plant Species Composition as Evidence of Alternate States
in the Sagebrush Steppe**

ABSTRACT

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. As STMs are created throughout the US, it is crucial to ensure that they are supported by ecological evidence. Plant species composition reflects ecosystem processes that are difficult to measure and may be a useful indicator of alternate states. This study aims to create data-driven STMs based on plant species composition for two ecological sites in northwestern Colorado. We sampled 76 plots with different management and disturbance histories. We hypothesized that 1) differences in species composition between the two ecological sites would be related to environmental factors and 2) differences in species composition within each ecological site would be related to management and disturbance history, consistent with the ecological site concept. Relationships between species composition, site history, and environmental variables were evaluated using multivariate statistics. We found that between ecological sites, species composition was related to

differences in soil texture, supporting our hypothesis and the creation of separate models of ecosystem dynamics. Planted grasslands differed in species composition from all other plots, regardless of ecological site. Evidence for the second hypothesis was equivocal. Species composition was related mostly to site history on one ecological site, consistent with alternate states at this scale. Species composition on the other ecological site is related to both site history and environmental factors, suggesting that this ecological site does not serve as a uniform physical template upon which plant community dynamics play out. This data-driven, plant species based approach created two objective, credible STMs with potential alternate states and transitions that are consistent with the sagebrush steppe literature. Our findings support the hierarchical view of landscapes currently applied in building STMs. An approach that acknowledges environmental heterogeneity within ecological sites is necessary to separate site history and environmental variability as drivers of species composition and 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 (Bestelmeyer et al. 2003; Suding and Hobbs 2009b; Westoby et al. 1989). STMs describe threshold shifts in ecosystems, which are especially likely in semi-arid rangelands with a short history of grazing

like the sagebrush steppe of western North America (Cingolani et al. 2005). Threshold shifts often have unexpected, negative impacts on ecosystem services (Scheffer et al. 2001). The US Department of Agriculture Natural Resources Conservation Service (NRCS) and partners are currently developing thousands of these models for use in land management across the US, and STMs are being developed and used in Mongolia, Africa, Australia, and elsewhere (Sasaki et al. 2008; Suding and Hobbs 2009a). Models are often developed based on expert knowledge with little published quantitative ecological evidence (Suding and Hobbs 2009b). As a consequence, the causes of vegetation change depicted in many models may reflect assumptions grounded in mainstream range management ideas rather than empirically derived or tested relationships (Rodriguez Iglesias and Kothmann 1997). Recent efforts have focused on creating models based on ecological data (Bestelmeyer et al. 2009; Martin and Kirkman 2009; Petersen et al. 2009). This study evaluates variation in species composition as evidence of alternate states for two sagebrush steppe soil types.

Alternate state theory suggests that ecosystems are self-organizing, meaning that strong interactions among biotic and abiotic components drive dynamics. Specifically, feedback mechanisms associated with individual states either maintain a persistent state (self-arresting negative feedbacks) or cause transitions to other states (self-reinforcing positive feedbacks; Briske et al. 2006). In semi-arid rangelands where resources are scarce, processes that influence water and nutrient storage in soils are major feedback mechanisms (e.g. infiltration; Huenneke et al. 2002; Ludwig et al. 2005b; Rietkerk et al. 2004). Plant

species composition is often related to differences in these key processes (Blackburn et al. 1992; Rietkerk et al. 2004; Schlesinger et al. 1990). Switches in feedbacks can be triggered by disturbances or management practices and cause transitions to other states. For example, increased grazing in Chihuahua desert grasslands increases grass mortality and triggers soil erosion, causing a shift to a patchy shrubland alternate state (Schlesinger et al. 1990). The self-organizing view of rangeland dynamics predicts that areas with similar environmental characteristics can support multiple, relatively stable (self-replacing) species assemblages that correspond to alternate states with unique feedback processes (Suding and Hobbs 2009b). Thus, if this view is correct, plots sampled at different locations can be grouped into alternate states based on species composition (Allen-Diaz and Bartolome 1998). The state of an area at a point in time should be determined by site history factors (i.e. disturbance and management history) that make states vulnerable to transitions. An important implication of this view is that management will not always trigger an alternate state, since thresholds where feedbacks switch will not be crossed every time a management practice occurs.

An alternative view is that heterogeneity in abiotic factors such as soil texture drives differences in plant species composition and changes over time in different locations (Gleason 1926; Whittaker 1967). Plant species have different demographic survival and growth rates in different environments due to physiological constraints imposed by those environments (Gleason 1926; Whittaker 1967). For example, soil parent material is a factor in the “lithic

inheritance” of a region which controls particle size distribution and nutrient status, and different soils provide different amounts of water, nutrients, and anchorage for plants (Monger and Bestelmeyer 2006). According to this gradient view of the landscape, every location will differ slightly in soils and/or other site characteristics, and plant species composition and responses to disturbance are driven by these differences. Thus, differences in species composition in plots sampled at different locations should be related to environmental variation.

Evidence suggests that arid and semi-arid landscapes are hierarchical: patterns arise from heterogeneity in abiotic factors at broader scales and from self-organizing dynamics driven by biotic and abiotic interactions at smaller scales (Bestelmeyer et al. 2006; McAuliffe 1994; O'Neill et al. 1986; Peters et al. 2006). The STM-building strategy being adopted by the NRCS and partners employs this hierarchy. Land is first classified into types with similar soils, climate, potential vegetation, and dynamics in response to management and disturbance, known as ecological sites (Bestelmeyer et al. 2009; NRCS 2003). Land within each ecological site is then classified into alternate states with different self-organizing processes (Bestelmeyer et al. 2009). In this study, we identify potential alternate states on two co-occurring ecological sites in the sagebrush steppe of Northwestern Colorado (Figure 2.1). Claypan is characterized by a thin clay loam or clay surface soil overlying deep clay subsoils, and is dominated by alkali sagebrush (*Artemisia arbuscula* ssp. *longiloba*). Mountain Loam is characterized by loam or clay loam surface soils

overlying deep clay loam or clay subsoils, with mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*).

Like many efforts to create data-driven STMs, we use plant species composition as evidence of differences in processes and thus alternate states (Allen-Diaz and Bartolome 1998; Jackson and Bartolome 2002; Oliva et al. 1998; West and Yorks 2002). Species data are widely available, easy to collect, and relevant for range management. Multivariate statistical methods are often used for identifying potential alternate states and transition triggers. Identifying states using multivariate analyses, rather than a priori based on expert knowledge, helps free this process from subjectivity or bias (Allen-Diaz and Bartolome 1998; Foran et al. 1986). An “indirect gradient approach” relating species composition to multiple management and disturbance factors is desirable for building STMs because it examines trends in species composition as evidence of alternate states, rather than assuming a priori that states exist (Keddy 1991).

This paper has three objectives: 1) to describe the differences in soils and plant species composition between the two sagebrush steppe ecological sites, 2) to identify the major trends in plant species composition within each ecological site and evaluate whether the self-organized or gradient view is supported by those trends, and 3) to construct a data-driven state and transition model for each ecological site. We sampled plots with similar climates but different management histories on two ecological sites to infer the effects of management on these areas. We describe major trends in plant species composition using ordination, and define potential states based on plant species composition using

hierarchical cluster analysis. By relating species composition to site history as well as soil and environmental characteristics, we evaluate which view of ecosystem dynamics is supported at each scale: between ecological sites and within ecological sites. We hypothesize that between ecological sites, environmental factors will be associated with differences in species composition (Hypothesis A). However, within ecological sites, site history should be associated with differences in species composition, corresponding to self-organized alternate states that repeat across the landscape (Hypothesis B). Alternatively, if Hypothesis A is false, then the abiotic factors on which these ecological sites are based are not good criteria for stratifying the landscape; if Hypothesis B is false, then environmental context is an important driver of species composition even within environmentally similar ecological sites and differences represent environmentally driven vegetation types rather than alternate states. We use this approach to build and compare two data-driven state and transition models based on plant species composition.

METHODS

We used point samples of soils and vegetation with different site (management and disturbance) histories to infer the effects of these practices and disturbances on sites with similar environmental characteristics. Space-for-time substitution is necessary in studies like this one that aim to describe long-term ecosystem responses to disturbance in areas where long-term data are lacking. Ewers and

Pendall (2008) found high replicability in vegetation responses to disturbance across three Wyoming sagebrush sites, supporting this design in burned and sprayed sagebrush steppe.

Site Selection

Data were collected on private and public rangelands in and around the Elkhead watershed of Northwestern Colorado (lat 40°38.5'N, long 107°12.5'W; Figure 2.1). Fifteen private landowners, the Bureau of Land Management (BLM), and the US Forest Service (USFS) permitted us to sample on their land (about 60% of the watershed). A detailed inventory of site management history was conducted through landowner interviews (Knapp and Fernandez-Gimenez 2009b) and review of agency (NRCS, BLM, USFS) records. Sampling focused on the Claypan and Mountain Loam ecological sites, two types of land with characteristic soils, climate, and vegetation (USDA NRCS 2003). While these currently only exist as range sites, an earlier concept, we refer to them as ecological sites throughout the paper because this work is conceptually grounded in the ecological site concept and this work is meant to contribute towards developing the revised ecological sites. Areas that represent all existing combinations of management histories were identified: historic grazing intensity, a qualitative estimate of typical stocking rate based on interviews with 26 local land managers (Knapp 2008); cultivation/seeding history; and shrub management practices including aerial spraying, mechanical treatment, or none.

Plot locations were stratified first by ecological site and then by management history and randomly located at least 200 m apart.

Soil and plant species data were collected within 20 x 50 m plots. We sampled 76 plots for vegetation in 2007 and 2008 and for soils in 2009.

Soil Data Collection

Soil data were collected to validate that sampled plots matched the Claypan and Mountain Loam ecological sites, and to relate trends in species composition to soil variability. Soil descriptions following NRCS protocols (Schoeneberger et al. 1998) were based on a soil pit or auger hole ≥ 50 cm deep in the center of each plot. We recorded texture, structure, color, root density, and carbonates in each layer. The ecological site was verified by matching each soil description with the Claypan and Mountain Loam range site soil descriptions (SCS 1975). Plots were removed from analysis if their soil characteristics were unusual for these ecological sites (shallow, rocky, etc). Claypan is characterized by a thin clay loam or clay A horizon and a fine-textured subsoil that restricts water movement and availability; Mountain Loam is characterized by a thicker loam or clay loam A horizon and clay loam or clay subsurface.

Plant Species Composition

We measured plant cover by species using 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.

Species names reported here correspond to the USDA PLANTS database (USDA 2010).

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. Categorical site history variables were determined by communicating with land managers and included historic grazing intensity (low to high), chemical shrub treatment (spraying), mechanical shrub treatment, seeding with grasses (including enrollment in CRP, Conservation Reserve Program), or none. 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). Static environmental factors, such as topographical context, are also related to species composition and may make certain transitions more likely in some areas within an ecological site relative to others. We recorded environmental variables in the field including slope, aspect, and hillslope position. Aspect was transformed into a continuous variable with higher values for more productive northeastern slopes and low values for southwest slopes (Beers et al. 1966).

Data Analysis

To compare Claypan and Mountain Loam soils, we report averages, standard deviations, and standard errors for soil characteristics. We average over each of

the top three soil horizons in order to give a general idea of the soil profiles and because we described these for all plots.

For multivariate analyses of plant cover data, plant cover values were square root transformed to reduce the influence of very common species. Species that occur in fewer than 5% of plots were omitted to reduce noise in the data (McCune and Grace 2002) and to ensure that more common species drove the definition of states. In addition, three annual forb species were omitted because of differences in abundance in different sampling years.

We used Non-metric Multi-dimensional Scaling (NMS; Kruskal 1964) to describe the relationship between plant species composition and site history and environmental variables (Hypotheses A and B). This indirect ordination method arranges plots in ordination space based on similarity in species composition. Environmental and site history variables are correlated with ordination axes after the ordination is performed. If there are important gradients that we did not measure, this method will reveal an unexplained trend in species data. NMS does not require assumptions about the underlying distribution of species along an environmental gradient, and is thus well suited for non-normal data on discontinuous scales often found in community ecology. NMS searches iteratively for the best positions of plots and species on a pre-defined number of axes while minimizing the “stress” of ordination. Conceptually, “stress” is a measure of how poorly distances in the original dissimilarity matrix and distance in the ordination space correspond to each other. Thus, NMS attempts to place the plots in ordination space such that the differences between plots correspond

to the pairwise dissimilarities in species composition between plots. We chose the number of dimensions beyond which reductions in stress are small, and used a Varimax rotation to maximize correlations between axes and environmental variables. We used Sorensen's (Bray-Curtis) proportional distance measure to calculate the dissimilarity matrices for species composition at different plots (Wishart 1969).

Potential alternate states were identified using agglomerative hierarchical cluster analysis of plant species cover data. Agglomerative hierarchical cluster analysis sequentially merges plots with similar species composition into larger groups (Dufrene and Legendre 1997; McCune and Grace 2002). We used Sorensen's distance measure to calculate the plot dissimilarity matrix that is the basis for merging similar groups. We used the flexible beta linkage method ($\beta = -0.25$) because this space-conserving method is compatible with Sorensen's distance (McCune and Grace 2002). Indicator species analysis, which generates an indicator value between 1-100 based on the faithfulness and exclusiveness of species to groups of plots, was used to prune the cluster dendrogram (Dufrene and Legendre 1997). Pruning occurred at the number of groups with the lowest average p value for species based on a randomization test (1000 randomizations), interpreted as the most ecologically meaningful number of groups (McCune and Grace 2002). Transitions between potential states were identified based on their management and disturbance histories and relationships to environmental variables. NMS assisted with this process by quantifying

associations of particular management practices, disturbances, and environmental variables with variation in plant species composition.

We compared species composition between ecological sites and among potential states using pairwise Multi-Response Permutation Procedure (MRPP) with a Bonferroni correction. MRPP tests the hypothesis of no differences among groups of plots (McCune and Grace 2002). This non-parametric method compares the observed weighted mean within-group distance in a distance matrix to the distance that would be expected by chance. The test statistic is the observed mean minus the expected mean divided by the expected standard deviation, similar to the Student's t. This test produces a p-value and a measure of effect size called the chance-corrected within-group agreement (A) which ranges from 0 (no effect) to 1. In ecological studies, a high value is greater than 0.3 and many values are less than 0.1 (McCune and Grace 2002).

RESULTS

Comparing Soils and Plant Species Composition in two Soil Types

Soils. We identified 41 Claypan and 35 Mountain Loam plots based on soil characteristics. The largest difference between soils in the two ecological sites is texture: Claypan has higher clay content in all horizons (Table 2.1). Other differences in soil properties are related to texture. Soil color is lighter in Claypan, indicating lower organic matter as expected on this lower-production

soil. Roots are generally denser in Mountain Loam soils. Carbonates are more common in the third horizon of Claypan soils.

Greater standard deviations in many soil properties indicated higher heterogeneity within Mountain Loam soils. Surface textures vary from loam to clay loam and subsurface textures vary from clay loam to clay. This heterogeneity is consistent with the Range Site Description (SCS 1975).

Trends in Species Composition. This analysis includes all plots in the Claypan and Mountain Loam ecological sites (N = 76). Environmental variables as well as soil properties were included as possible explanatory variables.

Species composition in the Claypan and Mountain Loam ecological sites differs more than expected by chance (MRPP; $A = 0.08701$; $p < 0.001$). NMS showed that variation in species composition was best explained along 2 axes (76 plots, 77 species; final stress = 18.99, final instability = 0.00001, 74 iterations; Figure 2.2). The cumulative variation explained by the ordination is 80.6% (Axis 1: $r^2 = 0.39$; Axis 2: $r^2 = 0.42$).

Axis 1 separates the Claypan from the Mountain Loam ecological site along a soil texture gradient. Total plant cover, species richness, basal cover of litter, and very fine roots in the top soil horizon increase with this axis ($r = 0.61$, 0.49 , 0.50 , and 0.47 , respectively) and field-determined percent clay in the top 3 soil horizons decreases ($r = -0.50$, -0.65 , and -0.63). The value of the soil color in the first horizon and the chroma of the second soil horizon both decrease ($r = -0.59$, $r = -0.56$), indicating darker and less intense colors. Claypan indicator

species include *Artemisia arbuscula* ssp. *longiloba*, *Koeleria macrantha*, and *Pascopyrum smithii*, while Mountain Loam indicator species include *Artemisia tridentata* spp. *vaseyana*, *Symphoricarpos rotundifolius*, and *Achillea millefolium* (Figure 2.2).

Axis 2 is related to seeding of forage grasses. CRP status is negatively related to this axis ($r = -0.60$). Some seeded plots were not enrolled in CRP, and they also are negatively associated with this axis. In contrast, cover of perennial forbs increases. Planted Grasslands were significantly different in species composition from all other plots ($A = 0.0402$, $p < 0.0001$). Indicator species of these grasslands were the non-native grasses *Thinopyrum intermedium* and *Bromus inermis* as well as *Elymus lanceolatus* and *Pseudoroegneria spicata*. Planted grasslands were removed from subsequent analyses because of their difference in species composition.

Trends in Species Composition within Ecological Sites

Claypan Ecological Site. Hierarchical cluster analysis and Indicator Species Analysis (ISA) of species composition by plot identified potential alternate states. Seven groups had the lowest average p value for species based on the randomization test (ISA; 0.13). We combined two groups that were similar in species composition and characteristics except for differences in ephemeral forb cover related to a late, moist spring in one sampling year. The resulting six potential states, referred to by their short names in parentheses from

here on, are: Diverse Alkali Sagebrush Shrubland (Diverse), Alkali Sagebrush/Bluegrass Shrubland (Bluegrass), Alkali Sagebrush/Western Wheatgrass Shrubland (Wheatgrass), Native Grassland (Native Grassland), Three-tip/Mountain Big Sagebrush Shrubland (Three-tip), and Alkali Sagebrush Shrubland with Sparse Understory (Sparse). The within-group similarity in species composition is greater than expected by chance (MRPP; $A = 0.2103$; $p < 0.0001$), and most groups are significantly different in species composition when compared pair-wise (Table 2.2). The largest differences in species composition are between Sparse and other potential states. Indicator species for each state are listed in Table 2.4. Total plant cover and site characteristics for each state are listed in Table 2.4. Total plant cover and site characteristics for each state are listed in Appendices 1 and 2, and average cover of particular species is listed in Appendix 3.

NMS identified major trends in species composition and associations with site history and environmental variables for Claypan potential states. The final stress for the three-dimensional NMS solution is 14.08 and the final instability is 0.00001 after 58 iterations on 39 plots and 41 species (Figure 2.3). The cumulative variation in plant species composition explained by the three axes is 84% (Axis 1: $r^2 = 0.07$; Axis 2: $r^2 = 0.11$; Axis 3: $r^2 = 0.66$). Along Axis 1, perennial grass cover ($r = 0.48$) increases and shrub cover ($r = -0.58$) decreases. Spraying ($r = 0.54$) increases with this axis. With Axis 2, basal bare ground cover decreases ($r = -0.52$) as does perennial forb cover ($r = -0.55$). Mechanical treatment increases with this axis ($r = 0.41$). With Axis 3, perennial grass and forb cover increase ($r = 0.64, 0.47$) and shrub cover decreases ($r = -0.70$), but no

site history factors were related to this axis. Proxies for grazing intensity were weakly related to trends in species composition; distance from water weakly decreases ($r = -0.21$) and historic grazing intensity weakly increases ($r = 0.11$) with Axis 1, suggesting a slight increase in grazing as this axis decreases.

Factors that influence transitions are suggested by the NMS and the management histories of the potential states (Table 2.4). The Grassland potential state is associated with aerial spraying of herbicide. While only weakly evident from the NMS, two out of four Three-tip plots were mechanically treated. The Bluegrass, Wheatgrass, and Diverse states overlap on the ordination and were not associated with site history. The Sparse potential state differed the most in species composition from all other potential states, but was also not related to site history.

Mountain Loam Ecological Site. Hierarchical cluster analysis and Indicator Species Analysis (ISA) of species composition by plot identified potential alternate states. Five groups had the lowest average p values for all species according to the randomization test (ISA; 0.0257), so the cluster dendrogram was pruned at this level. The resulting potential states, hereafter referred to by their short names in parentheses, are: Diverse Mountain Big Sagebrush Shrubland (Diverse), Mountain Big Sagebrush/Western Wheatgrass Shrubland (Wheatgrass), Three-tip/Mountain Big Sagebrush Shrubland (Three-tip), Mountain Big Sagebrush Shrubland with Sparse Understory (Sparse), and Dense Mountain Big Sagebrush Shrubland (Dense). The within-group similarity

in species composition is greater than expected by chance (MRPP; $A = 0.1889$; $p < 0.0001$), and all groups are significantly different in species composition when compared pair-wise (Table 2.3). Differences are greatest when comparing Dense to all other groups. Indicator species for each state are listed in Table 4. Total plant cover and site characteristics for each state are listed in Appendices 1 and 2, and average cover of particular species is listed in Appendix 3.

NMS identified major trends in species composition and associations with site history and environmental variables for Mountain Loam potential states. The final stress for the three-dimensional NMS solution on 33 plots and 56 species is 13.44 and the final instability is 0.00001 after 78 iterations (Figure 2.4). The cumulative variation explained by the ordination is 84% (Axis 1: $r^2 = 0.34$; Axis 2: $r^2 = 0.21$; Axis 3: $r^2 = 0.29$). With Axis 1, aggregate percent forb cover decreases ($r = -0.47$) and shrub cover increases ($r = 0.58$). Spraying is negatively associated with this axis ($r = -0.45$). Elevation decreases with this axis ($r = -0.47$). With Axis 2, perennial forb cover decreases ($r = -0.56$). Burning increases with this axis ($r = 0.51$). Field-determined percent clay in the top three horizons decreases ($r = -0.38, -0.55, -0.59$). With Axis 3, perennial grass cover decreases ($r = -0.65$) and perennial forb cover increases ($r = 0.48$). Mechanical treatment decreases with this axis, but the association is weak ($r = -0.19$). Historic grazing intensity, a qualitative measure of stocking rate over time, was weakly associated with Axis 3 ($r = 0.26$). Distance from water, another proxy inversely related to grazing intensity, was weakly associated with axis 2 ($r = 0.166$).

Factors that influence transitions are suggested by the NMS and the site histories of the potential states (Table 4). Aerial spraying of herbicides is associated with the Diverse state. Two burned plots fell into the Sparse potential state. One mechanically treated plot was in the Three-tip potential state. The Dense potential state is related to a lack of recent disturbance—one plot is known to have burned about 60 yr ago. In addition to site history, potential states were related to soil texture, with the Wheatgrass potential state at the clayey end of the gradient and Dense and Sparse at the other end.

DISCUSSION

Soil Texture and Seeding History Drive Species Differences across Ecological Sites

The largest difference between Claypan and Mountain Loam soils was texture, consistent with the fact that the two ecological sites are defined largely by texture (SCS 1975). Mountain Loam soils were more heterogeneous than Claypan soils, something that is evident also in the greater variety of soils that are classified as Mountain Loam in NRCS soil maps (USDA NRCS 2009).

Differences in plant species composition were associated with different soil characteristics and ecological sites, supporting our prediction that larger-scale patterns in species composition are driven by soil, climate, and topographic heterogeneity, as represented by ecological sites (Hypothesis A). In addition to species differences, Mountain Loam plots have higher shrub and total foliar cover

and higher species richness. These are consistent with the increased water infiltration and storage due to the coarser surface texture over a relatively fine subsurface texture in Mountain Loam vs. Claypan (Schaetzl and Anderson 2005). Unlike soil characteristics, Claypan and Mountain Loam plots have similar variability in species composition, as indicated by their relatively close grouping in the ordination (Figure 2.2).

Formerly cultivated plots that had been seeded with grasses drove the other major difference in plant species composition across ecological sites. Species composition in Claypan and Mountain Loam seeded grasslands are similar, despite the difference in soils. This likely reflects similar initial species seeded at these plots, taken from a recommended species list. While the soils are different, the medium term (25+ yr) effects of this management practice on species composition appear generalizable across ecological sites.

Site History is More Closely Related to Species Composition within the More Homogeneous Ecological Site

In Claypan, most differences in species composition were associated with site history and not environmental variables. This finding supports our prediction that species composition within this ecological site is related to differences in management and process rather than heterogeneity in abiotic factors (Hypothesis B), a hypothesis that is inherent in the way STMs are created and used. This is consistent with the self-organized view of plant community dynamics suggested by alternate state theory (Suding et al. 2004), with

endogenous biotic and abiotic interactions driving dynamics at the plot scale. In contrast, Mountain Loam species composition is related to both site history and environmental variation, contrary to our expectation (Hypothesis B). Soil texture drives trends in species composition: perennial forb cover increases with percent clay, and shrub cover decreases.

Contrasting findings for Hypothesis B in the two ecological sites may be related to the greater heterogeneity in soils within the Mountain Loam vs. the Claypan ecological site. There are two possible explanations of variation in species composition within Mountain Loam: 1) differences in species composition are related mainly to environmental variation (e.g. Gleason 1926); or 2) environmental characteristics interact with site history factors to make certain transitions more likely (e.g. Peters et al. 2006). We suspect the latter because management and environment were both related to trends in species composition, and not all plots with particular environmental characteristics are in the same potential state. This suggests a self-organizing view of ecosystem dynamics with transitions that are influenced by proximate environmental characteristics (e.g. Fynn and O'Connor 2000). STMs should note instances where environmental differences may influence dynamics.

Two Ecological Sites Have Similar and Contrasting States and Dynamics

Based on relationships between species composition-derived potential states and site history variables, we constructed two STMs of response to management and disturbance for the Claypan and Mountain Loam ecological sites (Figure

2.5). Management actions and disturbances were associated with potential states, consistent with the theoretical concept of alternate states. Environmental heterogeneity also has an influence and is noted within the models.

Comparison between the two STMs reveals many similarities in the effects of management on these ecological sites. The Diverse potential states in both ecological sites had greater cover and higher diversity of understory plant species than all other groups, granular soil structure, higher organic matter content, and no invasive species, consistent with others' descriptions of "reference states" for sagebrush steppe (Crawford et al. 2004; NRCS 2003). Wheatgrass potential states are the most frequent and were similar to reference states except for the dominance of western wheatgrass and lower sagebrush cover. Others have reported a wheatgrass-dominated state in Wyoming big sagebrush steppe related to heavy spring grazing (Cagney et al. 2010); more research is needed to establish this link on these ecological sites. Three-tip sagebrush characterized potential states associated with mechanical treatment on both soil types, consistent with the literature about this re-sprouting shrub (Winward 2004).

However, several key differences in response to management justify division of Claypan and Mountain Loam into two ecological sites (USDA NRCS 2003). Spraying herbicides that kill shrubs has a different effect on the two soil types. Claypan plots that were sprayed 20+ yrs ago are persistent Native Grasslands, and Mountain Loam plots are Diverse shrublands with abundant re-sprouting shrubs and forbs. The known short-term effect of spraying is a

decrease in shrubs and increase in grasses, but mountain big sagebrush re-establishes over 10-20 yrs (Crawford et al. 2004; Wambolt and Payne 1986). This finding is likely due to more rapid re-establishment and growth of mountain big sagebrush and re-sprouting shrubs relative to alkali sagebrush. The Claypan Bluegrass potential state was similar to Diverse except for a more homogeneous understory of *Poa secunda*; it has no analogue in Mountain Loam. Similarly, the Mountain Loam Sparse potential state is similar to the Dense but with higher grass cover; it has no analogue in Claypan.

The largest differences in species composition in both ecological sites remain unexplained by site history, except that they lack disturbance or management to reduce shrub cover. The Sparse Claypan potential state and the Dense Mountain Loam potential state were the most different from all others, with the highest shrub cover and low grass and forb cover. Both states also have a less clayey soil texture, but there are plots with similarly coarse textures that are not in these states. This further suggests that an interaction between environmental variation and management may trigger switches in processes and result in a transition to these potential states. For example, increased grazing has been shown to trigger soil erosion on steeper slopes (Fynn and O'Connor 2000), one possible mechanism for these states. Including measurements of processes at each site in addition to site history may reveal mechanisms for the species differences observed here (Kachergis et al. in press; Stringham et al. 2003).

Measures of grazing intensity at each plot (distance from water, grazed class, and historic grazing intensity) did not show strong associations with

species composition. Grazing patterns are a complex function of landscape characteristics and animal behavior that are difficult to approximate with simple measures (Bailey et al. 1996). The relatively strong effects of other management practices also may obscure the effects of grazing on species composition. Controlled grazing experiments, a sampling scheme that explicitly addresses grazing patterns, and/or expert and local knowledge are needed to determine grazing effects on these plant communities.

IMPLICATIONS

Plant species composition is useful as evidence of alternate states for creating data-driven STMs in the sagebrush steppe. Our findings support the hierarchical view of landscapes currently applied in building STMs (e.g. Bestelmeyer et al. 2009). In addition, we suggest several ways to improve STMs built using plant species composition. First, an approach that acknowledges soil and environmental heterogeneity is necessary to ensure that heterogeneity is not driving species composition and to elucidate cases where specific abiotic conditions make transitions more likely. Second, additional information to species composition is needed to differentiate between alternate states separated by ecological thresholds and communities that can shift continuously between each other. Process indicators like the Indicators of Rangeland Health can identify feedback mechanisms and distinguish between alternate states and communities (Kachergis et al. in press). The approach presented here,

comparing species composition and using space-for-time substitution, is one helpful tool in a diverse toolbox for understanding complex landscapes. These STMs will benefit from integration with and validation by additional types of information, including expert and local knowledge (Knapp and Fernandez-Gimenez 2009b; Knapp et al. 2011), long-term monitoring data (Allen-Diaz and Bartolome 1998), and dynamic models (Plant et al. 1999).

Table 2.1. Soil characteristics of Claypan and Mountain Loam plots in northwestern Colorado. For root density, numbers correspond to density classes as follows: 1 is < 1 per cm² (Few); 2 is 1-5 per cm² (Common); 3 is > 5 per cm² (Many). Carbonate stages are as follows: 0 is none; 1 is carbonate filaments and/or grain coatings; 2 is carbonate nodules.

Soil Property	Measurement	Horizon	Claypan			Mountain Loam		
			Mean	Std. Dev.	Std Error	Mean	Std Dev	Std Error
Texture	% Clay (top 10 cm)	-	52.4	8.4	1.3	30.9	9.9	1.6
	% Clay	1	42.8	11.9	1.9	24.3	9.1	1.5
	% Clay	2	59.2	7.1	1.1	36.3	12.0	2.0
	% Clay	3	63.9	5.3	0.8	46.5	13.2	2.2
Thickness	Thickness (cm)	1	4.3	2.0	0.3	5.4	3.4	0.6
	Thickness (cm)	2	12.1	6.2	1	15.1	7.3	1.2
Color	Value	1	3.7	0.8	0.1	2.9	0.6	0.1
	Chroma	1	2.1	0.5	0.1	1.9	0.6	0.1
	Value	2	3.9	0.6	0.1	3.6	0.6	0.1
	Chroma	2	2.8	0.5	0.1	2.2	0.6	0.1
	Value	3	4.1	0.6	0.1	3.8	0.6	0.1
	Chroma	3	2.9	0.5	0.1	2.7	0.8	0.1
Root Density	Very Fine Roots	1	2.3	0.5	0.1	2.9	0.4	0.1
	Fine Roots	1	1.9	0.8	0.1	2.2	0.7	0.1
	Very Fine Roots	2	2.7	0.5	0.1	2.7	0.5	0.1
	Fine Roots	2	2.2	0.7	0.1	2.3	0.6	0.1
	Very Fine Roots	3	1.8	0.6	0.1	2.1	0.5	0.1
	Fine Roots	3	1.5	0.6	0.1	1.5	0.5	0.1
Carbonates	Carbonate Stage	3	0.4	0.6	0.1	0.1	0.2	0.0

Table 2.2. Differences in species composition between potential states for the Claypan Ecological Site according to MRPP. Chance-corrected within-group agreement (*A*) values are in italics; *A* values of 1 indicate that all plots within a group have identical composition, while *A* values of 0 indicate that heterogeneity within groups equals that expected by chance. Numbers in bold are significant at Bonferroni corrected $p < 0.0033$.

	Grassland	Bluegrass	Wheatgrass	Three-tip	Sparse
Diverse	<i>0.1336</i> 0.0005	<i>0.1024</i> 0.0079	<i>0.0637</i> 0.0050	<i>0.1777</i> 0.0095	<i>0.1369</i> 0.0061
Grassland		<i>0.1036</i> 0.0004	<i>0.0758</i> 0.0000	<i>0.1133</i> 0.0004	<i>0.2354</i> 0.0000
Bluegrass			<i>0.1021</i> 0.0002	<i>0.1532</i> 0.0035	<i>0.1211</i> 0.0007
Wheatgrass				<i>0.1173</i> 0.0001	<i>0.1864</i> 0.0000
Three-tip					<i>0.2409</i> 0.0013

Table 2.3. Differences in species composition between potential states for the Mountain Loam Ecological Site according to MRPP. Chance-corrected within-group agreement (A) values are in italics; A values of 1 indicate that all plots within a group have identical composition, while A values of 0 indicate that heterogeneity within groups equals that expected by chance. P values in bold are significant at Bonferroni corrected $p < 0.0050$.

	Wheat	Three-tip	Sparse	Dense
Diverse	<i>0.0659</i> 0.0001	<i>0.1501</i> 0.0010	<i>0.1085</i> 0.0010	<i>0.2107</i> 0.0004
Wheat		<i>0.1052</i> 0.0001	<i>0.1018</i> 0.0000	<i>0.1508</i> 0.0000
Three-tip			<i>0.1847</i> 0.0024	<i>0.1870</i> 0.0027
Sparse				<i>0.1074</i> 0.0032

Table 2.4. Potential alternate states of the Claypan and Mountain Loam ecological sites with associated indicator species and management history. Potential alternate states were identified using hierarchical cluster analysis of plant species cover by plot. Species names are from the USDA PLANTS database (USDA 2010).

Claypan Potential States	No. Plots	Indicator Species ($p < 0.05$)	Management History (No. plots in parentheses)
Alkali Sagebrush Shrubland with Diverse Understory	3	<i>Melica bulbosa</i> , <i>Helianthella uniflora</i> , <i>Perideridia gairdnerii</i> , <i>Elymus elymoides</i> , <i>Achnatherum lettermanii</i> , <i>Symphoricarpos rotundifolius</i> , <i>Artemisia tridentata</i> ssp. <i>Vaseyana</i>	Ungrazed for 10 yr (1); Low grazing intensity (2)
Native Grassland	10	<i>Koeleria macrantha</i> , <i>Phlox longifolia</i>	Sprayed (8), Pocket gopher activity (4)
Alkali Sagebrush/ Bluegrass Shrubland	5	<i>Poa secunda</i>	Sprayed (2); Pocket gopher activity (2); Low-Med (1), High grazing intensity (4)
Alkali Sagebrush/ Western Wheatgrass Shrubland	11	<i>Pascopyrum smithii</i> , <i>Astragalus wetherillii</i> , <i>Lomatium grayi</i> , <i>Microseris nutans</i>	Sprayed (1); Medium (5), Med-High (2), High (4) grazing intensity
Three-tip/ Mountain Big Sagebrush Shrubland	4	<i>Artemisia tripartita</i> , <i>Poa nemoralis</i> ssp. <i>interior</i> , <i>Achillea millefolium</i> , <i>Bromus tectorum</i>	Mechanical treatment of shrubs (2)
Alkali Sagebrush Shrubland/Sparse Understory	6	<i>Artemisia arbuscula</i> ssp. <i>longiloba</i> , <i>Arenaria hookeri</i> , <i>Gutierrezia microcephala</i> , <i>Orthocarpus luteus</i>	Burn ~10 yr ago (1)
Mountain Loam Potential States	No. Plots	Indicator Species ($P < 0.05$)	Management History (No. plots in parentheses)
Mountain Big Sagebrush Shrubland with Diverse Understory	7	<i>Symphotrichum spathulatum</i> , <i>Melica bulbosa</i> , <i>Achillea millefolium</i> , <i>Achnatherum lettermannii</i> , <i>Symphoricarpos rotundifolius</i>	Sprayed (5); Low-Med (2), Med-High (5) Grazing Intensity

Mountain Loam Potential States	No. Plots	Indicator Species ($p < 0.05$)	Management History (No. plots in parentheses)
Mountain Big Sagebrush/Western Wheatgrass Shrubland	12	<i>Lomatium grayi</i> , <i>Microseris nutans</i> , <i>Astragalus wetherilli</i> , <i>Wyethia amplexicaulis</i>	Sprayed (2); Low-Med (6), Med-High (3), High (3) Grazing Intensity
Three-tip/Mountain Big Sagebrush Shrubland	4	<i>Artemisia tripartita</i> , <i>Phleum pratense</i> , <i>Poa nemoralis</i> ssp. <i>interior</i>	Mechanical Treatment (1); Low-Med (2), Med-High (1), High (1) Grazing Intensity
Mountain Big Sagebrush Shrubland/Sparse Understory	5	<i>Chrysothamnus viscidiflorus</i> , <i>Leymus cinereus</i> , <i>Erodium cicutarium</i>	Burned 2 yr ago (2); Low-Med (2), Med-High (2), High (1) Grazing Intensity; Steep slopes between agricultural fields (3)
Dense Mountain Big Sagebrush Shrubland	5	<i>Artemisia tridentata</i> var. <i>vaseyana</i> , <i>Bromus marginatus</i>	Low-Med (1), Med-High (1), High (3) Grazing Intensity
Planted Grasslands (both soil types)	4	<i>Thinopyrum intermedium</i> , <i>Bromus inermis</i> , <i>Elymus lanceolatus</i> , <i>Pseudoroegneria spicata</i>	Seeded with non-native grasses (4); CRP (2); sprayed and mechanically treated (1); Burned ~10 yr ago (1)

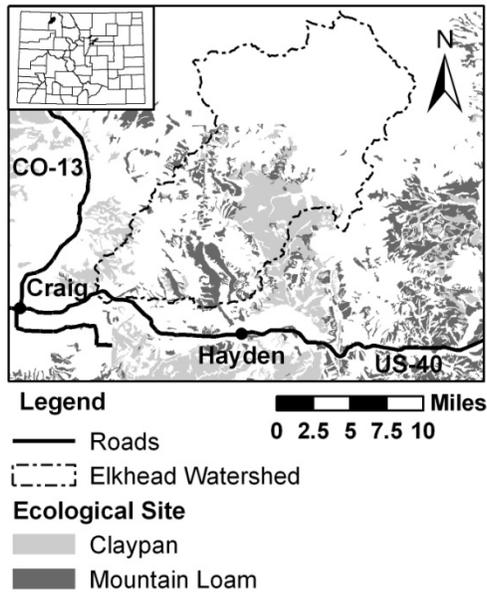


Figure 2.1. The Elkhead watershed in northwest Colorado. Claypan and Mountain Loam ecological sites were mapped based on on NRCS soil data. The Elkhead mountains on the Routt National Forest (the area in white at the top of the map) was not considered in this study because the elevation and climate differed from those of our study area.

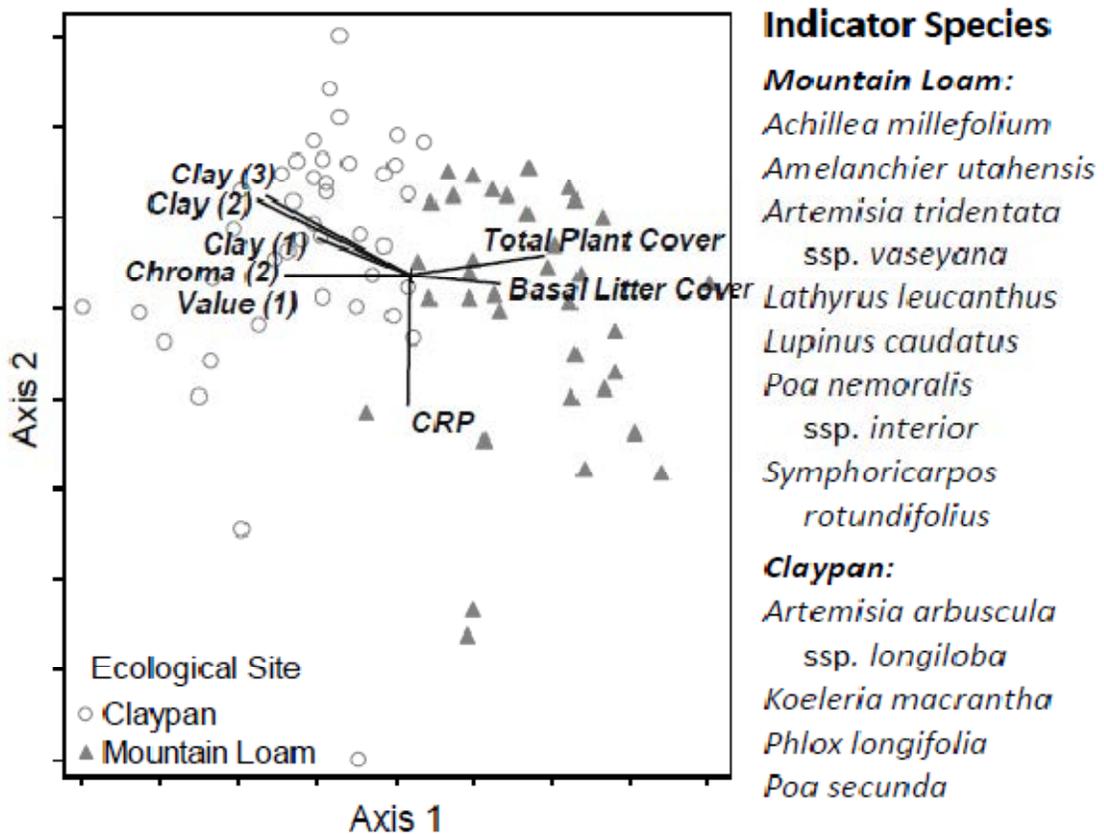


Figure 2.2. Differences in species composition and environmental variables between the Claypan and Mountain Loam ecological sites. Non-metric multi-dimensional scaling results on the left show differences in plant species foliar cover for each plot, grouped by ecological site. Distances between plots (circles and triangles) are related to magnitude of differences in species composition. Axis 1 separates alkali sagebrush-dominated shrublands associated with the Claypan ecological site from mountain big sagebrush shrublands associated with the Mountain Loam ecological site. Axis 2 separates formerly cultivated, seeded rangelands at the bottom from all others. Vectors represent correlations of other variables with species composition ($r^2 > 0.25$). Indicator species for each ecological site according to Indicator Species Analysis are listed on the right.

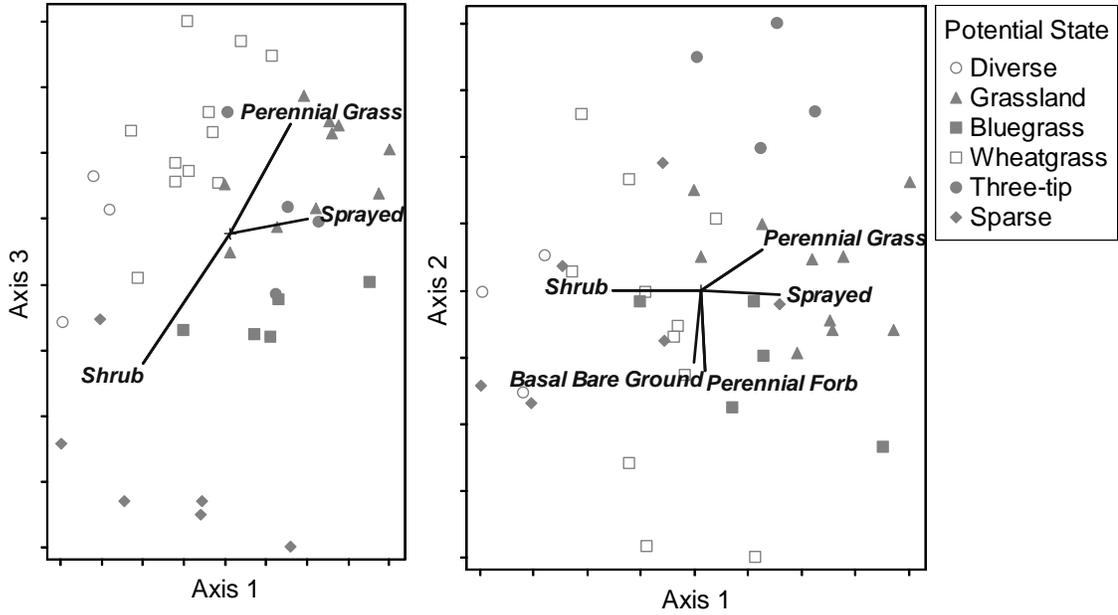


Figure 2.3. Non-metric multidimensional scaling results for plant species foliar cover by plot in the Claypan ecological site. Symbols represent plots, with different symbols for plots in different potential states identified using hierarchical cluster analysis. Distances between plots are related to magnitude of differences in species composition. Vectors show correlations ($r^2 > 0.25$) between the ordination and environmental and site history variables.

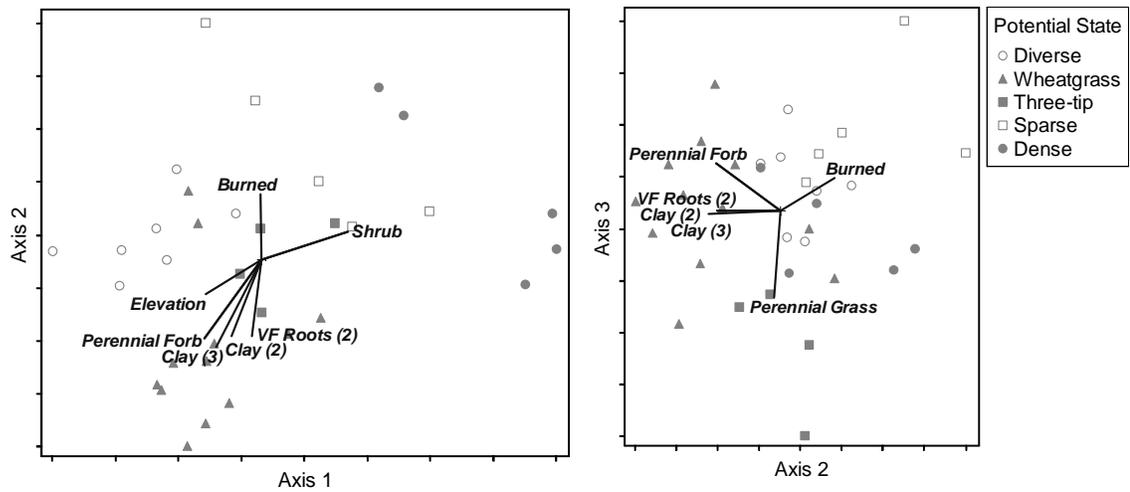


Figure 2.4. Non-metric multi-dimensional scaling results for plant species foliar cover by plot in the Mountain Loam ecological site. Symbols represent plots, with different symbols for plots in different potential states identified using hierarchical cluster analysis. Distances between plots are related to magnitude of differences in species composition. Vectors show correlations ($r^2 > 0.25$) between the ordination and environmental and site history variables.

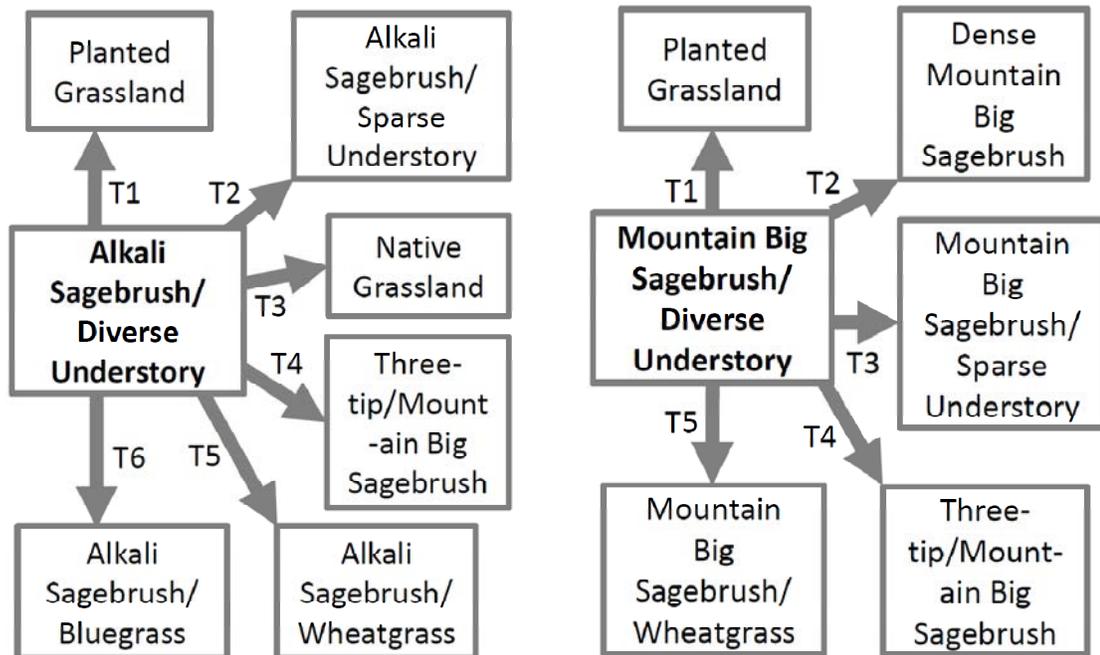


Figure 2.5. Data-driven state-and-transition models for the Claypan and Mountain Loam ecological sites in Northwestern Colorado. Boxes are potential alternate states with different species composition identified using hierarchical cluster analysis. Arrows mark associations with site history and environmental variation that may make transitions more likely; these were identified using non-metric multidimensional scaling and qualitative analysis (Figs. 2 and 3; Table 4).

Claypan Transitions. Maintenance of Reference State: No grazing to low long-term grazing intensity. **T1:** Planting non-native grasses (includes CRP). **T2:** Lack of shrub disturbance (spraying or fire); more likely with less clayey soil textures. **T3:** Aerial spraying with herbicide. **T4:** Mechanical treatment. **T5:** Moderate to high long-term grazing intensity. **T6:** High long-term grazing intensity; also associated with spraying shrubs, but alkali sagebrush still present.

Mountain Loam Transitions. Maintenance of Reference State: Aerial spraying with herbicide. **T1:** Planting non-native grasses (includes CRP). **T2:** Lack of shrub disturbance (spraying or fire); more likely with less clayey soil textures. **T3:** Recent fire; also associated with steep slopes between agricultural fields. **T4:** Weakly associated with mechanical treatment. **T5:** Low to moderate long-term grazing; higher soil clay content.

Chapter 3.
Indicators of ecosystem function identify alternate states in the sagebrush steppe

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 US, 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 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.

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 (Bestelmeyer et al. 2009; Suding and Hobbs 2009b; Westoby et al. 1989). 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 semi-arid rangelands with a short history of grazing like the sagebrush steppe of western North America (Cingolani et al. 2005). The US Department of Agriculture Natural Resources Conservation Service (USDA NRCS) together with partners are currently developing thousands of these models for use in land management across the US, and STMs are being developed and used in Mongolia, Africa, Australia, and elsewhere (Hobbs and Suding 2009; Sasaki et al. 2008). However, models are often developed based on expert knowledge with little published quantitative ecological data (Suding and Hobbs 2009b). 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.

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) (Allen-Diaz and Bartolome 1998; Jackson and Bartolome 2002; Oliva et al. 1998; 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 (Chartier and Rostagno 2006; Petersen et al. 2009; Stringham et al. 2001; 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 seventeen 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 and the USA).

To identify transitions and ways to manage them, the relationship between management and potential alternate states must be identified (Fig. 3.1). 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 includes 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. 3.1) 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, US (Major Land Resource Area 48A, Southern Rocky Mountains). 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. 3.1). 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 (Figs. 3.1a, 3.1b)? Finally, how are IRH and species composition related to site history and environmental variables

(Figs. 3.1c, 3.1d)? In answering these questions, we outline a data-driven approach to constructing STMs.

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 US 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 2009a) 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: historic 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 x 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 ≥ 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; 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 (Appendix 4) 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 weight 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 lab 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 fifteen 0.1 m² circular subplots and clipped in a subset of three of them. Estimates were corrected by a ratio estimator of dry to estimated weights (Reich et al. 1993), and further adjusted for percent utilization at each plot by the grazed class method (Coulloudon et al. 1999; Schmutz et al. 1963). 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 a good substitute 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*, percent litter cover is related to *Litter Amount*, and percent bare ground is related to *Bare Ground*. Line-point intercept, described above, 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). Percent litter cover and percent bare ground are correlated with runoff and susceptibility to water erosion (Blackburn and Pierson 1994; Smith and Wischmeier 1962). 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 greater than 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 historic grazing intensity (below medium vs. medium-high to high), chemical shrub treatment (spraying), mechanical shrub treatment, seeding with grasses, or none. We were only able to sample two plots that had been seeded with grasses, so this practice is not included in statistical analyses but is 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). 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 southwest 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 state (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).

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. 3.1a) using MRPP. We explored which IRH predict membership in each potential state defined by plant species composition (Fig. 3.1b) relative to all other states

using logistic regression. Significant effects were identified using backwards selection with an alpha of 0.10 to ensure that all meaningful variables remain in the model and given our relatively small sample size. IRH were excluded from analysis when they did not vary across a potential state because this prevented the model from converging. Finally, we used logistic regression to discover which site history and environmental variables could predict states and IRH (Fig. 3.1c, 3.1d). 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 because this prevented the model from converging. *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 3.1). 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 cover greater than 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 3.2). 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 pair-wise with Bonferroni correction, a conservative test (Table 3.3). 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. Average IRH ratings for each potential state are listed in Appendix 5.

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 twelve uncorrelated ones (correlation coefficient <0.5 ; Table 3.4). *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* ($r = 0.72$).

Many potential states were predictable based on levels of IRH (Table 3.4). *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 3.5), 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 environmental variables predicted occurrence of the Diverse or Bluegrass potential states. Both Planted Grasslands plots were former wheat fields that had been planted with mostly non-native 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 3.5). 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 historic 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 after plant and litter cover were measured. 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. 3.2), consistent with our conceptual model (Fig. 3.1). 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 historic range of variation under a natural disturbance regime for the Claypan ecological site (Bestelmeyer et al. 2009).

Site History and Environmental Factors Affect Structure and Function

Specific management practices are associated with three potential states (Fig. 3.2), 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 ten 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. 3.2). Rodent activity, mechanical treatment, spraying, historic 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. 3.1). However, our findings suggest more complex relationships between management and ecosystem structure and function, which are also modified by environmental factors like slope (Fig. 3.2). 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. 3.1). We were likely unable to capture some of the important drivers and interaction effects within the scope of this study. Experimental approaches (Firn et al. 2010; Martin and Kirkman 2009) 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. 3.3) 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 2009b), 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, Firm et al. 2010), thousands of these models are being created for land management in the US (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 consistent with alternate state theory, and thus improve future models.

Table 3.1. Correlations between the qualitative Indicators of Rangeland Health (IRH ratings) and quantitative measures of related ecosystem properties.

Indicator	Quantitative Measure	Correlation Coefficient (Pearson's R)	P
<i>Water Flow Patterns</i>	% Basal Gaps >20 cm	0.56	<0.001
	% Basal Gaps 20-50 cm	NS	
	% Basal Gaps 50-100 cm	0.63	<0.001
	% Basal Gaps 101-200 cm	0.47	<0.01
	Mean Basal Gap Size	0.53	<0.001
	% Bare Ground	NS	
<i>Bare Ground</i>	% Basal Gaps >20 cm	0.69	<0.001
	% Basal Gaps 20-50 cm	0.44	<0.01
	% Basal Gaps 50-100 cm	0.67	<0.001
	% Basal Gaps 100-200 cm	0.56	<0.001
	Mean Bare Ground Gap Size	0.31	<0.05
	% Bare Ground	NS	
<i>Litter Movement</i>	% Basal Gaps >20 cm	0.56	<0.001
	% Basal Gaps 20-50 cm	0.36	<0.05
	% Basal Gaps 50-100 cm	0.55	<0.001
	% Basal Gaps 100-200 cm	0.43	<0.01
<i>Plant Mortality and Decadence</i>	Proportion of Live-to-Dead Canopy Cover	NS	
<i>Litter Amount (+ too much, - too little)</i>	Litter Basal Cover	NS	
<i>Invasive Plants</i>	Invasive Plant Foliar Cover	0.69	<0.001

Note: NS= Not Significant. There are no quantitative indicators for *Reproductive Capability of Perennial Plants*. We did not measure any for *Pedestals and Terracettes, Gullies, Compaction, or Soil Surface Loss or Degradation*.

Table 3.2. Descriptive names for potential states of the Claypan ecological site, as identified with 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	<i>Melica bulbosa</i> , <i>Helianthella uniflora</i> , <i>Perideridia gairdnerii</i> , <i>Cirsium eatonii</i> , <i>Elymus elymoides</i> , <i>Achnatherum lettermanii</i> , <i>Symphoricarpos rotundifolius</i> , <i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	38.3
Alkali Sagebrush/ Bluegrass Shrubland (Bluegrass)	5	<i>Poa secunda</i>	34.8
Native Grassland	10	<i>Koeleria macrantha</i> , <i>Phlox longifolia</i>	28.3
Alkali Sagebrush/Western Wheatgrass Shrubland (Wheatgrass)	11	<i>Pascopyrum smithii</i> ; <i>Amelanchier utahensis</i> , <i>Astragalus wetherillii</i> , <i>Delphinium nuttallianum</i> , <i>Lomatium grayi</i> , <i>Microseris nutans</i>	29.3
Three-tip Sagebrush Shrubland (Three-tip)	4	<i>Artemisia tripartita</i> , <i>Poa interior</i> , <i>Achillea millefolia</i>	32.0
Alkali Sagebrush Shrubland with Sparse Understory (Sparse)	6	<i>Artemisia arbuscula</i> ssp. <i>longiloba</i> , <i>Gutierrezia microcephala</i> , <i>Orthocarpus luteus</i>	34.7
Planted Grassland	2	<i>Elymus lanceolata</i> , <i>Bromus inermis</i> , <i>Pseudoroegneria spicata</i>	24.0

Note: 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 $P < 0.05$, unless otherwise indicated. Species names are from the USDA PLANTS database (USDA NRCS, 2010).

Table 3.3. 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	-					
Wheatgrass	-	0.0133				
Three-tip	-	-	0.0005			
Sparse	-	0.0029	0.0000	-		
N. Grassland	-	-	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).

Table 3.4. Significant relationships between processes (IRH deviations from reference conditions: None-to-Slight, Slight-to-Moderate, and Moderate or higher) and potential states according to logistic regression.

State	IRH	P	Odds Ratio
Sparse	<i>Water Flow Patterns</i>	0.03	9.8
Native Grasslands	<i>Litter Movement</i>	0.02	12.9
	<i>Invasive Plants</i>	0.09	0.1
	<i>Soil Surface Loss or Degradation</i>	0.06	0.2
Wheatgrass	<i>Water Flow Patterns</i>	0.01	0.1
	<i>Soil Surface Resistance to Erosion</i>	0.09	0.4
Bluegrass	None	--	--

Note: IRH were selected using backwards selection at $p < 0.10$. Odds ratios greater than one show that IRH deviations from references conditions increase the odds of being in a particular state, and vice versa. Diverse, Three-tip, and Planted Grassland states had too few observations for this analysis.

Table 3.5. Relationships between site history, environment, processes (IRH ratings: None-Slight, Slight-Moderate, and Moderate or higher) and potential states according to logistic regression.

INDICATORS OF RANGELAND HEALTH			
IRH	Site History and Environmental Variables	P	Odds Ratio
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
STATES			
Native Grassland	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

Note: Variables included were significant at $p < 0.10$ according to backwards selection. Odds ratios greater than one show that management practices or increasing values of environmental variables increase the odds of IRH deviation from reference conditions and state occurrence, and vice versa. *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.

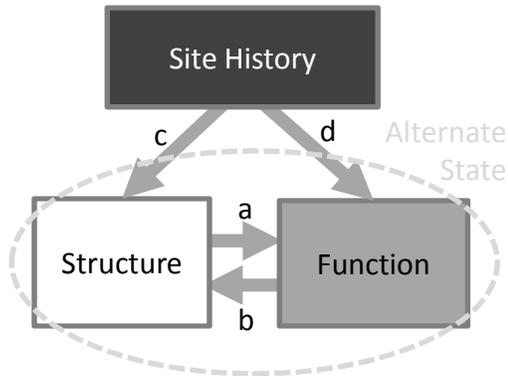


Figure 3.1. Hypothesized relationships between site history and ecosystem structure and function, approximated by plant species composition and Indicators of Rangeland Health (IRH) in this study. Site history (including management and disturbance history) directly impacts structure (species composition) and function (IRH). Structure and function influence each other through negative or positive feedbacks. 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.

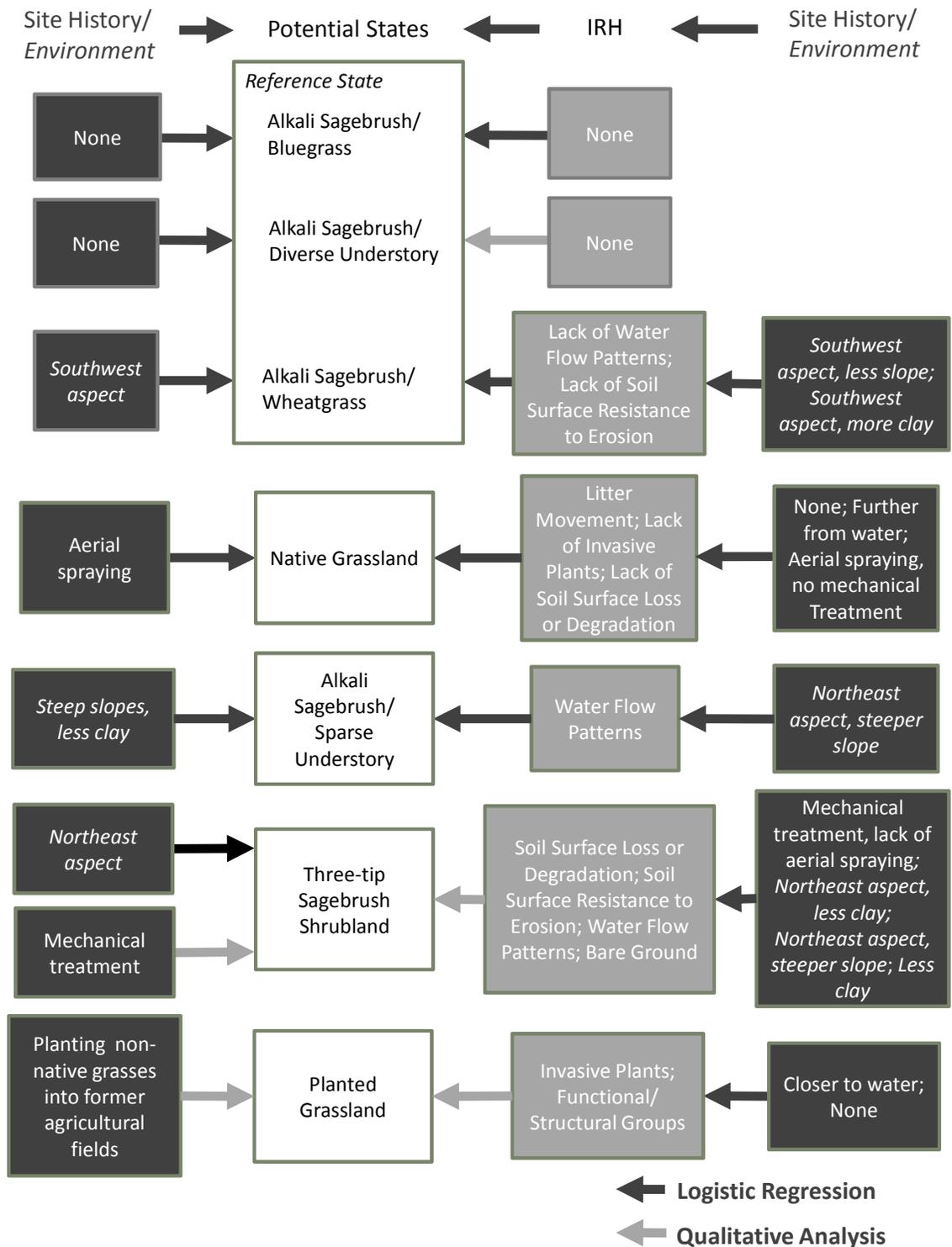


Figure 3.2. Flowchart showing data-driven relationships between potential alternate states of the Claypan Ecological Site in NW Colorado, US and processes (IRH ratings), site history, and environmental factors. Dark arrows show statistically significant relationships according to logistic regression (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. 3.1). However, relationships were often not exclusive, implying that links are not as tight as expected in theory.

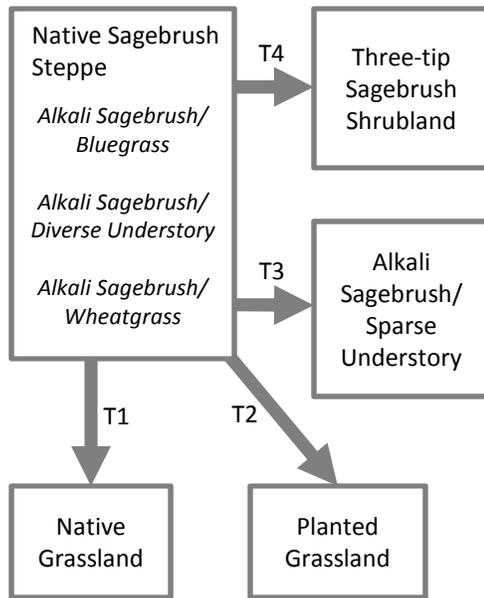


Figure 3.3. Data-driven state-and-transition model for the Claypan ecological site in Northwestern Colorado. The grey boxes represent alternate states with unique processes as measured by the Indicators of Rangeland Health ratings (Table 4). Causes of transitions between states according to relationships with site history and process (Fig. 3.2) are marked with grey arrows. When environmental factors are important for state occurrence (Fig. 3.2) they are also noted. **T1:** Aerial spraying with herbicide. **T2:** Planting non-native grasses. **T3:** Erosion by water; occurs on steep slopes. **T4:** Mechanical treatment; also associated with northeast aspects.

Chapter 4.
Comparison of Species and Trait-Based Approaches for Describing Sagebrush Steppe Response to Range Management

ABSTRACT

Is there an advantage to using plant trait-based group composition rather than species composition to identify potential alternate states and describe plant community response to range management? We 1) compare potential states defined by species composition to those defined by trait-based groups of differing complexity and 2) determine how management and environmental variation relate to species- and trait group-defined states. We sampled 76 plots with different grazing and spraying histories on two soil types in the sagebrush steppe of Colorado, USA. We measured plant species composition in each plot and categorized species into trait groups using three different classification schemes, which represented increasing numbers of traits and levels of complexity in classification. The classifications were based on traits that are easy to measure and affect plant response to grazing and herbicide spraying: life form, life history, resprouting ability, height, vegetative reproduction, and N-fixing ability. Using hierarchical cluster analysis, we identified potential states separately based on similarity in species or trait group cover. Then, we explored relationships between each set of potential states and site history and environmental factors

using logistic regression. We found that trait-based group composition and species composition identified many of the same potential states and responses to grazing and herbicide treatment of shrubs as species composition. Relationships between species and trait group composition and management differed on the two soil types. Species composition was sensitive to more different management practices, on average, than was trait group composition, and both were related to environmental variation. States defined by simple trait groups based on life form were related to management on one soil type but not the other. This study reveals that species and trait-based group composition are both useful for understanding sagebrush steppe response to management. A combination of approaches provides the most complete understanding, because species composition and trait group composition were sensitive to different management practices. Groups that combine five or more easily-measured traits mechanistically related to management and disturbance may be sufficient for detecting many vegetation patterns and responses to disturbance.

INTRODUCTION

Understanding plant community responses to land management is crucial because plant communities can alter ecosystem function (Chapin et al. 1997) and the provisioning of ecosystem services (Scheffer et al. 2004). However, the time involved with studying individual species' responses and the complexity of scaling responses up to the community or region necessitates alternative

approaches (Suding et al. 2008). One promising way to understand community response to management is through groups of plant species with similar traits (hereafter, trait groups; TGs). A growing literature links disturbances to changes in abundance of plant traits at the community level. For example, a global analysis of trait responses to grazing showed that heavier grazing favors short, prostrate, and annual plants versus tall, erect, or perennial plants (Diaz et al. 2007). TGs that integrate these traits therefore provide a quasi-mechanistic understanding of ecosystem change (Quetier et al. 2007). Although changes in species abundances are localized to the area where that species occurs, many changes in TG composition are generalizable across local environmental variability and regions (Bond et al. 2005; Cornwell et al. 2008; Diaz et al. 2004). For these reasons, TGs are commonly used to understand and predict vegetation change in Global Vegetation Models and other large-scale modeling efforts (Bond et al. 2005; Euskirchen et al. 2009) and to enable better predictions of how ecosystems will respond to changes in environment and management. In this paper, we compare plant species and trait-based group composition as indicators of plant community response to range management in a sagebrush steppe in the western US.

Globally, numerous efforts are underway to develop state-and-transition models (STMs) to assist with land management decision-making (Bestelmeyer et al. 2009; Hobbs and Suding 2009). These conceptual models describe plant community change in response to disturbance as a set of shifts between alternate states. Differences in species composition are often used to identify

alternate states in STMs (e.g. Allen-Diaz and Bartolome 1998), under the assumption that changes in species correspond to changes in underlying processes maintaining states. This approach requires careful sample stratification by land units with uniform soils and climate, often called *ecological sites* in the US (USDA NRCS 2003). However, ecological sites inevitably encompass some environmental variability that affects species composition (Kachergis et al. in prep). TGs may provide a useful alternative approach to STM-building (Gondard et al. 2003; Quetier et al. 2007). They may be less related to environmental variation than species, reducing the potential for confounding the effects of management with underlying environmental gradients. Also, they may be more related to management, partially because they are mechanistically tied to positive feedbacks that drive transitions between alternate states. For example, in the sagebrush steppe, heavy grazing reduces perennial bunchgrass populations; the release from competition allows shrubs to increase and further prevents grass population recovery, eventually leading to a shrub-dominated state where grasses cannot establish (Laycock 1991; West and Young 2000). Threshold shifts like this one also result in changes in species composition. However, if TGs are more closely related to management and less related to environmental variation than species composition, then they are better indicators of alternate states. In addition, using TGs that can be quickly identified in the field would expedite the STM building process and create models that are more easily accessible to land managers.

Although many TGs are identified using a data-driven process, *a priori* approaches have been more commonly applied in the sagebrush steppe. The data-driven approach employs quantitative measures of traits to identify “clusters” of plant species with similar traits using multivariate statistics (e.g. Diaz et al. 2004; e.g. Lavorel et al. 1997; McIntyre et al. 1999). Data-driven studies have found that life form (grass, forb, shrub) is related to many other plant traits (e.g. Westoby et al. 1989), and therefore they recommend a hierarchical approach to TG classification based on life form (Lavorel et al. 1997). Life form has been found to be related to disturbance in previous studies of the sagebrush steppe (Blaisdell 1953; Harniss and Murray 1973; Mueggler and Blaisdell 1958). Most TG classifications used in sagebrush steppe have followed this recommendation, with grass, forb, and shrub groupings further subdivided by photosynthetic pathway (Derner et al. 2008), annual vs. perennial life histories (Bates et al. 2006; Derner et al. 2008; Pellant et al. 2005), N-fixation (Goergen and Chambers 2009; Pellant et al. 2005), growth form (e.g. bunch vs. rhizomatous, Pellant et al. 2005), re-sprouting vs. not (Riegel et al. 2006), and height differences (Bates et al. 2006; Pellant et al. 2005). These TGs respond differently to changes in precipitation (Bates et al. 2006; Derner et al. 2008), burning (Blaisdell 1953; Mueggler and Blaisdell 1958), and spraying (Harniss and Murray 1973; Mueggler and Blaisdell 1958). They also affect functional attributes such as ecosystem resistance to invasion (Davies 2008) and carbon cycling (Knapp et al. 2008).

This study compares the utility of plant species and trait group composition as indicators of ecosystem response to disturbance in the sagebrush steppe. The ideal indicator would define states that are related to management but not to underlying environmental variation. We sampled plant cover by species in 76 plots representing two ecological sites and a variety of management histories to infer the effects of management on the abundance of plant species and TGs. Three simple TG classification schemes were defined *a priori*, drawing on previous studies of response to disturbance in sagebrush steppe. In order of ascending complexity, they are: Simple, Practical (chosen to be identified quickly in the field), and Complex (Figure 4.1). Species are actually a very complex TG classification. First, we compare potential alternate states based on TG composition with potential states based on species composition and ask, *do the two approaches identify the same overall vegetation patterns?* Next, we explore how potential alternate states based on TG composition are related to site history and environment. We predicted that the Complex and Practical TGs would identify alternate states that are most related to management and least sensitive to environmental variation; species will be related to environmental variation as well as management, and Simple TGs will be too general to detect management effects. This study has important implications for designing monitoring studies to detect shifts between alternate states in the sagebrush steppe.

METHODS

Study Area

This study was conducted on private and public rangelands in and around the Elkhead Watershed of Northwestern Colorado. Fifteen private landowners, the Bureau of Land Management (BLM), and the US Forest Service (USFS) participated. We inventoried site management history through landowner interviews (Knapp and Fernandez-Gimenez 2009b) and review of agency (NRCS, BLM, USFS) records. Sampling focused on the Claypan and Mountain Loam ecological sites, defined as two different types of land with characteristic soils, climate, and vegetation (USDA NRCS 2003). Areas that represent all existing combinations of management practices were identified: historic grazing intensity, a qualitative estimate of typical stocking rate based on interviews with 26 local land managers (Knapp 2008); and shrub management practices, including aerial spraying, mechanical treatment, or none. Plot locations were stratified first by ecological site, then by management history, and randomly located at least 200 m apart.

We collected soil and plant species data within 20 x 50 m plots. We sampled 76 plots for vegetation in 2007 and 2008 and for soils and indicators in 2009.

Soil Data Collection

Soil data were collected to verify the ecological site and to relate plant species and TG composition to environmental variation. A pit or auger hole ≥ 50 cm deep was dug in the center of each plot, and each horizon was described according to NRCS protocols (Schoeneberger et al. 1998). We recorded texture, structure, color, root density, and carbonates in each layer. The ecological site was verified by matching soil descriptions with the Claypan and Mountain Loam ecological site soil descriptions (SCS 1975). Claypan is characterized by a thin clay loam or clay A horizon over a clay subsoil that restricts water movement and availability. Mountain Loam is characterized by a thicker loam or clay loam A horizon and a clay loam or clay subsurface.

Plant Species and Trait Group Composition

We measured plant cover by species using 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). Functional characteristics for each species were identified using species descriptions from the USDA PLANTS database “Characteristics” sheets (USDA 2010), supplemented by XID (height and rhizomatous/stoloniferous growth form; Flora ID Northwest 2009) and the Fire Effects Information System (resprouting capability of shrubs; USFS 2010). Traits were chosen to use in the classifications based on their relationship to major management practices/disturbances and ease of use in monitoring: plant height (Short <1.5 feet, Tall >4 feet), whether they are rhizomatous or not, and

annual/perennial life history are related to grazing, and life form and whether shrubs are re-sprouting or not are related to spraying. Species were categorized into TGs at three different levels of complexity within life form (Figure 4.1).

Site History and Environment

Categorical site history variables were determined through communication with land managers and included historic grazing intensity (below medium vs. medium high vs. high), chemical shrub treatment (spraying), and mechanical shrub treatment. We also 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 southwest slopes (Beers et al. 1966).

Data Analysis

First we compared potential states based on TG composition with potential states based on species composition to determine whether the two approaches identified the same overall differences among plots. We used agglomerative hierarchical cluster analysis to identify potential states based on similarity in species and TG composition. The cluster dendrograms were pruned quantitatively based on Indicator Species Analysis (ISA), which generates an indicator value of 1-100 based on each species' faithfulness and exclusivity to that group (Dufrene and Legendre 1997). Dendrograms were pruned at the number of groups with the lowest average p value for all species based on a

randomization test (1000 randomizations), interpreted as the most ecologically meaningful number of groups (McCune and Grace 2002), up to a maximum of seven groups. To identify how similar cluster results based on species and TG composition are, we used the adjusted Rand index (Hubert and Arabie 1985) in R 2.8.1 with the MCLUST package (Fraley and Raftery 2002, 2006). The adjusted Rand index assesses the agreement between two groupings of the same sets of objects, with a maximum value of 1 indicating perfect agreement and a minimum of 0 representing random clusters. This method is appropriate even when cluster results are compared across different hierarchical levels (e.g. when they are pruned at different numbers of groups; Milligan and Cooper 1986).

To identify how potential states based on TG composition are related to site history (management and disturbance) and environment, we used logistic regression, with site history and environmental variables as predictors of potential state membership.

RESULTS

Comparison of Species and Trait Group-Defined States

On both soil types, similarity between species- and TG-defined potential states increases with the complexity of the TG classification, as shown by the adjusted Rand index (Table 4.1). Complex TG-defined states are substantially more similar to species-defined states than Practical or Simple ones. Simple TG-

defined states were more similar to species-defined states on Claypan than on Mountain Loam.

Several Mountain Loam and Claypan potential states defined by Complex TGs are similar to species-defined states (Tables 4.2 and 4.3). States are similar when indicator species of the species-defined potential state correspond to the indicator trait group of the TG-defined potential state. For example, Mountain Loam CO1 and PR1 are characterized by non-resprouting shrubs and are the same as SP1 which is characterized by the non-resprouting shrub *Artemisia tridentata* ssp. *vaseyana*. On Claypan only, some Simple TG-defined potential states are over 50% similar to species-defined potential states (meaning that over 50% of plots are in the same groups; Table 4.3). Both SP1 and SP2 have analogues in all TG classification schemes, with shrubs and grasses as indicator TGs respectively. Despite many similarities, there are also many TG-defined potential states that differ from species-defined states on both soil types.

Management and Environment Predict Species and Trait Group-Defined State Membership

For both Mountain Loam and Claypan ecological sites, most Species, Complex, and Practical potential states were related to site history and/or environmental variation (Tables 4.4 and 4.5). These variables explained the most variation in occurrence of Species-defined states. Simple TG-defined potential states were generally not related to management or environmental variation on Mountain Loam, but they were on Claypan.

Sensitivity to management practices differed among the trait grouping schemes, as evidenced by the fact that management practices differ in their relationships to potential states defined using each (Table 4.6). Historic grazing intensity is more closely related to TG composition than species composition in Mountain Loam, but it is only related to one Practical state in Claypan. Species composition is more closely related to spraying in ML, but species and TG are equally related to spraying in Claypan. Overall, number of management practices related to potential states declined with the complexity of the trait group scheme in Mountain Loam, but remained high even with Simple TGs in Claypan (Figure 4.2).

Sensitivity to environmental variation was surprisingly similar among trait grouping schemes (Figure 4.2), with states related to at least two of the three environmental variables in each except Claypan Practical.

DISCUSSION

Species and Trait-Based Approaches Identify Many of the Same Patterns in Plant Community Composition

The trait grouping schemes that we examined in this study are hierarchical; each TG is a combination of more complex TGs. We found that as TGs decrease in complexity, similarity of TG-defined states to species-defined states decreases further. This pattern appears generalizable across both soil types, and is not surprising, given that as TG complexity increases, fewer species are included in

each group. Clifford and Dale (1976) also found that similarity between plot composition based on species and higher taxonomic units decreased as higher taxonomic units were used (e.g. family vs. genus). Information is lost when TG classifications are used in place of species composition, and more information is lost with coarser TGs. This information could elucidate patterns of response to management and allow a more complete understanding of ecosystem dynamics.

Species and TG approaches identified many of the same patterns in plant community composition (Table 4.2), especially Complex TGs. This supports previous research that has found agreement in vegetation patterns identified using species- and TG-based approaches using multivariate methods (Webb et al. 1970; Werger and Sprangers 1982). A mechanism for the agreement is that dominant species often compose a majority of their TGs (Walker et al. 1999), driving some similarities between states defined by species and TG composition. For example, several species of *Artemisia* (sagebrush) are the primary non-resprouting shrubs on these soil types, and non-resprouting shrubs are indicators of TG-defined states that correspond to sagebrush-dominated potential states on both soil types. Likewise, *Pascopyrum smithii* is the dominant medium-height clonal grass in the area, and a species- and a complex TG-defined state are characterized by these on both soil types.

Simple TGs captured similar vegetation patterns as species on Claypan but not Mountain Loam. This occurred when a single simple trait group dominated potential states, corresponding to multiple species. For example, states were identified in all three TG classifications which are similar to Claypan

SP1, a native grassland; even though SP1 is not characterized by one dominant species, it is characterized by a dominant TG (grasses) that corresponds with species differences. The difference in the overlap between Species and Simple TGs on the two soil types is likely related to the higher species and TG diversity of Mountain Loam relative to Claypan, and suggests that Simple trait groups may not be as useful on soil types with more diverse plant communities.

In contrast, some species-defined states did not correspond to TG-defined states. These states had many co-dominant species in multiple TGs (Claypan SP5 and SP6) or were defined by an uncommon shrub (*Artemisia tripartita*). Werger and Sprangers (1982) noted that the disagreement between their species- and TG-based classifications of plots tended to be around “atypical” or “locally restricted” communities. However, several of these potential states are found in the Claypan reference state (Kachergis et al. in prep), or set of plant communities where ecological processes are operating within their historic range of variation under a natural disturbance regime for the Claypan ecological site (Bestelmeyer et al. 2009). This state is very important for an overall understanding of vegetation dynamics on that ecological site, but it is less likely to be distinguished by characteristic trait groups because it is diverse and contains a more balanced composition of different trait groups. An approach to monitoring based on trait group composition may, therefore, miss reference conditions.

Species and Trait Group Approaches Describe Plant Community

Responses to Management

Species and TG approaches are complementary in describing plant community responses to management on the two soil types. While they agree in many cases, taking multiple approaches provides more information than one approach. However, the fact that species and TG approaches do not always agree implies that STMs created using species and TGs will sometimes describe different dynamics.

Plant community responses to management differed on the two soil types. Where we found related patterns in species and TG composition, we often also found similar relationships to management practices and environmental variables. Mountain Loam dense *Artemisia* shrublands (SP1, CO1, and PR1) are all related to higher historic grazing intensity and lower slopes. Claypan dense *Artemisia* shrublands (SP2, CO2, PR2, and SI2) generally occur on steeper slopes with less clayey soils. Claypan native grasslands (SP1, CO1, PR1, and SI1) are related to spraying herbicide that kills shrubs. In contrast, spraying Mountain Loam is related to a state with diverse grasses, forbs, and shrubs (SP3, CO3). TG-defined potential states that overlapped with species defined-states tended to have the strongest relationships with management, with some notable exceptions. Mountain Loam PR2, characterized by Tall Grasses, is related to lower historic grazing intensity. Claypan SP7, an *Artemisia tripartita* shrubland, is qualitatively related to mechanical treatment.

Usefulness of the Two Approaches for Describing Sagebrush Steppe Dynamics

We expected that trait groups would be more related to management and less related to environmental variation, and therefore more useful than species composition for describing plant community response to management and identifying potential alternate states. We found that there are trade-offs in the usefulness of different approaches, and a combination of approaches gives the most complete understanding of sagebrush steppe dynamics.

Contrary to our expectations, TG composition, like species composition, is related to environmental variation within soil types (Figure 4.2). These findings contradict many authors' predictions that TG responses to disturbance are generalizable across environmental gradients (Bond et al. 2005; Cornwell et al. 2008; Diaz et al. 2004). Others have also reported relationships between TGs and environmental variation at similar scales (Anderson and Hoffman 2007); indeed, using functional attributes of plants to identify important environmental gradients structuring communities has been the purpose of many past studies (e.g. Werger and Sprangers 1982). This presents a challenge for finding TGs that can be used as a "universal language" of plant community response to disturbance (Anderson and Hoffman 2011).

Sensitivity of a trait grouping scheme to many different management practices is also desirable for describing plant community response to management. No single TG classification was related to all management practices on both soil types (Figure 4.2). Species-based groups are related to at

least two management practices on both soil types, whereas TG-based groups were related to fewer management practices on average. Differences in sensitivity between the two soil types are largely related to differences in plant community response to management. Sprayed Claypan plots are a persistent grassland, whereas sprayed Mountain Loam plots have abundant shrubs and forbs (Kachergis et al. in prep)—thus Claypan response to spraying is expressed in terms of simple TGs (increase in grasses and decrease in forbs), whereas Mountain Loam response is not. Neither species nor TG composition is related to distance from water, a proxy for grazing intensity, possibly because water is abundant in this landscape and all plots were relatively close to water (<0.6 km).

This study reveals that species and trait group composition are both useful for understanding sagebrush steppe response to management. However, no single approach is ideal--there are tradeoffs between approaches that affect interpretations of community dynamics. TGs that employ five or more plant traits related to the disturbances of interest appear sufficient for identifying major vegetation patterns. The traits we use here can be quickly measured in the field and do not require species identification in order to identify the trait group. Sampling should be stratified by soil type since responses of trait groups to disturbance vary by soil type. Simple TGs are useful in cases where a strong, single life-form based response to disturbance is expected, but not when responses are expected to be mixed among life forms. More complex TG's are useful for detecting a broader range of responses to management, especially grazing. Species composition was sensitive to more individual management

practices and often had the strongest relationships with management. If identifying diverse potential states is a key monitoring objective, then species-based monitoring is more appropriate. A combination of approaches provides the most complete information, but may not be justified depending on the objectives and funding of the monitoring project at hand. For example, a species approach may be best for identifying alternate states, but an TG approach could be used to monitor changes over time, especially when transitions involve large changes in TG composition.

Table 4.1. Similarity between potential states identified using hierarchical cluster analysis on species and trait-based group composition based on adjusted Rand index. A value of 1 indicates complete agreement between potential states identified using two approaches, while a value of 0 indicates no more agreement than expected by chance. Similarity to species-defined states increases with the complexity of the trait group classification.

<i>Ecological Site</i>	<i>Trait Group Class.</i>	Adjusted Rand Index		
		<i>Complex</i>	<i>Practical</i>	<i>Simple</i>
Mountain Loam	Species	0.40	0.29	0.14
	Complex		0.59	0.26
	Practical			0.17
Claypan	Species	0.38	0.26	0.23
	Complex		0.31	0.27
	Practical			0.42

Table 4.2. Potential states of the Mountain Loam ecological site and their characteristic species and trait-based groups. States were identified using hierarchical cluster analysis of species composition and Complex, Practical, and Simple trait group composition. Significant indicator species and trait groups according to Indicator Species Analysis are listed next to the name of each state. Grey shading indicates potential states that are over 50% similar to each other, meaning that $\geq 50\%$ of plots in one state are also in the other. Species names are from the USDA PLANTS database (USDA 2010).

Species	Complex	Practical	Simple
SP1: <i>Artemisia tridentata</i> var. <i>vaseyana</i> , <i>Bromus marginatus</i>	CO1: Non-sprouting Shrub	PR1: Non-sprouting Shrub	SI1
SP2: <i>Lomatium grayi</i> , <i>Microseris nutans</i> , <i>Astragalus wetherillii</i> , <i>Wyethia amplexicaulis</i>	CO2: Perennial Medium Clonal Grasses; Perennial Short Bunchgrasses	PR2: Tall Grasses	SI2: Perennial Grass
SP3: <i>Chrysothamnus viscidiflorus</i> , <i>Leymus cinereus</i> , <i>Erodium cicutarium</i>	CO3: Perennial Tall Bunchgrass	PR3: Short and Medium Grasses	SI3
SP4: <i>Symphyotrichum spathulatum</i> , <i>Melica bulbosa</i> , <i>Achillea millefolium</i> , <i>Achnatherum lettermannii</i> , <i>Symphoricarpos rotundifolius</i>	CO4	PR4: 12 Short and Medium Forb	SI4: Shrub
SP5: <i>Artemisia tripartita</i> , <i>Phleum pratense</i> , <i>Poa nemoralis</i> ssp. <i>interior</i>	CO5: Resprouting Shrubs	PR5	SI5: Perennial Forb
	CO6	PR6	SI6
	CO7		

Table 4.3. Potential states of the Mountain Loam ecological site and their characteristic species and trait-based groups. States were identified using hierarchical cluster analysis of species composition and Complex, Practical, and Simple trait group composition. Significant indicator species and trait groups according to Indicator Species Analysis are listed next to the name of each state. Grey shading indicates potential states that are over 50% similar to each other, meaning that $\geq 50\%$ of plots in one state are also in the other. Species names are from the USDA PLANTS database (USDA 2010).

Species	Complex	Practical	Simple
SP1: <i>Koeleria macrantha</i> , <i>Phlox longifolia</i>	CO1: Perennial Short Bunchgrasses	PR1	SI1: Perennial Grass
SP2: <i>Artemisia arbuscula</i> ssp. <i>longiloba</i> , <i>Arenaria</i> <i>hookeri</i> , <i>Gutierrezia</i> <i>microcephala</i> , <i>Orthocarpus luteus</i>	CO 2: Non- resprouting shrubs	PR2: Non- resprouting shrubs	SI2:
SP3: <i>Pascopyrum smithii</i>	CO 3: Perennial Medium Clonal Grasses	PR3	SI3: Shrub
SP4: <i>Astragalus</i> <i>wetherillii</i> , <i>Lomatium</i> <i>grayi</i> , <i>Microseris nutans</i>	CO 4: Perennial Short Non-N Fixing Forb	PR4	SI4: Annual Grass
SP5: <i>Melica bulbosa</i> , <i>Helianthella uniflora</i> , <i>Perideridia gairdnerii</i> , <i>Elymus elymoides</i> , <i>Achnatherum lettermanii</i> , <i>Symphoricarpos</i> <i>rotundifolius</i> , <i>Artemisia</i> <i>tridentata</i> ssp. <i>Vaseyana</i>	CO 5	PR5: Medium Grass	SI5: Perennial Forb
SP6: <i>Poa secunda</i>	CO 6: Perennial Medium N-Fixing Forbs (0.10)	PR6: Short Grass	SI6
SP7: <i>Artemisia tripartita</i> , <i>Poa nemoralis</i> ssp. <i>interior</i> , <i>Achillea</i> <i>millefolium</i> , <i>Bromus</i> <i>tectorum</i>	CO 7: Perennial Medium Bunchgrass, Perennial Medium Clonal Non-N-Fixing Forbs	PR7: Short Forb	SI7

Table 4.4. Relationships among site history, environmental variables, and potential states for the Mountain Loam ecological site. States are based on species composition and Complex, Practical, and Simple trait-based group composition. Relationships are significant according to logistic regression at $p < 0.10$; italics indicate qualitative analysis (e.g. *All sprayed*). Grey shading indicates potential states that are over 50% similar to each other.

Species		Complex		Practical		Simple	
State (N)	Site History/ Enviro.	State (N)	Site History/ Enviro.	State (N)	Site History/ Enviro.	State (N)	Site History/ Enviro.
SP1 (5)	Grazing Intensity (+) Slope (-)	CO1 (5)	Grazing Intensity (+) Slope (-)	PR1 (5)	Grazing Intensity (+) Slope (-)	SI1 (8)	Slope (+) Clay (-)
SP2 (12)	Clay (+) Slope (-)	CO2 (7)	Clay (+)	PR2 (11)	Grazing intensity (-) Slope (+)	SI2 (3)	-
SP3 (5)	Clay (-) Slope (+)	CO3 (4)	Slope (+)	PR3 (5)	-	SI3 (15)	-
SP4 (7)	Spray (+)	CO4 (8)	Grazing intensity (-)	PR4 (10)	Clay (+)	SI4 (4)	-
SP5 (4)	-	CO5 (7)	-	PR5 (1)	<i>Burned 2 yr ago</i>	SI5 (2)	-
		CO6 (1)	<i>Burned 2 yr ago</i>	PR6 (1)	<i>Burned 2 yr ago</i>	SI6 (1)	<i>Burned 2 yr ago</i>
		CO7 (1)	<i>Burned 2 yr ago</i>				

Table 4.5. Relationships among site history, environmental variables, and potential states for the Claypan ecological site. States are based on species composition and Complex, Practical, and Simple trait-based group composition. Relationships are significant according to logistic regression at $p < 0.10$; italics indicate qualitative analysis (e.g. *All sprayed*). Grey shading indicates potential states that are over 50% similar to each other.

Species		Complex		Practical		Simple	
<i>State (N)</i>	<i>Site History/ Enviro.</i>	<i>State (N)</i>	<i>Site History/ Enviro.</i>	<i>State (N)</i>	<i>Site History/ Enviro.</i>	<i>State (N)</i>	<i>Site History/ Enviro.</i>
SP1 (10)	Spray (+)	CO1 (6)	<i>All sprayed</i>	PR1 (9)	Spray (+)	SI1 (12)	Spray (+) Distance from water (-)
SP2 (6)	Slope (+) Clay (-)	CO2 (9)	Slope (+) Clay (-)	PR2 (6)	-	SI2 (3)	-
SP3 (7)	Transformed Aspect (-)	CO3 (9)	-	PR3 (9)	Grazing Intensity (-)	SI3 (9)	-
SP4 (4)	-	CO4 (2)	-	PR4 (6)	-	SI4 (4)	Spray (+) Transformed Aspect (-)
SP5 (3)	-	CO5 (8)	-	PR5 (3)	-	SI5 (5)	-
SP6 (5)	-	CO6 (1)	-	PR6 (4)	-	SI6 (5)	Slope (-)
SP7 (4)	Transformed Aspect (+) <i>2/4 Mechanically Treated</i>	CO7 (4)	Transformed Aspect (+)	PR7 (2)	-	SI6 (1)	-

Table 4.6. Sensitivity of each trait grouping scheme to different management and environmental variables. “Yes” and “No” indicate whether or not there was a significant relationship between a management practice or environmental variable in that trait grouping scheme. Potential states were defined by Species, Complex, Practical, and Simple trait groupings.

	Species		Complex		Practical		Simple	
	ML	CP	ML	CP	ML	CP	ML	CP
Management								
Grazing Intensity	Yes	No	Yes	No	Yes	Yes	No	No
Distance from Water (proxy for grazing intensity)	No	No	No	No	No	No	No	Yes
Spraying	Yes	Yes	No	Yes	No	Yes	No	Yes
Mechanical Treatment (CP Only)	-	Yes	-	No	-	No	-	No
Sensitivity (No. Management Factors Associated with a State)	2	2	1	1	1	2	0	2
Average Sensitivity	2		1		1.5		1	
Environment								
Clay	Yes	Yes	Yes	Yes	Yes	No	Yes	No
Slope	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes
Aspect	No	Yes	No	Yes	No	No	No	Yes
Sensitivity (No. Environmental Factors Associated with a State)	2	3	2	3	2	0	2	2
Average Sensitivity	2.5		2.5		1		2	

	Grass	Forbs	Shrubs
Simple (4)	Annual vs. Perennial	Perennial	
Practical (9)	Short vs. Medium vs. Tall	Short vs. Medium vs. Tall	<u>Resprouting</u> vs. Non
Complex (17)	Vegetative Reproduction vs. None	Vegetative Reproduction vs. None, N-Fixing vs. Not	<u>Resprouting</u> vs. Non
Species (44)			

Figure 4.1. Trait-based group classification schemes used to define potential alternate states in this study, increasing in complexity from Simple groups based on growth form and life history to Species.

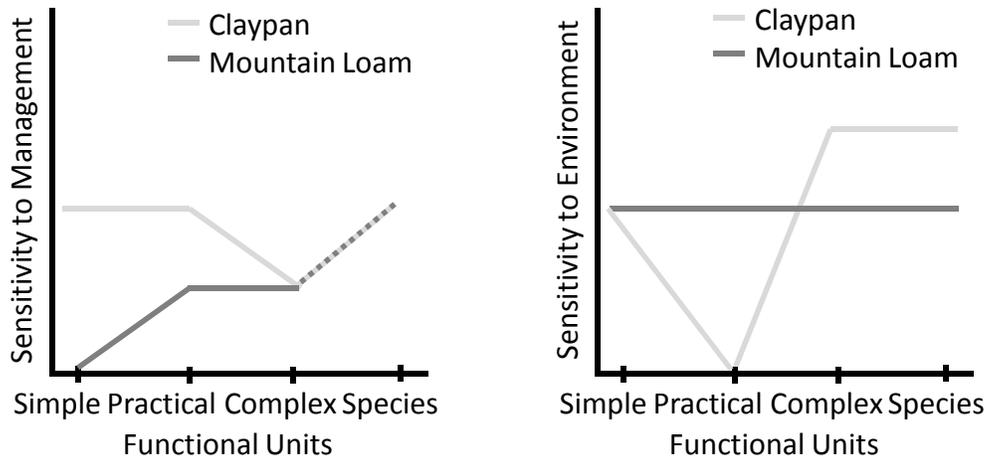


Figure 4.2. Sensitivity of species and trait-based group composition to range management practices and environmental variation on two different soil types. Functional units used to define states increase in complexity with the x axis. Sensitivity is defined by the number of different management practices and environmental variables related to states in each grouping scheme (Table 6). While species and trait group approaches were complementary, no single approach gave a complete picture of sagebrush steppe responses to management.

**Chapter 5.
Long Term Vegetation Change in California Park: Evidence for Alternate States?**

ABSTRACT

Describing and predicting shifts between alternate states in ecosystems is a frontier in ecology with important implications for land management and human well-being. The sagebrush steppe, one of the most extensive vegetation types in North America, may have shifted states when it experienced heavy livestock grazing in the nineteenth century. The goals of this study are 1) to describe long-term vegetation change in a high-elevation sagebrush steppe park and 2) evaluate evidence that this ecosystem exhibits alternate state dynamics. We examine vegetation change over the last 50 years in California Park, Colorado, USA using monitoring data from 15 permanent transects at six sites on two soil types. We analyzed change in species composition over time and related it to management and climate drivers using non-metric multidimensional scaling. We found that species composition has changed over time in response to management practices but not to climate. Spraying the herbicide 2,4-D resulted in decreases of shrubs and a dominant, unpalatable forb (*Wyethia*), but shrubs recovered. Spraying also resulted in a short term (10-20 year) increase in native palatable grasses and forbs. Native grasses have since decreased again in

conjunction with increases in cattle stocking rate and elk populations. The non-native pasture grass *Phleum* has increased to become one of the dominant grasses in California Park today. Changes in species composition generally did not match patterns expected based on alternate state theory. Instead of sudden jumps, changes were small and gradual; furthermore, rather than experiencing persistent shifts, composition fluctuated through time. Two possible exceptions are 1) lack of recovery of the dominant forb *Wyethia* after spraying at the beginning of the time series, possibly indicating a shift from an overgrazed state and 2) the recent increase in the non-native grass *Phleum*. Analyses of long term data can help determine whether alternate state dynamics are the appropriate model of change for land management decision-making. Long-term changes in species composition suggest that high-elevation sagebrush steppe experiences gradual changes in response to management rather than sudden shifts between alternate states. Regardless of whether this system exhibits alternate states, the long-term increase in the non-native pasture grass *Phleum* raises the question of whether gradual changes can still be irreversible.

INTRODUCTION

Describing and predicting shifts between alternate states in ecosystems is a frontier in ecology with important implications for natural resource management and human well-being (Scheffer et al. 2001). Rangelands with a short evolutionary history of grazing and low resource availability are especially likely

to respond non-linearly to disturbances and undergo irreversible transitions (Bestelmeyer et al. 2006; Chartier and Rostagno 2006; Cingolani et al. 2005; Kefi et al. 2007). Since rangelands provide many important ecosystem services including provisioning of food and clean water (Havstad et al. 2007), irreversible transitions can have serious impacts on social as well as ecological systems. Recognizing the importance of threshold dynamics, the range profession has recently adopted a management approach based on alternate state theory. The Natural Resource Conservation Service (NRCS) and partners are creating state and transition models, conceptual models that describe shifts in ecosystems, for many types of land throughout the US. Long-term data are valuable for model building because they can provide evidence for the existence of alternate states and relate transitions to specific management practices and weather patterns. The goals of this study are to 1) describe long-term vegetation change in a high-elevation sagebrush steppe park and relate changes to management practices and climate and 2) evaluate evidence that this ecosystem exhibits alternate state dynamics.

Assessments of whether alternate states exist in ecosystems are important because alternate state dynamics have major implications for ecosystem management and sustaining ecosystem services. A one-state system implies that the effects of disturbance are temporary, and with sufficient time the system will return to the only equilibrium possible (Scheffer et al. 2002). A multi-state system, however, requires energy inputs to shift from one state to another. Alternate state theory is largely based on mathematical systems theory

and makes specific predictions about how system variables change over time (Scheffer 2009). Observational evidence of alternate states identifies behavior of ecological systems that is similar to predicted patterns (Scheffer 2009). First, sudden jumps in a time series can be evidence of alternate states. For example, lakes in Wisconsin suddenly increase in phosphorous concentrations when anoxic conditions caused by algae blooms cause a release of phosphorous from soil into water (Carpenter and Gunderson 2001). This triggers a shift to an alternate, eutrophic state. Second, an external disturbance or perturbation often triggers the shift to a different, permanent state. In semi-arid rangelands, herbivory and drought are often triggers of ecosystem shifts (Bestelmeyer et al. 2003; Cingolani et al. 2005; West and Young 2000). A third prediction of alternate state theory is that the system does not recover to its original state even when the disturbance is removed. For example, a long-term (26 year) spring-grazed three-tip sagebrush rangeland with high shrub cover and little forb understory relative to other grazing treatments did not recover its forb understory when grazing was removed or when it was fall-grazed after 40 years (Bork et al. 1998). Similarly, rangeland experiments have shown that once a critical soil erosion threshold has been crossed, vegetation is unable to recover (Chartier and Rostagno 2006). Although this general pattern--sudden changes triggered by disturbance in a state variable that then doesn't resume its original values when the disturbance is removed--supports the existence of alternate states in long-term data sets, evidence can never be definitive (Scheffer 2009). However, the economic and ecological consequences of shifting to an undesirable

alternate state make it an important question to investigate in different ecosystems.

Long-term change in plant species composition offers a unique opportunity to explore evidence of alternate states in the sagebrush steppe. Heavy grazing in the second half of the 19th century represented an intense and novel perturbation to the ecosystem (Mack and Thompson 1982; West and Young 2000). Historical documents indicate widespread reduction in native perennial grasses and expansion of native shrubs after only 10-15 years of grazing (West and Young 2000). In addition, persistent changes in ecological processes such as erosion suggest that thresholds may have been crossed. Grazing was reduced following implementation of the Taylor Grazing Act, passed in 1934. The long-term dataset in this study that begins in 1953 therefore represents a time when the intensity of perturbation had been reduced (Figure 5.1). This study focuses on California Park, a 4,400 acre sagebrush park at 8,500 feet in the Elkhead Mountains of northwestern Colorado. This area received particularly heavy grazing due to the fact that it was a driveway for over 10,000 cattle as well as sheep (USFS 2011). At the start of the time series, range managers noted two major problems that they took action to correct: 1) soil erosion, often forming gullies, and 2) dominance of the unpalatable native forb *Wyethia amplexicaulis* (*Wyethia*) to the detriment of other native species (USFS 2011). In addition to reducing grazing, Forest Service managers sprayed herbicide (2,4-D) to kill *Wyethia* (e.g. Mueggler and Blaisdell 1951) and sagebrush. Permanent transects were established throughout the Park in the

1940's and 1950's in order to evaluate rangeland response to these management actions (USFS 2011). These are a few of the over 16,500 permanent monitoring transects the US Forest Service (USFS) established on 5307 National Forest allotments by 1967 (Reppert and Francis 1973).

The goal of this study is to describe changes in plant species composition in California Park over the last 50-60 years in an alternate state context. We use loop frequency data to describe changes in composition, and draw on photos and other supplementary information to confirm loop frequency findings. This case study will complement extensive work on nearby private lands that describe vegetation dynamics using local knowledge (Knapp and Fernandez-Gimenez 2009b), an observational field study (Kachergis et al. in press), and participatory model building (Knapp et al. 2011). These studies suggested that, as in other areas of the sagebrush steppe (West and Young 2000), long-term heavy grazing causes over-abundance of sagebrush and reduction of desirable perennial species (Knapp et al. 2011), and erosion on a clay soil type (Kachergis et al. in press). We hypothesized that we would see two changes in species composition related to the management history of California Park. We first hypothesized that sagebrush and *Wyethia* cover would initially decrease after spraying, and then increase over time but not to previous levels. We also hypothesized that we would see an increase throughout the time period in frequency of herbaceous species due to the reduction in grazing pressure compared to a century ago combined with spraying. Finally, we hypothesized that changes in composition would match the characteristics of alternate state dynamics: they would occur as

jumps in the time series, they would be related to disturbance (grazing, spraying and drought history), and they would not resume their original values once disturbance was removed. In contrast, gradual changes in species composition that eventually return to original values after disturbance would support a one-state view of this system. This case study will provide valuable insights into the long-term dynamics of sagebrush rangelands that are recovering from historic overgrazing.

METHODS

Study Area

This study takes place in California Park on the Routt National Forest (UTM zone 13, Easting 319000, Northing 4510500; 2500 m elevation). Mean annual temperature and precipitation for Elk River, a nearby SNOTEL site, are 2.3 C and 722 mm. This high-elevation sagebrush park is dominated by silver sagebrush with some mountain big sagebrush (*Artemisia cana* and *Artemisia tridentata* ssp. *vaseyana*). The management history of the area is similar to many other areas in the Intermountain West: following heavy grazing by domestic livestock in the second half of the 19th century, the US government began regulating grazing in the area in the early 1900's. However, significant reductions in stocking did not occur until after the implementation of the Taylor Grazing Act in the 1940s. The highest recorded stocking rate was 1.9 AUMs/acre in 1927, the first year for which there are grazing records (Figure 5.1); stocking rate was dramatically

reduced after that, reaching a low of 0.1 AUMs/acre from 1951-1968, and then increased to current levels at 0.18 AUMs/acre in 1969 (USFS 2011). Land managers also sprayed many of the sites with 2,4-D to control *Wyethia* and sagebrush. Management history variables for each site are: time since spraying; current year's stocking rate; and three-year, ten-year, and twenty year average stocking rates based on grazing allotment records (USFS 2011). As an indicator of climatic conditions, we also included Palmer Drought Severity Index (PDSI), an indicator of long-term drought (months to years) based on both precipitation and temperature (NOAA 2007). PDSI ranges from -6 to +6 with negative numbers indicating drought and positive numbers indicating a wet period. We also qualitatively discuss possible effects of herbivory from elk, whose populations in the area are known since 1980 and peaked in 1999 (Figure 5.1; data provided by D. Finley of the Colorado Division of Wildlife for Data Analysis Unit E-2; calculated using the method of White and Lubow 2002) .

Site Characteristics

Three sites (eight transects total) had clayey soils (Table 5.1). Some variation in soils is worth noting: sites C3 and C4 had vertic soils with clay within 10 cm of the surface, while California Park Enclosure had clay loam to at least 40 cm. No sagebrush was present at C3 or C4 throughout the time series. The sites also had different management histories. California Park Enclosure had one transect inside a domestic livestock enclosure that has existed since 1942 and one outside. California Park Enclosure and C4 were sprayed with 2,4-D to kill Mule's-

ear in the early 1950's, but C3 was never sprayed so that it could serve as a reference site.

Three sites (seven transects) had loamy soils (Table 5.1). All transects were sprayed with 2,4-D in the early 1960s. In addition, Transects 1 and 2 at the Elkhead Enclosure have had domestic livestock excluded since 1942. In contrast to the clay sites, all of the loamy sites had sagebrush present at the beginning and the end of the study period.

Vegetation

Long-term data are from fourteen 30.48 m permanent transects at the six sites within California Park (Table 5.1). Vegetation measurements were taken using the Parker Three-step method (Parker 1950, 1951; USFS 1985). Our analysis focuses on Step 1 of this method, which involves recording vegetation within a 1.9 cm diameter loop at 100 points along each 30.48-m transect according to the following set of rules. Grasses and forbs are recorded as a "hit" when their root crown falls within the loop. If more than one species is present, the dominant species is recorded. Annuals are recorded only when perennial vegetation is not present, but annuals were not recorded until the 1970s in this dataset. If more than 50% of the loop is covered with litter or moss, then litter or moss is "hit"; otherwise bare ground, erosion pavement, or rock are recorded. Shrubs are recorded separately as "overstory" when the perennial portion of the shrub crown falls within the loop. Each permanent transect, marked by rebar stakes, was measured at different time intervals (generally at least every 10 years) beginning

1950-1960 through 2010. Step 2 of Parker's method involves collection of supplementary information such as plant vigor and utilization and a record of range condition and trend. Step 3 involves taking 2 photos at each transect: a landscape photo from the start of the transect looking towards the end, and a close-up photo of a 0.91x0.91 m plot starting 1.07 m from the beginning of the transect. Our quantitative analyses rely on Step 1, with supporting qualitative evidence from Steps 2 and 3.

Although loop frequency data from Parker's method contains valuable information about changes in species composition over time, it is not a measure of vegetation cover and cannot be compared directly with other conventional measures of plant abundance (Coughenour et al. 1994). It overestimates plant basal cover because of the area of the loop (Hutchings and Holmgren 1959; Smith 1962). It is also influenced by plant size, shape and numbers, so that even with constant basal area, Parker frequencies vary with the size and shape of plants (Hutchings and Holmgren 1959). These effects are most important for infrequent plants with large individual basal area, but are less important for grasses and forbs with smaller and less variable individual sizes (Hutchings and Holmgren 1959). When Parker data have been used to analyze changes in species composition over time, they have revealed important trends related to climate (Coughenour et al. 1994). In addition, as one of the earliest and most widespread vegetation data collection methods on western US rangelands, it is often the only source of quantitative information about vegetation change on these rangelands. We took several measures to improve data quality. We

checked that all datasheets were summarized in the same way, as follows: all shrub canopy cover hits were recorded; and all understory and shrub basal hits were summarized separately and checked to ensure that they added up to 100. Measurements from 1958 were removed because plants that occurred in the shrub understory were not recorded. In addition, we combined species where there was reason to question species identification due to patterns in species occurrence in the time series. As a result our species list is a mixture of species and genus: for example, *Festuca idahoensis* and *Festuca thurberi* were identified consistently, but *Bromus marginatus* and *Bromus inermis* are combined into *Bromus* because they were not differentiated in several of the sampling years.

In addition to loop frequency estimates, local managers began monitoring vegetation cover along permanent transects using Daubenmire ocular estimates in 1999. This well-established method assists with interpretation of Parker data. In this method, plant canopy cover is visually estimated by species in twenty 20x50 cm frames along each 30.48 m transect (Daubenmire 1959; USFS 1996). Each species was placed in one of seven cover classes (0-1, 1-5, 5-25, 25-50, 50-75, 75-95, 95-100% cover), and the sum of the products of abundance and frequency in each class was used to determine percent canopy cover. Each transect was measured 2-3 times 1999-2010; we only report 2010 measurements.

Analysis

We described changes in species composition over time and whether they matched patterns predicted by management history (spraying and grazing) and alternate state theory using non-metric multi-dimensional scaling (NMS). This method is ideal for revealing simultaneous changes in multiple species, as would be expected if a threshold was crossed, rather than relying on analysis of individual species. This unconstrained ordination method arranges plots in ordination space based on similarity in species composition, so similar plots are close together. Management and climate variables are correlated with ordination axes after the ordination is performed. If there are important gradients influencing species composition that we did not measure, this method will reveal an unexplained trend in species data. NMS does not require assumptions about the underlying distribution of species along an environmental gradient, and is thus well suited for non-normal data on discontinuous scales such as most species data. NMS searches iteratively for the best positions of species and plots on k dimensions while minimizing the stress of the k -dimensional ordination. NMS was performed using R 2.8.1 and the `vare.mds` function of package `vegan`, which uses up to 20 random starts to find a stable NMS solution. It also centers points, rotates the solution so that axes explain maximum variance, and standardizes the scaling in the result to increase interpretability. We chose the maximum number of dimensions beyond which reductions in stress are less than five. Dissimilarity matrices were calculated using Sorenson's (Bray-Curtis) proportional distance measure, which retains more sensitivity to changes in

species composition than other distance measures (Wishart 1969). Loop frequency values were square root transformed to reduce the influence of very common species and high loop frequency values. Species that occur in fewer than 5% of plots were omitted to reduce noise in the data (McCune and Grace 2002). Annuals were also omitted because they were not measured at the beginning of the time series.

RESULTS

Changes in Sagebrush Canopy and *Wyethia* Loop Frequency

Sagebrush canopy loop frequency in 2010 was strongly correlated with Daubenmire estimates of sagebrush canopy cover ($r^2=0.91$, $p<0.001$), so in this study, sagebrush canopy loop frequency can be considered an index of sagebrush cover. Sagebrush canopy decreased after each site was sprayed with 2,4-D (Figure 5.2). Sagebrush often reached pre-spraying canopy loop frequencies within 20-40 years, although re-colonization was quite variable among sites, and some sites still have very little sagebrush. Interestingly, there is evidence of fairly dramatic sagebrush die-off in the California Park Enclosure and at one C6 transect in the last 10-15 years. Sagebrush did not occur on the sites with the most clayey soil texture (C3 and C4).

Wyethia loop frequency also decreased after spraying (Figure 5.2). In most cases it has remained present but not recovered, except at one transect on

C4 in 2010. The unsprayed California Park Exclosure transect has had consistently high *Wyethia* loop frequency over time.

Changes in Herbaceous Species Composition on Clay Soils

NMS shows trends in species composition according to loop frequency over time (final stress 16.67 along 3 axes; Figures 5.3 and 5.4). Axis 1 differentiates sites, with the California Park exclosure having lower values and higher *Wyethia*, *Eriogonum*, *Geranium*, *Potentilla*, and *Vicia/Lathyrus* loop frequencies than the other two sites. While sites are not identical in initial species composition, the dominant trend across all sites over time is similar, moving from high values to low values on Axis 2. Based on the species scores (Figure 5.5), these changes are related to a decrease in *Wyethia* and an increase in *Poa*, *Phleum* and *Astragalus* loop frequencies. In addition, sites tend to increase and then decrease along Axis 3 over time; this is related to changes in *Bromus*, *Melica*, *Festuca idahoensis* and *Achillea* which increase initially but decline in loop frequency towards the end of the time series. The largest changes occurred at the beginning of the time series along Axis 3. C4 and the California Park exclosure were sprayed at that time. Axis 3 also separates the ungrazed from the grazed transect in the California Park exclosure, with the grazed transect having higher values associated with *Bromus*, *Delphinium* and *Geranium*.

Change in species composition over time according to NMS is strongly related to multiple management and environmental drivers (Figures 5.2 and 5.3; Table 5.2). Axis 1 is negatively related to sagebrush overstory loop frequency

and years since spraying. Axis 2 is negatively related to year and 3-year average stocking rate. Axis 3 is negatively related to the 10- and 20-year moving averages of stocking rate in the California Park allotment. PDSI was not strongly related to trends in species composition over time.

These trends in species composition are confirmed with the photos (Figure 5.5). They show a strong increase in native perennial grass cover and vigor after spraying, especially at site C4, which persisted for 10-20 years. *Wyethia* has remained present in the area, but has not reached pre-spraying levels. In the California Park enclosure, which has had domestic livestock excluded since 1942 and was never sprayed, *Wyethia* is abundant. The vigor and cover of native perennial grasses decreased in the 1970s and 1980s. An increase in *Phleum* is evident at C4 and the California Park enclosure beginning in the mid-1990s.

Changes in Herbaceous Species Composition on Loamy Soils.

NMS shows trends in species composition according to changes in loop frequency over time (final stress 13.8 along 3 axes; Figures 5.6 and 5.7). The overall trend at all three sites is an increase along Axis 1 and a decrease along Axes 2. This corresponds to an increase in *Poa* and *Phleum* and decreases in Wheatgrass, *Festuca idahoensis*, *Bromus* and *Festuca thurberi* (Figure 5.6). This trend reverses somewhat in the 1999 and 2010 measurements at C1 and C6, corresponding to a decrease in *Phleum* in recent years. Axis 3 separates the ungrazed from the grazed transect in the Elkhead Enclosure, with the grazed

transect having higher values associated with *Fragaria*, *Viola*, and *Potentilla* and the ungrazed transect having lower values associated with *Festuca thurberi*.

Many environmental and management variables are correlated with trends in species composition according to loop frequency. Year increased along Axis 1 and decreased along Axis 2 and had the strongest correlation with the ordination (Table 5.3). All measures of stocking rate (this year, last year, and 3-, 10-, and 20-year moving averages) increase along all axes, especially Axis 1. Years since spraying and overstory sagebrush cover increase with Axis 3. PDSI was not related to trends in species composition.

These trends in species composition are confirmed by the photos (Figure 5.8). After spraying, there was a decrease in sagebrush cover and an increase in native grass cover and vigor, although the increase is not as dramatic or persistent (~10 years) as on the clay sites. *Phleum* becomes evident in the 1970s, earlier than at the clay sites, and increases over time until recent years. The photos also show that sagebrush recovery is variable at different sites, which is also clear from the sagebrush canopy hits over time (Figure 5.1). Some sites have not recovered to pre-spraying canopy levels (Figure 5.8). *Wyethia* is generally not present on the loam sites. It is important to note that all loam sites also appear to have maintained a productive grass and forb understory throughout the time that they have been monitored, contrary to our prediction that the grass and forb understory would be sparse at the beginning of the measurement period due to heavy grazing at the turn of the century.

Current Conditions—2010 Cover Estimates

As a measure of absolute abundance and in order to validate the patterns that we observed in loop frequencies, we include Daubenmire estimates of cover for the dominant species (Table 5.4). These estimates confirm the overall species trends. *Phleum* is a dominant grass on both soil types, and *Poa* is a dominant grass on the loamy soil type. Other native grasses are present, but are less abundant, with the exception of *Festuca thurberi* at the Elkhead Exclosure. Forb cover is variable across sites and soil types, although they are generally more abundant on the loamy soil type. Total cover is also higher on the loamy soil type.

DISCUSSION

Long-Term Changes in Plant Species Composition are Related to Grazing and Spraying History

Long term loop frequency data and historic photographs revealed species change over time in relation to grazing and spraying history in California Park. Drawing on previous studies in the region as well as the sagebrush steppe literature (Knapp et al. 2011; West and Young 2000), we hypothesized that sagebrush and *Wyethia* cover would decrease initially after spraying, and increase afterwards but not to previous levels. In addition, we hypothesized that palatable understory native grasses and forbs would increase, due to reduced

grazing intensities relative to the 60 years before this study began in addition to spraying.

The responses of sagebrush and *Wyethia* to spraying over time differed on different soil types. On sites with coarser soils where it was present initially, shrub cover decreased after spraying and then increased gradually over time. In many cases it reached the same levels as before spraying after 20-40 years, but dynamics varied by site. This calls into question the idea that sagebrush had reached especially high densities in this area due to heavy grazing, as has been described in other areas (Blaisdell 1953; Laycock 1994; Stoddart 1941).

Sagebrush has not colonized sites where it was not present initially; these are the heaviest clay sites, which may be unsuitable for sagebrush growth. In contrast, *Wyethia* was present on clay soils, and when sprayed it decreased and generally did not recover. At one unsprayed clay site, *Wyethia* remained abundant throughout the study period. This supports other research as well as local knowledge that suggests the dominance of *Wyethia* is induced by heavy grazing and will persist until *Wyethia* is treated (Knapp et al. 2011; Mueggler and Blaisdell 1951).

Understory composition also changed through the study period, but dynamics were more complex than our simple hypothesis that palatable native plants would increase. Initially, many palatable native perennial grasses such as *Bromus*, *Festuca idahoensis* and wheatgrasses increased in both abundance (based on NMS) and vigor (based on photos). This increase coincided with spraying 2,4-D and the reduction in stocking rate in 1951 to its lowest levels in at

least 50 years. These changes are consistent with other studies which have found dramatic short-term effects of spraying on grass abundance (Mueggler and Blaisdell 1958). This also underlines the importance of refugia that may harbor native species even under long-term heavy grazing and when undesirable plants are dominant (Anderson and Inouye 2001). Over time, however, abundance of palatable native perennial grasses decreased again. This decrease is associated with stocking rate on both soil types, as stocking increased to its current levels around 1970. Changes in species composition are more strongly related to long-term stocking rate averaged over 3, 10, and 20 years than current-year stocking rate. This supports previous research that suggests native sagebrush steppe grasses are sensitive to long-term grazing even at moderate rates (Miller et al. 1994). While we lack elk population numbers for the entire time series, the elk population in the area doubled between 1980 and 2000 (Figure 5.1), which likely also contributed to this trend.

Coinciding with the decrease in native perennial grasses, there has been an increase in the non-native pasture grass *Phleum* across all sites starting in the 1970s on the loam sites and the 1990s on the clay sites. *Phleum* was seeded in the park as recently as the 1990s according to local land managers, although records are not specific about location and timing. It is also a major component of hay in the area and has naturalized on many surrounding rangelands, so it may also be brought in by herbivores. To our knowledge, this is the first time a long-term increase in this grass has been documented in native sagebrush steppe. The increase in *Phleum* coincides with the increase in the stocking rate

in California Park in 1969 and the decrease in native perennial grasses—it is possible that livestock grazing has facilitated the increase in this species. Elk herbivory may have also contributed to this trend.

Evidence of Alternate States

In general, long-term changes in species composition at California Park were not consistent with the predictions of alternate state theory. Rather than sudden jumps in the time series, most changes in composition were gradual and occurred as small shifts in a few species; this is visualized on the ordinations by the fact that the succession vectors tend to cycle about the same points over time (Figures 5.3 and 5.6). The larger jumps that did occur were generally related to a specific spraying event. In addition, instead of being persistent, composition continued to change even after sudden shifts. Sagebrush recovered to pre-spraying levels within several decades (Figure 5.1). These changes in species composition suggest that high-elevation sagebrush steppe experiences continuous changes in response to management rather than sudden shifts between alternate states (Scheffer and Carpenter 2003). This pattern may be better described as a dynamic equilibrium (Huston 1979), with fluctuations in individual species due to management rather than shifts between alternate states. West and Yorks (2002) similarly observed using long-term data that burned and grazed sagebrush steppe experienced temporary fluctuations in species abundance but not large shifts in composition that indicated alternate states. Further studies are needed to prove or disprove the existence of alternate

states in the sagebrush steppe. In addition, comparative studies of change in species composition over time in different ecosystems are needed to discern which systems are more likely to exhibit alternate states.

While there was not clear evidence of alternate state dynamics in this system, two possible exceptions are worth examining. On the clay site which was historically dominated by *Wyethia*, changes in composition were largest just after spraying (Figures 5.3b, 5.3f). *Wyethia* has not returned to its former dominance on this site. Erosion was noted in the first several years at this site, suggesting that ecological processes were altered in addition to species composition, but erosion ended as perennial grasses re-established (Table 5.1). Local knowledge of the area has suggested a *Wyethia*-dominated state as a persistent, alternate state (Knapp et al. 2011). There are examples of a similar condition in the literature also (Mueggler and Blaisdell 1951) and evidence that spraying can cause a transition from *Wyethia* to perennial grasses. It is possible that we observed this site transition away from a *Wyethia*-dominated alternate state at the very beginning of this time series.

In addition, the long-term increase in the non-native pasture grass *Phleum* raises the question of gradual changes and whether they can be irreversible. Although this change was not sudden on the timescale of most ecological studies, it is large and has occurred across multiple sites over the last 40 years. Non-native plants often alter site processes such as nutrient cycling (Prober et al. 2005) and plant invasions have often been cited as evidence of alternate states (Suding et al. 2004). Further work is needed to establish whether *Phleum* is

affecting ecosystem function in California Park and may represent a new alternate state.

Table 5.1. Descriptions and history for the six sites and 15 long-term transects in California Park. Soil types are based on hand textures of surface layers in summer 2010 at each site. Exclosure, spray history and comments are from Forest Service records. Erosion history is taken from a checklist that was part of the Parker Three-step method but was only filled out at ~50% of visits; missing data and years where no erosion were noted are not listed.

Site & Transect	Exclosure?	Spray History	Rills	Gullies	Soil Movement	Comments
Clay Soil Type						
C3	1	-	-	1958 -	1971 -	Soil is vertic (deep cracks)
	2	-	-	Few	Occasional	
	3	-	-			
C4	1	-	1954	1955-	1953-Frequent;	Soil is vertic (deep cracks); 1953 – Erosion attributed to grazing; 1956-1964 – Numerous annuals noted
	2	-	1954	1959 -	1958-1959 -	
	3	-	1954	Few	Occasional; 1986 - Occasional	
CA Park	1	Yes	-	1987 -	1987 -	1942 – Exclosure established; 1953 – Some drift from spraying of outside transect
	2	-	1953	-	Occasional	
					1987 and 1986 -	1999 - Slight
					Slight	1953 - Active erosion also noted and attributed to grazing; not a complete kill of wyethia
Loamy Soil Type						
Elk-head	1	Yes	1963	-	1982 -	1942 – Exclosure established; 1982 – Thurber fescue plants large with dead centers
	2	Yes	1963		Occasional	
	3	-	1963	-	1976 and 1982 -	
					Occasional	

C1	1	-	1963	1968 and 1977 - Few	1968 and 1977 - Occasional	1965 - Slight	1968 – Much rodent activity resulting in death of bunchgrasses; 1977 – grass recovering, recommend spray sagebrush again
	2	-	1963				
C6	1	-	1961	1961 - Few	1961 - Occasional	1961 and 1976 - Slight	
	2	-	1961				

Table 5.2. Relationships between management and environmental factors and differences in species composition on the clay soil type according to non-metric multi-dimensional scaling. NMDS1, 2, and 3 refer to correlations between each variable and each of the axes of the ordination. Significant relationships according to the permutation test (1000 permutations) indicate a stronger relationship with species composition than expected by chance.

	NMDS1	NMDS2	NMDS3	r²	Pr(>r)
Year	-0.336	-0.942	-0.000	0.61	0.000999***
PDSI	-0.679	-0.511	-0.527	0.13	0.017982 *
Graz20Yr	0.544	0.276	-0.792	0.26	0.000999 ***
Graz10Yr	0.171	-0.273	-0.946	0.14	0.003996 **
Graz3Yr	0.225	-0.835	-0.503	0.19	0.001998 **
GrazLastYr	0.153	-0.931	-0.330	0.19	0.000999 ***
AUMs	0.626	0.058	0.778	0.04	0.382617
Overstory.Sagebrush	-0.960	-0.234	0.153	0.48	0.000999 ***
YrsSinceSpray	-0.682	-0.413	-0.604	0.25	0.000999 ***
Site	-0.915	0.088	0.393	0.60	0.000999 ***

Table 5.3. Relationships between management and environmental factors and differences in species composition on the loam soil type according to non-metric multi-dimensional scaling. NMDS1, 2, and 3 refer to correlations between each variable and each of the axes of the ordination. Significant relationships according to a permutation test (1000 permutations) indicate a stronger relationship with species composition than expected by chance.

	NMDS1	NMDS2	NMDS3	r²	Pr(>r)
Year	0.836	-0.476	-0.272	0.58	0.000999 ***
PDSI	0.878	-0.472	0.082	0.07	0.286713
Graz20Yr	0.587	0.360	0.725	0.53	0.000999 ***
Graz10Yr	0.792	0.223	0.568	0.50	0.000999 ***
Graz3Yr	0.836	0.233	0.496	0.60	0.000999 ***
GrazLastYr	0.734	0.363	0.574	0.56	0.000999 ***
AUMs	0.389	0.760	0.520	0.25	0.002997 **
Overstory.Sagebrush	0.214	-0.077	0.974	0.19	0.014985 *
YrsSinceSpray	0.087	-0.560	0.824	0.21	0.010989 *
Site	-0.446	-0.858	-0.254	0.12	0.113886

Table 5.4. Daubenmire cover values for selected species at all sites in 2010.

	Clay sites						Loamy sites							
	C3		C4			CalPark		Elkhead			C1		C6	
Species	T1	T2	T1	T2	T3	In	Out	1In	2In	3Out	T1	T2	T1	T2
Shrub														
<i>Artemisia</i>	0	0	0	0	0	4.2	29	10	3.9	20	33	17	8.9	12
<i>Chrysothamnus</i>	0	0	0	0	0	0	0	3.9	6.3	1.1	0	0	0	0
Perennial Grass														
Wheatgrass	4.5	1.4	4.4	1.3	3.1	2.6	3.5	1.3	3.3	0	0.9	0.1	3.3	0.2
<i>Bromus</i>	0.5	0	0	0.2	0	2.5	0.5	2.3	3.4	0.5	1.3	9.2	7.8	1.1
<i>Festuca idahoensis</i>	2.9	1.7	6.7	1.8	9.1	16	3.2	0.2	3.5	1.6	5	1.4	1	0
<i>Festuca thurberi</i>	0	0	0	0	0	0	0	11	4.9	0	0	1.9	0	0
<i>Phleum</i>	16	2.2	3.2	0	8.2	5.6	5	1.6	3.8	6.4	11	6.2	7.6	10
<i>Poa</i>	0	0.2	0.2	0	0	2	0	5	0.6	6.2	3.6	12	5.9	20
<i>Stipa</i>	2.4	0.9	0	0.2	0.6	0	3.3	0.2	4.4	3	0.8	0.8	0.9	0
Forbs														
<i>Achillea</i>	0.8	3.6	5	1.5	2	2.4	2.5	6.2	5.5	6.7	4.1	7.6	6.1	3.4
<i>Aster/Erigeron</i>	0.9	0	0.3	0	2.1	6.1	6.8	0.9	0.2	1.3	0.9	5.2	0.4	3
<i>Delphinium</i>	0.1	0	0	0	0	0	0.2	0	0.9	0.3	1.2	0	0	0
<i>Eriogonum</i>	0	0	0	0	0	0	1.6	8.3	5.9	12	0	3.5	0	0
<i>Geranium</i>	0	0	0	0	0	0	0	2.8	2.2	7.8	2.9	4	2	3.9
<i>Lomatium</i>	2.1	0.9	3.5	2	0.1	0	0	0	0	0	0	0	0	0
<i>Perideridia gairdneri</i>	0.5	0.2	0	0	0.1	0.3	0.2	0	0	0	0.3	0.2	1.5	0.2
<i>Potentilla</i>	0	0	3.8	5.8	8.7	11	0.9	0	0	4.2	2.7	0.4	0.3	3.7
<i>Vicia/Lathyrus</i>	0	0	0	0	0	0.7	4.2	2.9	6.3	7.9	4	2.4	4.2	3.6
<i>Wyethia</i>	0.8	0	1.6	4.3	0	17	0	0	0	0	0	0	0	0
<i>Madia</i> (annual)	19	2.9	8.4	4.4	11	5.1	0.2	0	0	0	0	0	7.9	8.2
Total	57	21	38	23	48	81	64	71	63	84	81	81	67	110

Figure 5.1. Known history of grazing in California Park. Cattle use is from existing records for the California Park allotment (USFS 2011), which show that it was generally grazed July-late September by cow-calf pairs. Elk population numbers are for Colorado Division of Wildlife Data Analysis Unit E-2, which California Park is at the east end of and covers <1% of the area. California Park is occupied by elk late spring-fall.

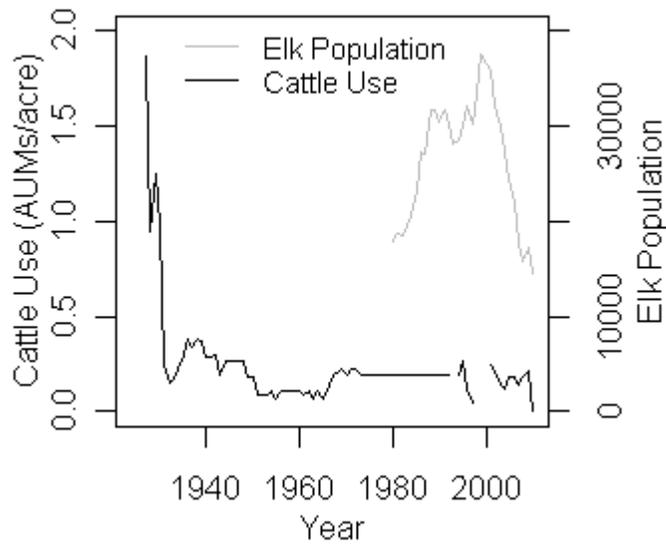


Figure 5.2. Changes in sagebrush canopy and *Wyethia* loop frequency over time. Most long-term monitoring transects were sprayed in the 1950s and 1960s to remove these species and improve rangeland grass production.

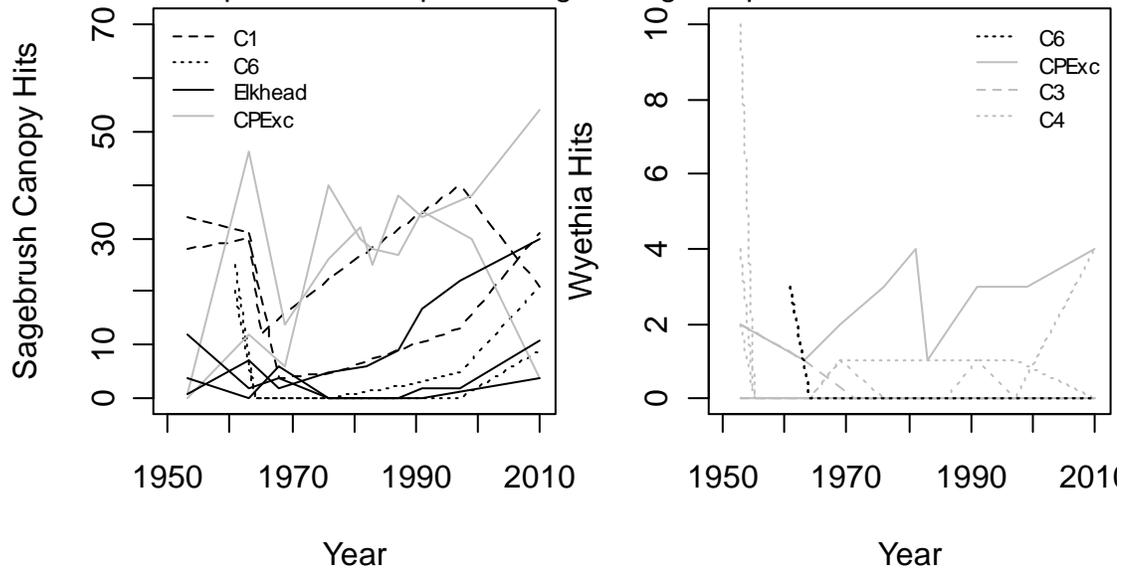


Figure 5.3. Non-metric multi-dimensional scaling results for all transects with clay soils (Axis 2 vs. 1 a-d, Axis 2 vs 3 e-h; sites a-c and e-g; correlations with management and environmental factors d and h). For each site, open circles represent individual measurements, and lines connect each measurement to the next one through time. The last measurement (2010) is marked with an arrow. Sites were analyzed simultaneously but are graphed separately.

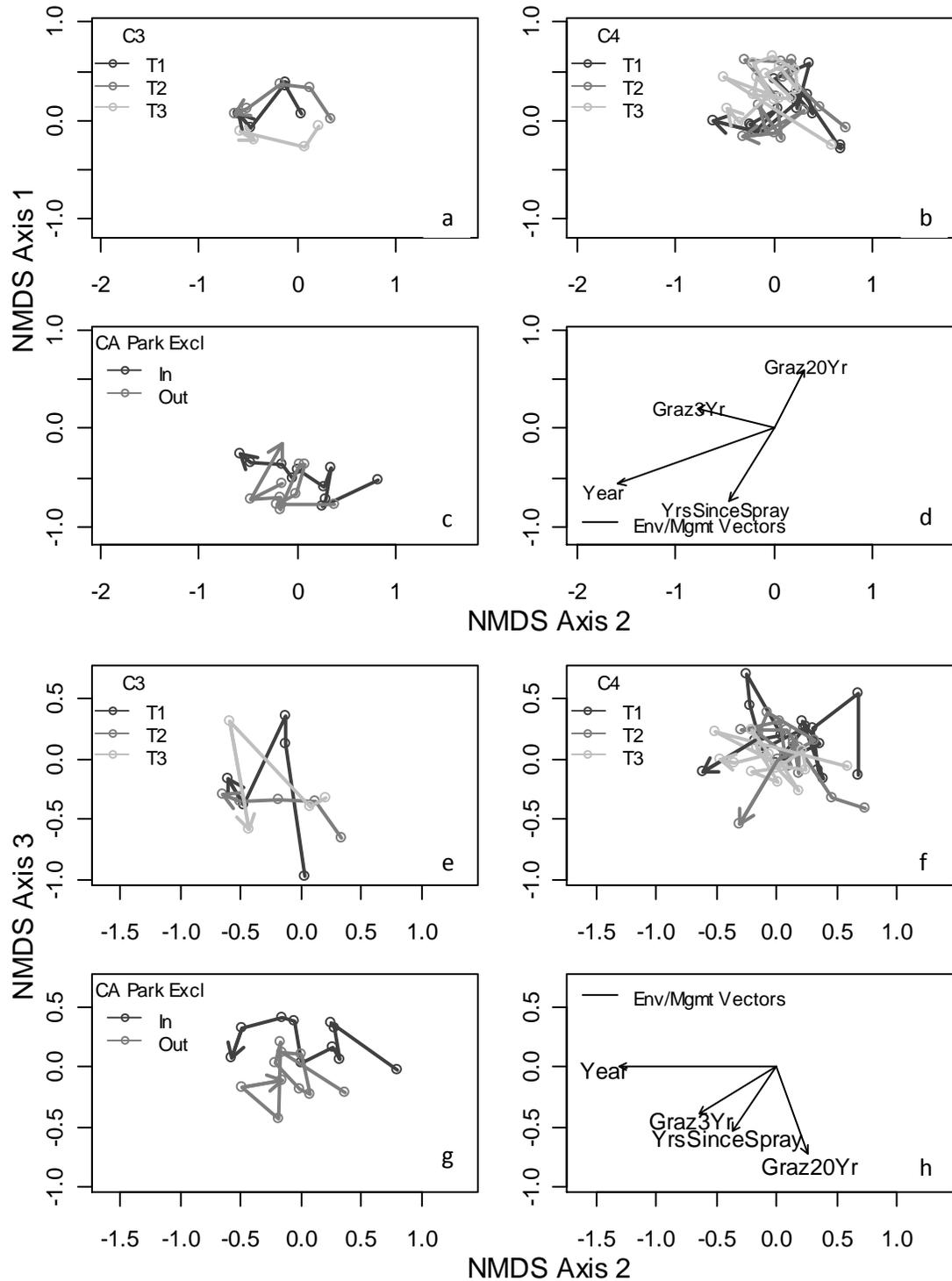


Figure 5.4. Selected species locations on the non-metric multidimensional scaling ordinations for the clay sites. A shift in the position of a particular site through time on Figure 5.3 shows that it has generally increased in the species that occur near its new position.

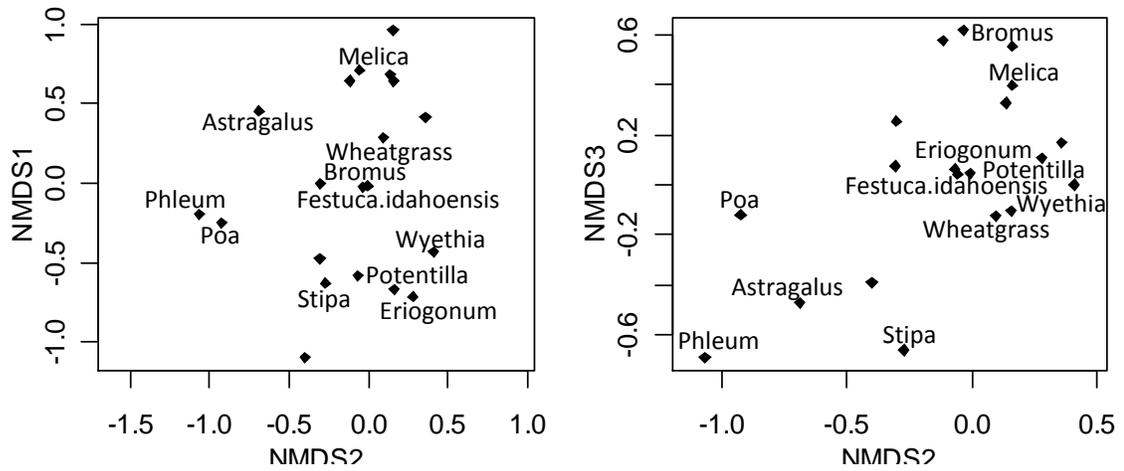


Figure 5.5. Site C4 in 1953 (a, b), 1956 (c, d; two years after spraying with 2-4,D) and in 2010 (e, f). The 1953 photos (a, b) show the extreme abundance of the broad-leaved forb *Wyethia* which was the reason the spraying program was implemented. The tall grasses in this and other closeup photos from 1956 appear to be *Bromus* and wheatgrasses, which increased for 1-2 decades after spraying but have declined since.

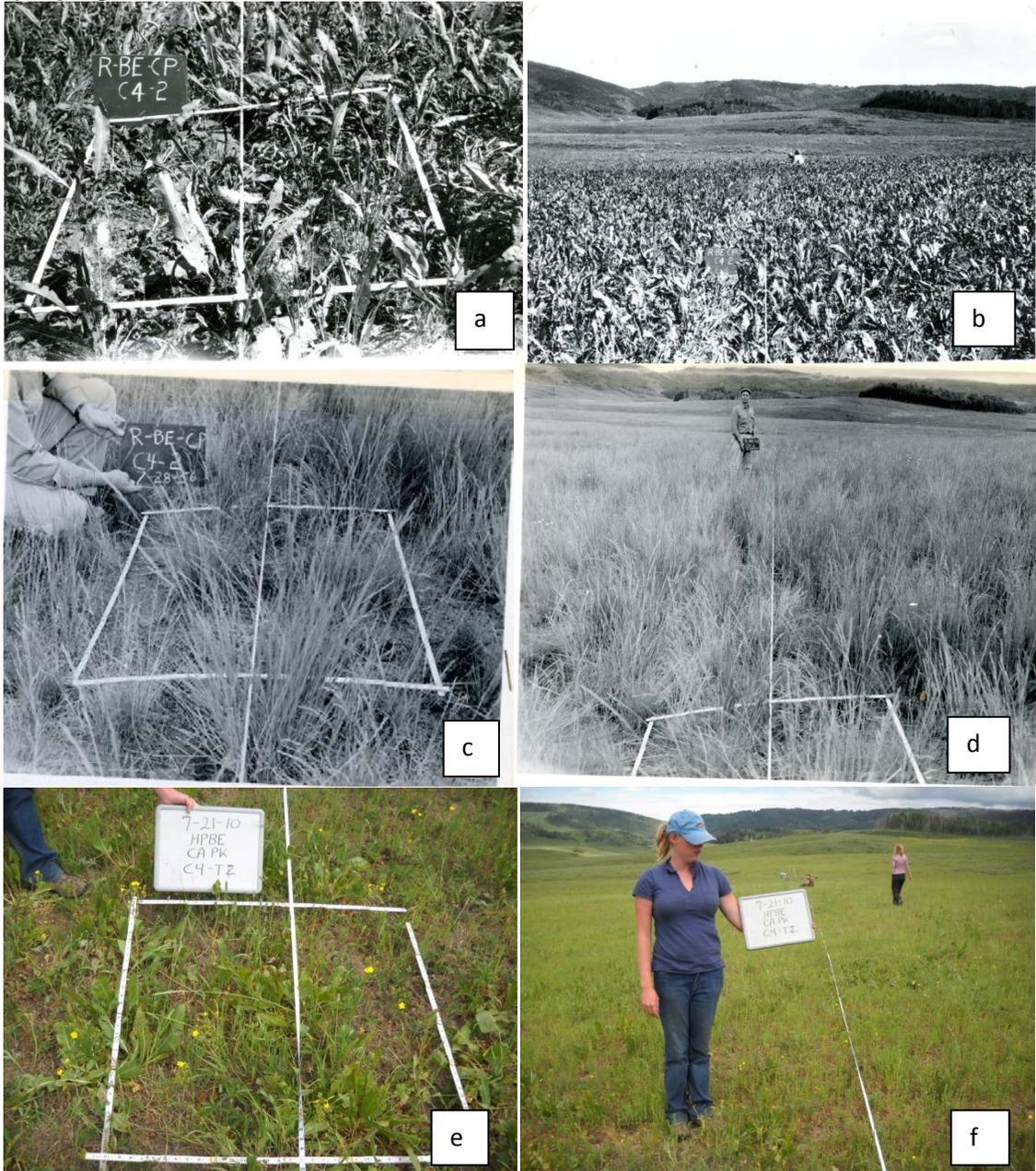


Figure 5.6. Non-metric multi-dimensional scaling results for all transects with loam soils (Axis 2 vs. 1 a-d, Axis 2 vs. 3 e-h; sites a-c and e-g; correlations with management and environmental factors d and h). For each site, open circles represent individual measurements, and lines connect each measurement to the next one through time. The last measurement (2010) is marked with an arrow. Sites were analyzed simultaneously but are graphed separately.

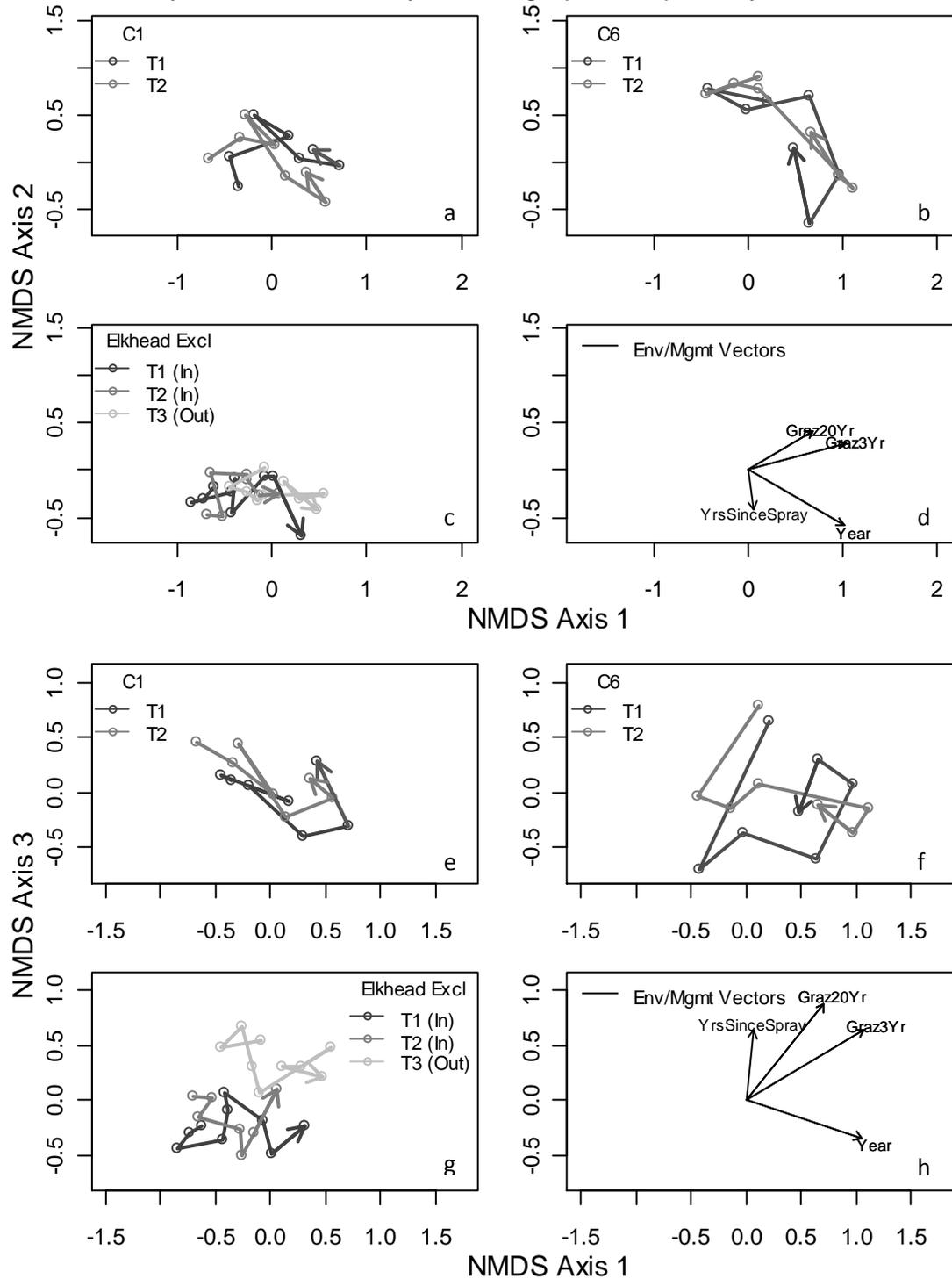


Figure 5.7. Selected species locations on non-metric multidimensional scaling ordinations for the loamy soil type. A shift in the position of a particular site through time on Figure 5.3 shows that it has generally increased in the species that occur near its new position.

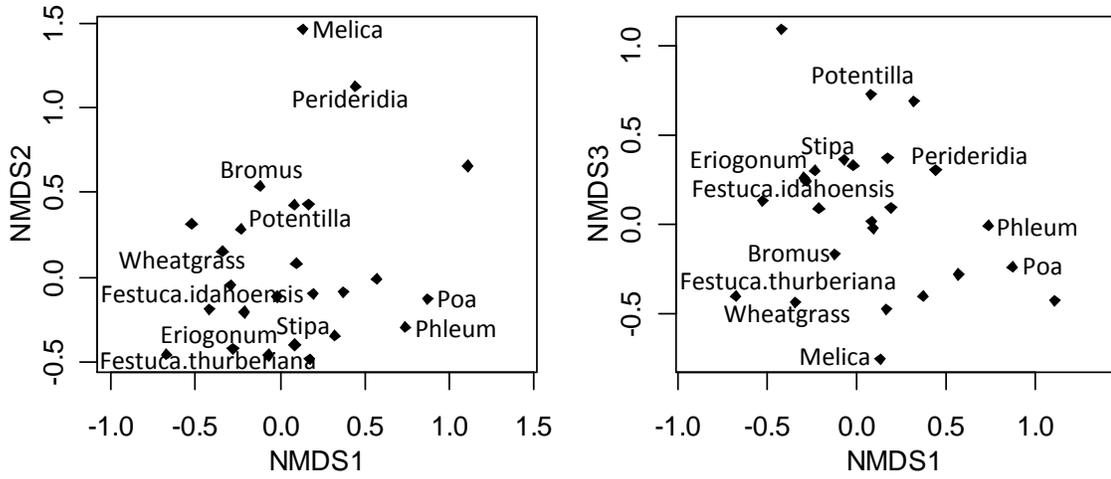
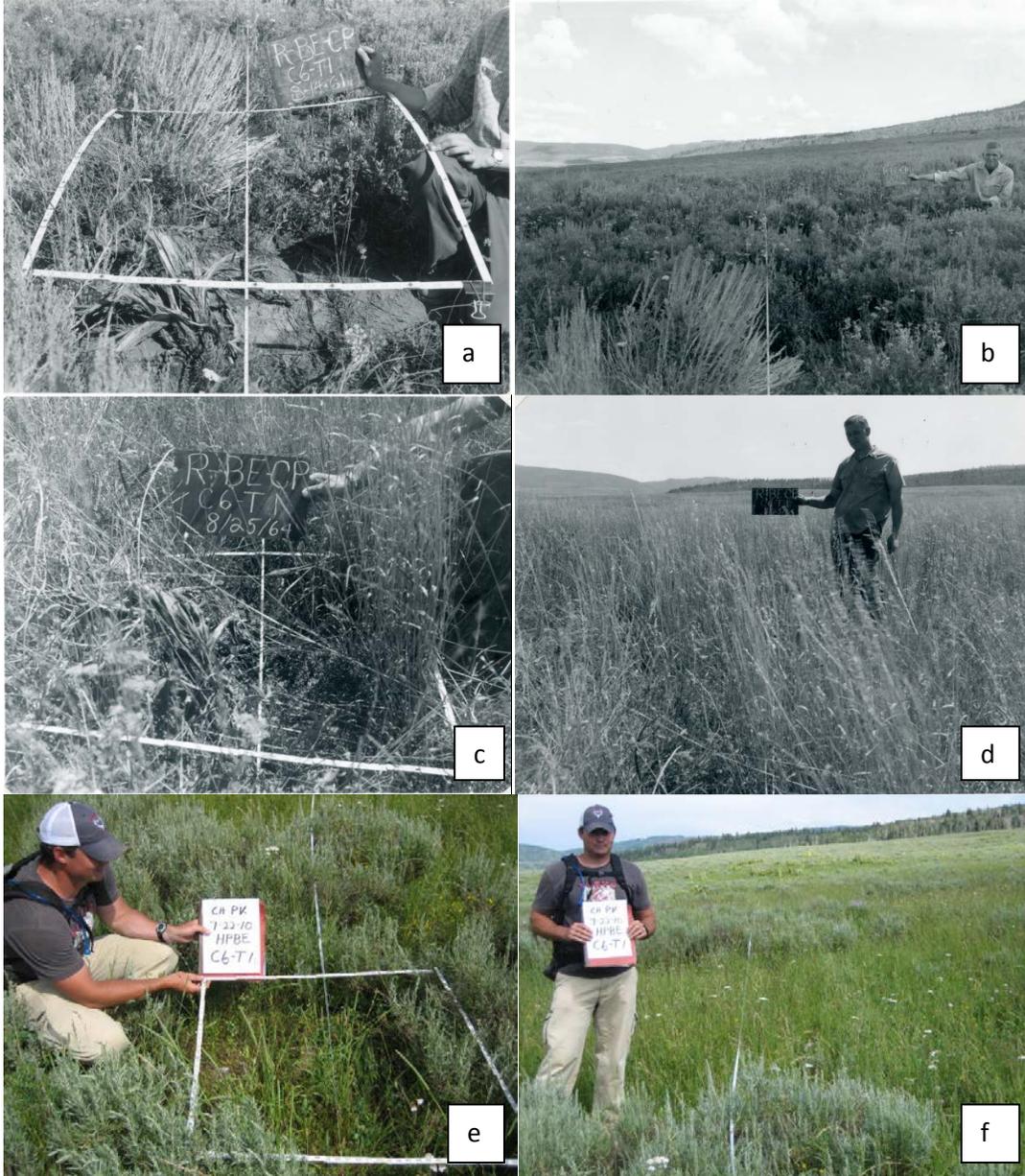


Figure 5.8. Close-up and landscape photos taken at one of the loamy sites (C6) just before spraying in 1961 (a, b), 3 years after spraying in 1964 (c, d), and 49 years after spraying in 2010 (e, f). Native grass cover and vigor increased after spraying. Much of the understory grass today is *Phleum*, a non-native pasture grass.



Chapter 6. Conclusion

INTRODUCTION

Motivated by the national STM-building effort, this dissertation had two practical objectives: 1) to create data-driven STMs that describe sagebrush steppe ecosystem response to management, and 2) to develop guidelines for STM creation. A third objective grew out of the need to create theoretically accurate STMs: to determine whether spatial and temporal patterns of vegetation in northwest Colorado sagebrush steppe are consistent with predictions of alternate state theory. Below I summarize the findings related to these objectives, beginning with the third and followed by the first and second.

VEGETATION PATTERNS AND ALTERNATE STATE THEORY

Although it is difficult to prove whether alternate states exist in an ecosystem, it is an important question because of the implications of threshold dynamics for management. For this reason, current literature and NRCS guidelines suggest that STMs should be consistent with theory. In identifying the states in the STMs, I aimed to verify several of the predictions of alternate state theory and refute

other explanations using spatial and temporal variation in species composition. These are important first steps for accumulating evidence for alternate states that could be applied in ongoing STM-building efforts.

Alternate state theory predicts, first, that the frequency distribution of states will be multimodal; second, that shifts between states are often triggered by disturbance; and, third, that feedback processes are the mechanisms that maintain unique states. The observational study on sagebrush steppe rangelands in the Elkhead watershed showed that there are large differences in species and functional group composition that are related to management within the Claypan and Mountain Loam ecological sites, consistent with the first and second predictions. On Claypan, some of these differences in species composition are related to processes which could provide mechanisms for maintaining alternate states, consistent with the third prediction. Other differences in species composition were not related to differences in process, showing that some differences in species composition do not indicate alternate states. This study also found several deviations from theoretical predictions, which may be specific to this system. First, species and functional group composition are not only related to management but also to environmental variation, suggesting that interaction between management and landscape heterogeneity may drive transitions between alternate states. In addition, relationships among potential states, processes, and site history were often not exclusive, implying that they are not as tightly linked as suggested by theory.

Long-term data provided a more direct look at whether there are alternate states in northwestern Colorado sagebrush steppe. Changes in species composition in the high-elevation sagebrush shrublands of California Park do not match all characteristics of alternate state dynamics: sudden changes are triggered by spraying, but generally they are not persistent. Instead, most species change appears to be gradual and directional at all sites. However, the long-term increase of a non-native grass raises the question of whether a gradual change may still be irreversible and lead to an alternate state.

Combined, the two studies provide weak support for the existence of alternate states in the sagebrush steppe. Long-term monitoring of the lower elevation sagebrush steppe plots in addition to experimental manipulations would be valuable additions to the evidence collected in this dissertation.

SAGEBRUSH STEPPE RESPONSE TO MANAGEMENT AND DISTURBANCE IN THE ELKHEAD WATERSHED

The literature review reported evidence of alternate states in the sagebrush steppe and described several specific states. Species and functional group approaches for describing sagebrush steppe response to disturbance revealed many biotically distinct potential states that were consistent with the literature. In addition to a diverse reference state, I found dense sagebrush shrublands, eroding sagebrush shrublands and planted grasslands on both soil types and a native grassland on one soil type. Relationships with management and process

generally confirmed the mechanisms of transitions between these literature-based states: herbivory that alters biotic interactions between sagebrush and the understory, erosion that prevents plant understory growth and establishment, historic cultivation and subsequent planting of grasses which alters both biotic and abiotic conditions, and spraying herbicides. Differences are related to different species and abiotic responses to management on clayey and loamy soil types. I did not find a cheatgrass-dominated potential state as has been reported in many lower-elevation sagebrush steppe sites. However, I did find several other potential states that had not been reported in the literature, related to particular species like western wheatgrass and three-tip sagebrush. These may be specific to these soil types in this region of the sagebrush steppe. I also found that environmental variation is important for predicting variation in species and functional group composition, suggesting that environmental variation is an important filter on species and functional group composition at different sites and may make some transitions between states more likely on some areas within an ecological site.

GUIDELINES FOR DEVELOPING STMs

An emergent question is whether STMs need to be consistent with alternate state theory to be useful. Spatial and temporal vegetation patterns were not entirely consistent with alternate state theory. Furthermore, the observational approach taken in this study and by the NRCS and partners does not allow a strong test of

whether alternate states occur. Nevertheless, the vegetation patterns identified have clear relevance to management of northwestern Colorado sagebrush steppe. Based on these findings, I want to emphasize that the new STMs developed here are intended to be a set of hypotheses about system behavior. As such, procedures for updating models should be built in to the STM development process. Future studies should focus on quantifying and identifying mechanisms of thresholds, one aspect of theory that many scientists argue has important implications for management (Bestelmeyer 2006; Briske et al. 2006; Suding and Hobbs 2009b).

The observational study allowed us to compare approaches to creating data-driven STMs on two different soil types. A plant species composition-based approach created two objective, credible STMs with potential alternate states and transitions that are consistent with the sagebrush steppe literature. Differences in species composition between and within ecological sites support the hierarchical view of landscapes currently applied in building STMs and the creation of separate models for different soil types. Composition of functional groups that combine several easily-measured traits identified many of the same patterns as species composition on both soil types and may provide a way to expedite model creation, but differences among the findings from the two approaches suggest that the tradeoffs between the two should be considered. An approach to STM building that acknowledges environmental heterogeneity within ecological sites is necessary to ensure that site history and environmental variability are not confounded in identifying triggers of transitions between states.

Whichever approach is taken to identify potential states, functional indicators are a simple, efficient way to identify the mechanisms of ecosystem degradation that need to be addressed by management actions. The Indicators of Rangeland Health approximate ecosystem processes, and can distinguish between alternate states and communities and identify transitions when building data-driven STMs.

FINAL THOUGHTS

An alternate state approach to range management shows promise for describing sagebrush steppe dynamics and assisting with decision-making. Species, trait-based approaches and indicators of ecosystem processes identified many potential alternate states and transitions that were consistent with the sagebrush steppe literature and important for range management. These complementary approaches are simple, quick additions to current model-building methods that may help expedite the national STM building effort. In addition to practical utility, the observational study confirmed three predictions of alternate state theory for one ecological site: that the frequency distribution of states is multimodal, that shifts between potential states are triggered by disturbance, and that unique feedback processes are associated with each state. However, incomplete support on the other ecological site and lack of strong evidence for alternate states in long-term data raise the question of whether STMs need to be theoretically accurate to be useful. Long-term directional change associated with increase of a non-native grass on higher-elevation rangelands also highlights the

lack of predictive power of STMs, especially in the face of novel disturbances like invasive species. Additional studies, including long-term monitoring, modeling, and experiments are needed to validate and update models as we learn more about the sagebrush steppe.

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Appendix 1. Vegetation characteristics of potential states of the Claypan (CP) and Mountain Loam (ML) ecological sites, Elkhead Watershed, NW Colorado. Foliar and basal plant cover were measured using the line-point intercept method (five 50 m transects, 250 points). Species richness was derived from a whole-plot search of each 20 x 50 m plot. Means \pm standard errors are reported.

States	N	Foliar Cover				Basal Cover			Species Richness
		Total Perennial	Shrub	Perennial Grass	Perennial Forb	Plant	Bare Ground	Litter	
CP Bluegrass	5	53.9 \pm 3	19.7 \pm 5.8	19.7 \pm 2.3	14.5 \pm 5.5	7.4 \pm 2.9	37.5 \pm 5.7	55 \pm 4.2	34.8 \pm 3.5
CP Diverse	3	73 \pm 10	27.4 \pm 9.5	23.4 \pm 7.6	22.2 \pm 12.6	5.6 \pm 2.6	26 \pm 5.8	68.4 \pm 7.3	38.3 \pm 0.3
CP Native Grassland	10	61.2 \pm 1.6	4.1 \pm 2.4	41 \pm 2.6	16.1 \pm 1.9	14.7 \pm 2	24.9 \pm 1.3	58.4 \pm 2.6	28.3 \pm 1.3
CP Planted Grassland	2	54.4 \pm 10.4	0.4 \pm 0.4	30.8 \pm 12.4	23.2 \pm 22.4	0.2 \pm 0.6	36 \pm 12.4	63.4 \pm 12.2	24 \pm 6
CP Sparse	6	47 \pm 5.2	30.6 \pm 3	9.8 \pm 2.1	6.6 \pm 1.6	10 \pm 3.2	39.7 \pm 6.1	51.4 \pm 5.4	34.7 \pm 2.5
CP Three-tip	4	62.9 \pm 4.4	15.5 \pm 4.9	31.2 \pm 6.7	16.2 \pm 2.4	17.8 \pm 7.7	21.9 \pm 2.8	59.7 \pm 7.8	32 \pm 1.8
CP Wheatgrass	11	58.4 \pm 3.9	7.4 \pm 1.4	27.6 \pm 4.4	23.4 \pm 4.4	13.5 \pm 2.5	36.3 \pm 6.5	49.4 \pm 4.5	29.3 \pm 1.2
ML Dense	5	73.1 \pm 3.3	41.8 \pm 4.9	19.1 \pm 2.5	12.2 \pm 3.8	4.5 \pm 1.7	20.5 \pm 5	75 \pm 3.6	38.2 \pm 1.6
ML Diverse	7	75.3 \pm 3.9	26.6 \pm 4.2	22.7 \pm 4.9	25.9 \pm 4.5	11.1 \pm 5	16.4 \pm 4.5	72.4 \pm 4.6	41.4 \pm 2.5
ML Planted Grassland	2	50 \pm 12.8	6.6 \pm 0.6	37.6 \pm 7.2	5.8 \pm 5	6.4 \pm 1.6	18 \pm 1.2	75.6 \pm 2.8	17.5 \pm 0.5
ML Sparse	5	57.1 \pm 9.6	26.9 \pm 5.6	13.9 \pm 1.7	16.3 \pm 3.9	6.6 \pm 4.2	30.6 \pm 13.3	62.5 \pm 11.9	41.6 \pm 3.7
ML Three-tip	4	76.4 \pm 4	36.4 \pm 3	31 \pm 2.8	9 \pm 2.7	24.2 \pm 2.6	12.2 \pm 2	63.5 \pm 2.5	36.8 \pm 4.9
ML Wheatgrass	12	74.3 \pm 3.3	20.3 \pm 2.9	22.3 \pm 3.7	31.7 \pm 3.3	8.4 \pm 2.6	24.1 \pm 5.2	65.9 \pm 4.6	43.4 \pm 2.3

Appendix 2. Site characteristics of potential states of the Claypan (CP) and Mountain Loam (ML) Ecological Sites, Elkhead Watershed, NW Colorado. Means \pm standard errors are reported. For explanations of individual measurements, see the Methods sections of Chapters 2 and 3.

State	N	Trans- formed Aspect	Slope (%)	Elev- ation (m)	% Clay	Soil Aggregate Stability			Percent Basal Bare Ground Gaps			
						Site Ave- rage	Shrub Inter- space	Under Shrub	Total Gaps >20	20-50 cm	50- 100 cm	100- 200 cm
CP Bluegrass	5	0.82 \pm 0.31	9.2 \pm 2.9	2066.4 \pm 16.9	57.8 \pm 4	3.8 \pm 0.4	3.7 \pm 0.5	3.8 \pm 0.4	17.4 \pm 2.2	13 \pm 1.5	3.8 \pm 0.7	0.6 \pm 0.6
CP Diverse	3	0.43 \pm 0.41	10.3 \pm 4.7	2128.3 \pm 36.2	51.1 \pm 9.2	4 \pm 0.6	3.8 \pm 0.6	4.2 \pm 0.7	17.5 \pm 6.1	9.7 \pm 1.7	4.9 \pm 3.4	2.2 \pm 1.4
CP Native Grassland	10	0.56 \pm 0.18	10 \pm 0.8	2081 \pm 5.2	51.9 \pm 1.6	3.8 \pm 0.2	3.7 \pm 0.2	3.9 \pm 0.3	25.8 \pm 2.5	16.2 \pm 1.5	7.5 \pm 0.9	1.7 \pm 0.6
CP Planted Grassland	2	1.25 \pm 0.67	9 \pm 0	2065.5 \pm 5.5	51.1 \pm 4.9	3 \pm 0.4	2.9 \pm 0.6	3.1 \pm 0.2	16.8 \pm 5.9	10.7 \pm 1.1	5.4 \pm 4.2	0.7 \pm 0.7
CP Sparse	6	0.88 \pm 0.3	12.5 \pm 0.9	2079.3 \pm 38.9	44.7 \pm 2	3.7 \pm 0.3	3.5 \pm 0.4	3.9 \pm 0.3	38.6 \pm 4.5	16 \pm 1.5	15 \pm 2.3	6.8 \pm 2.3
CP Three- tip	4	1.42 \pm 0.31	7 \pm 2.1	2062.5 \pm 8.2	50.1 \pm 6.2	4 \pm 0.4	4.3 \pm 0.6	3.6 \pm 0.4	22.6 \pm 6.9	16.4 \pm 4.3	6.1 \pm 2.7	0 \pm 0
CP Wheatgrass	11	0.33 \pm 0.14	8.7 \pm 1.5	2198.2 \pm 15.4	55.8 \pm 2.1	4.3 \pm 0.3	4.1 \pm 0.3	4.4 \pm 0.3	14.3 \pm 2.3	11.2 \pm 1.7	2 \pm 0.5	0.2 \pm 0.2
ML Dense	5	1.25 \pm 0.22	7.2 \pm 1.3	2075.6 \pm 21.7	25.5 \pm 2.9	4.2 \pm 0.4	4 \pm 0.5	4.3 \pm 0.4	26.4 \pm 6.9	11.9 \pm 2	10.5 \pm 3.5	2.6 \pm 1.6
ML Diverse	7	1.07 \pm 0.19	14.4 \pm 1.2	2145.9 \pm 22.6	33.9 \pm 3.8	4.1 \pm 0.4	4.3 \pm 0.3	3.8 \pm 0.4	9.1 \pm 2.5	7.9 \pm 2	1 \pm 0.4	0.2 \pm 0.2
ML Planted Grassland	2	0.87 \pm 0.55	6.5 \pm 3.5	2014.5 \pm 0.5	12.3 \pm 2.3	5.1 \pm 0.5	5.1 \pm 0.2	5.1 \pm 0.7	16.9 \pm 3.7	13.2 \pm 2.2	3.7 \pm 1.5	0 \pm 0
ML Sparse	5	1.07 \pm 0.44	15.8 \pm 2.2	2062.8 \pm 22.2	28.1 \pm 3.5	4.5 \pm 0.3	4.6 \pm 0.2	4.4 \pm 0.4	22.5 \pm 12.1	8.3 \pm 2.8	9 \pm 5.5	4.3 \pm 3.4

<i>State</i>	<i>N</i>	<i>Trans- formed Aspect</i>	<i>Slope</i>	<i>Elevation</i>	<i>% Clay</i>	<i>Soil Aggregate Stability</i>			<i>Percent Basal Bare Ground Gaps</i>			
						<i>Site Ave- rage</i>	<i>Shrub Inter- space</i>	<i>Under Shrub</i>	<i>Total Gaps >20 cm</i>	<i>20-50 cm</i>	<i>50-100 cm</i>	<i>100- 200 cm</i>
ML Wheatgrass	12	0.96 ± 0.23	10.3 ± 1.3	2177.3 ± 19.7	36.7 ± 2.6	4 ± 4 ± 0.2	4 ± 0.2	4 ± 0.3	13 ± 2.2	8.3 ± 1.2	3.9 ± 1	0.9 ± 0.6
ML Three-tip	4	1 ± 0.29	8.5 ± 1.3	2053.8 ± 9	25 ± 3.9	3.3 ± 0.2	2.9 ± 0.2	3.7 ± 0.2	11.4 ± 1.6	7.4 ± 1.3	2 ± 0.6	1.6 ± 0.4

Appendix 3. Foliar plant cover of dominant species in potential states of the Claypan (CP) and Mountain Loam (ML) Ecological Sites, Elkhead Watershed, NW Colorado. Means \pm standard errors are reported. Foliar cover was measured using the line-point intercept method (five 50 m transects, 250 points). The following tables report dominant species of shrubs, grasses, and forbs.

SHRUBS

State	N	<i>Artemisia arbuscula</i> ssp. <i>longiloba</i>	<i>Artemisia cana</i>	<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	<i>Artemisia tripartita</i>	<i>Amelanchier utahensis</i>	<i>Symphoricarpos</i> <i>rotundifolius</i>
CP Bluegrass		19.4 \pm 5.6	0 \pm 0	0.1 \pm 0.1	0 \pm 0	0 \pm 0	0 \pm 0
CP Diverse	3	15 \pm 5.1	0 \pm 0	11.7 \pm 6	0.1 \pm 0.1	0 \pm 0	0.6 \pm 0.2
CP Native Grassland	10	3.9 \pm 2.3	0 \pm 0	0.1 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
CP Planted Grassland	2	0.4 \pm 0.4	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
CP Sparse	6	30.1 \pm 2.7	0 \pm 0	0.2 \pm 0.1	0 \pm 0	0 \pm 0	0.1 \pm 0.1
CP Three-tip	4	1.4 \pm 1.1	0 \pm 0	9.1 \pm 4.3	5 \pm 2.1	0 \pm 0	0 \pm 0
CP Wheatgrass	11	5.5 \pm 1.3	0 \pm 0	1.2 \pm 0.5	0 \pm 0	0.3 \pm 0.2	0.4 \pm 0.3
ML Dense	5	0.7 \pm 0.7	0 \pm 0	40.6 \pm 4.6	0.2 \pm 0.2	0 \pm 0	0 \pm 0
ML Diverse	7	2.2 \pm 2.2	0 \pm 0	8.7 \pm 3	0.5 \pm 0.5	1.2 \pm 0.6	14 \pm 2.3
ML Planted Grassland	2	0 \pm 0	0 \pm 0	4.6 \pm 1.4	0 \pm 0	0 \pm 0	0 \pm 0
ML Sparse	5	0 \pm 0	0.1 \pm 0.1	12.4 \pm 5.1	0 \pm 0	0.5 \pm 0.3	12.6 \pm 5.8
ML Three-tip	4	1.7 \pm 1.7	0 \pm 0	20.2 \pm 6	11.7 \pm 3.6	0.6 \pm 0.5	1 \pm 0.8
ML Wheatgrass	12	0.4 \pm 0.3	0 \pm 0	10.9 \pm 1.6	0.5 \pm 0.4	0.9 \pm 0.4	6.3 \pm 2.6

Note: Common names for shrub species, from left to right, are: Alkali sagebrush; Silver sagebrush; Mountain big sagebrush; Three-tip sagebrush; Serviceberry; and Snowberry.

State	N	NATIVE GRASSES								NON-NATIVE GRASSES				
		<i>Melica bulbosa</i>	<i>Bromus montana</i>	<i>Elymus lanceolatus</i>	<i>Koeleria macrantha</i>	<i>Pascopyrum smithii</i>	<i>Poa secunda</i>	<i>Poa interior</i>	<i>Elymus elymoides</i>	<i>Stipa lettermanii</i>	<i>Bromus inermis</i>	<i>Bromus tectorum</i>	<i>Elytrigia intermedia</i>	<i>Pheum pratense</i>
CP Bluegrass	5	0.6 ± 0.3	0.6 ± 0.6	0 ± 0	0.6 ± 0.3	5.6 ± 1.2	5.4 ± 2.1	2.9 ± 0.3	0 ± 0	0.4 ± 0.4	0 ± 0	0.7 ± 0.5	0 ± 0	0 ± 0
CP Diverse	3	3.2 ± 2	0 ± 0	0 ± 0	2.1 ± 1.1	7.9 ± 2.8	1.3 ± 0.6	2.5 ± 0.5	0.7 ± 0.5	3.8 ± 1.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0
CP Native Grassland	10	1.1 ± 0.4	0 ± 0	0 ± 0	4.5 ± 0.5	26.2 ± 2.2	3.7 ± 0.7	4 ± 0.9	0 ± 0	1.2 ± 0.6	0 ± 0	0.3 ± 0.2	0 ± 0	0 ± 0
CP Planted Grassland	2	0 ± 0	0 ± 0	5.4 ± 1.8	0 ± 0	2.6 ± 2.6	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	13.4 ± 12.2	1.2 ± 1.2	3.6 ± 3.6	0 ± 0
CP Sparse	6	0.1 ± 0.1	0 ± 0	0 ± 0	2 ± 1	1.9 ± 0.7	2.7 ± 1.2	0.5 ± 0.2	0.1 ± 0.1	0.3 ± 0.3	0 ± 0	1.4 ± 1.1	0 ± 0	0 ± 0
CP Three-tip	4	0 ± 0	0 ± 0	0 ± 0	1.1 ± 0.4	15.7 ± 2.4	1.1 ± 0.4	7.4 ± 1.8	0 ± 0	0.5 ± 0.3	0 ± 0	2.1 ± 1	0 ± 0	0 ± 0
CP Wheatgrass	11	0.3 ± 0.1	0 ± 0	0 ± 0	2.1 ± 0.7	22.2 ± 3.9	0.4 ± 0.4	1.4 ± 0.9	0 ± 0	0.4 ± 0.2	0 ± 0	0.1 ± 0.1	0 ± 0	0.6 ± 0.5
ML Dense	5	0.3 ± 0.2	4.2 ± 1.6	0 ± 0	0 ± 0	0.7 ± 0.4	0 ± 0	4.2 ± 1.6	0 ± 0	0 ± 0	5 ± 2.2	0.3 ± 0.2	0 ± 0	0 ± 0
ML Diverse	7	2.6 ± 0.9	0.5 ± 0.4	0 ± 0	0.6 ± 0.4	2.5 ± 0.8	1.1 ± 0.4	7.5 ± 2.8	0.2 ± 0.1	4.3 ± 1.8	0.1 ± 0.1	0 ± 0	0 ± 0	0.3 ± 0.2

Note: Common names for native grasses, from left to right, are: Oniongrass; Mountain brome; Slender wheatgrass; Junegrass; Western wheatgrass; Sandberg bluegrass; Inland bluegrass; Squirreltail; and Letterman's needlegrass. Common names for non-native grasses, from left to right, are: Smooth brome; Cheatgrass; Intermediate wheatgrass; and Timothy.

State	N	NATIVE GRASSES							NON-NATIVE GRASSES					
		<i>Melica bulbosa</i>	<i>Bromus montana</i>	<i>Elymus lanceolatus</i>	<i>Koeleria macrantha</i>	<i>Pascopyrum smithii</i>	<i>Poa secunda</i>	<i>Poa interior</i>	<i>Elymus elymoides</i>	<i>Stipa lettermanii</i>	<i>Bromus inermis</i>	<i>Bromus tectorum</i>	<i>Elytrigia intermedia</i>	<i>Pheum pratense</i>
ML Planted Grassland	2	0 ± 0	0 ± 0	9.2 ± 1.2	0 ± 0	0 ± 0	0 ± 0	1.2 ± 0.8	0 ± 0	0 ± 0	6 ± 2	0.4 ± 0.4	9.4 ± 1	0 ± 0
ML Sparse	5	0.5 ± 0.5	0 ± 0	0 ± 0	0.6 ± 0.3	1.3 ± 0.6	0.2 ± 0.2	5.3 ± 1.4	0 ± 0	0 ± 0	2.1 ± 1	1.4 ± 1.4	0 ± 0	0 ± 0
ML Three-tip	4	0 ± 0	0.1 ± 0.1	0 ± 0	0.4 ± 0.2	5.5 ± 1.7	0.9 ± 0.7	13.7 ± 1.4	0 ± 0	1.4 ± 1.1	0 ± 0	0 ± 0	0 ± 0	3.9 ± 2.2
ML Wheatgrass	12	0.9 ± 0.3	1.6 ± 0.8	0 ± 0	0.8 ± 0.3	6.6 ± 1.4	0.6 ± 0.3	4.5 ± 0.6	0.1 ± 0.1	5.6 ± 3.3	0.1 ± 0	0.5 ± 0.3	0 ± 0	1 ± 1

Note: Common names for native grasses, from left to right, are: Oniongrass; Mountain brome; Slender wheatgrass; Junegrass; Western wheatgrass; Sandberg bluegrass; Inland bluegrass; Squirreltail; and Letterman's needlegrass. Common names for non-native grasses, from left to right, are: Smooth brome; Cheatgrass; Intermediate wheatgrass; and Timothy.

State	N	NATIVE FORBS										NON-NATIVE		
		<i>Achillea millefolium</i>	<i>Aster spathulatus</i>	<i>Astragalus bisulcatus</i>	<i>Astragalus ssp. haydenianus</i>	<i>Helianthella wetherilli</i>	<i>Lomatium uniflora</i>	<i>Lupinus grayi</i>	<i>Perideridia caudatus</i>	<i>Phlox longifolia</i>	<i>Viola praemorsa</i>	<i>Wyethia amplexicaulis</i>	<i>Cynoglossum officinale</i>	<i>Cardaria draba</i>
CP Bluegrass	5	1.1 ± 0.5	3.8 ± 1.6	0.2 ± 0.2	1.8 ± 1.6	0 ± 0	1.5 ± 0.8	0.1 ± 0.1	0.7 ± 0.7	3.2 ± 0.7	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0
CP Diverse	3	0.3 ± 0.3	2.5 ± 1.6	0.1 ± 0.1	2.3 ± 1	7 ± 6.9	1.2 ± 1.2	0.1 ± 0.1	0.4 ± 0	0.5 ± 0.5	0 ± 0	2 ± 1.3	0 ± 0	0 ± 0
CP Native Grassland	10	1.6 ± 0.5	1 ± 0.3	0.6 ± 0.3	2.6 ± 1	0 ± 0	5.5 ± 2.3	0 ± 0	0 ± 0	3.4 ± 0.6	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0
CP Planted Grassland	2	0 ± 0	0 ± 0	0.4 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
CP Sparse	6	0.5 ± 0.5	0.1 ± 0.1	0.3 ± 0.2	0.6 ± 0.4	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0 ± 0	0 ± 0
CP Three-tip	4	2.8 ± 1.1	1.6 ± 0.8	2.9 ± 1.9	0.9 ± 0.5	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	1.2 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0
CP Wheatgrass	11	0.2 ± 0.2	2.3 ± 0.8	0.9 ± 0.5	4.2 ± 1.5	0.1 ± 0.1	8.2 ± 3.3	0.1 ± 0	0.1 ± 0.1	1.6 ± 0.4	0 ± 0	2.8 ± 0.9	0.4 ± 0.3	0 ± 0
ML Dense	5	1.8 ± 1	0.5 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	8.4 ± 3.8	0 ± 0	0.2 ± 0.1	0.1 ± 0.1	0 ± 0	0.8 ± 0.7	0.6 ± 0.6

Note: Common names for native forbs, from left to right, are: Yarrow; Western mountain aster; Hayden's milkvetch; Wetherill's milkvetch; One-flower helianthella; Gray's lomatium; Tailcup lupine; Yampa; Longleaf phlox; Canary violet; and Mule's-ears. Common names for non-native forbs, from left to right, are: Hounds-tongue and White-top.

State	N	NATIVE FORBS										NON-NATIVE		
		<i>Achillea millefolium</i>	<i>Aster spathulatus</i>	<i>Astragalus bisulcatus</i>	<i>Astragalus</i> ssp. <i>haydenianus</i>	<i>Helianthella wetherilli</i>	<i>Lomatium uniflora</i>	<i>Lupinus grayi</i>	<i>Perideridia caudatus</i>	<i>Perideridia gairdneri</i>	<i>Phlox longifolia</i>	<i>Viola praemorsa</i>	<i>Wyethia amplexicaulis</i>	<i>Cynoglossum officinale</i>
ML Diverse	7	6.6 ± 1.2	4.6 ± 1	0.4 ± 0.3	2.3 ± 0.9	2.9 ± 2.9	0 ± 0	1.2 ± 0.9	3.3 ± 1.2	1.5 ± 0.7	1.3 ± 0.8	0.8 ± 0.5	0 ± 0	0 ± 0
ML Planted Grassland	2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3.6 ± 3.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
ML Sparse	5	3 ± 1	1.3 ± 1.1	0 ± 0	0 ± 0	1.2 ± 0.8	0 ± 0	5.2 ± 1.2	0 ± 0	1.2 ± 0.6	0.1 ± 0.1	0.1 ± 0.1	0.5 ± 0.5	0 ± 0
ML Three-tip	4	3.2 ± 0.6	1.3 ± 0.5	0 ± 0	0.7 ± 0.7	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.1	1 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0
ML Wheatgrass	12	3.4 ± 0.9	1.9 ± 0.5	0.1 ± 0.1	1.9 ± 0.6	1.6 ± 0.9	4.4 ± 2.1	0.7 ± 0.2	1.3 ± 0.4	0.8 ± 0.2	0.6 ± 0.2	9 ± 1.7	0 ± 0	0 ± 0

Note: Common names for native forbs, from left to right, are: Yarrow; Western mountain aster; Hayden's milkvetch; Wetherill's milkvetch; One-flower helianthella; Gray's lomatium; Tailcup lupine; Yampa; Longleaf phlox; Canary violet; and Mule's-ears. Common names for non-native forbs, from left to right, are: Hounds-tongue and White-top.

Appendix 4. Evaluation matrix used to rate the Indicators of Rangeland Health for the Claypan and Mountain Loam Ecological Sites, Elkhead Watershed, NW CO. The evaluation matrix defines evidence for deviation from reference conditions for each rating of each indicator.

**Rangeland Health Indicators Evaluation Matrix
CSU State-and-Transition Model Project, Elkhead Watershed,
Colorado**

Adapted from *Interpreting Indicators of Rangeland Health* (Version 4), by M. Pellant, D. Pyke, P. Shaver, and J. Herrick. (2005). pp. 82-87.
Online at <ftp://ftp-fc.sc.egov.usda.gov/GLTI/technical/publications/IIRH_v4_8-15-05.pdf>

- RILLS**- small erosional rivulets; usually linear, and don't follow microtopography that water flow patterns do.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Rill formation is severe and well defined throughout most of site.	Rill formation is moderately active and well defined throughout most of the site.	Active rill formation is slight or at infrequent intervals; mostly in exposed areas.	No recent formation of rills; old rills have blunted or muted features.	Little to no evidence of past formation of rills.

- WATER FLOW PATTERNS** – The path that water takes as it moves across the soil surface during overland flow (i.e. when soil is saturated or has a very low infiltration rate). Evidence: litter, soil or gravel redistribution, or pedestalling of vegetation or stones in the flow pattern.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Water flow patterns extensive and numerous; unstable with active erosion;	Water flow patterns more numerous than the description for 0 ; deposition and cut areas	Number and length of water flow patterns nearly match the description for	Number and length of water flow patterns match the description for 0 ; some	Flow patterns are few, short (<1 m), >5 m apart; slightly longer/more numerous on steeper

usually connected.	common; occasionally connected.	0 ; erosion is minor with some instability and deposition.	evidence of minor erosion. Flow patterns are stable and short.	slopes; minimal evidence of past or current soil deposition or erosion.
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3. **PEDESTALS** – Pedestals are rocks or plants that appear elevated because of loss by wind or water erosion. Terracettes are benches of soil deposition behind obstacles, caused by water movement.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Abundant active pedestalling. Many rocks and plants are pedestaled; exposed plant roots are common.	Moderate active pedestalling. Some rocks and plants are pedestaled with occasional exposed roots.	Slight active pedestalling; most pedestals are in flow paths and interspaces and/or on exposed slopes.	Active pedestalling is rare; some evidence of past pedestal formation, especially in water flow patterns on exposed slopes.	Current or past evidence of pedestaled plants or rocks is rare.

4. **TERRACETTES**- Benches of soil deposition behind obstacles, caused by water movement.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Numerous terracettes.	Terracettes common.	Occasional terracettes present.	Active terracette formation is rare, but present in water flow patterns on exposed slopes.	Terracettes absent or uncommon.

5. **BARE GROUND** – Bare mineral or organic soil.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Many bare areas. Bare areas large and generally	A moderate number to many bare areas. Bare	Moderate number of bare areas. Bare areas	Few bare areas. Bare areas are small and	Very few bare areas, almost never connected.

connected.	areas are large and occasionally connected.	are of moderate size and sporadically connected.	rarely connected.	
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6. **GULLIES** – A gully is a channel that has been cut into soil by moving water. They generally follow natural drainages and are caused by accelerated water flow and the resulting downcutting of soil. “Active” erosion will be evidenced by sharp gully edges and headcuts; older gullies will have rounded edges.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Common with indications of active erosion and downcutting; vegetation is infrequent on slopes and/or bed. Nickpoints and headcuts are numerous and active.	Moderate in number to common with indications of active erosion; vegetation is intermittent on slopes and/or bed. Headcuts are active; downcutting is not apparent.	Moderate in number with indications of active erosion; vegetation is intermittent on slopes and/or bed. Occasional headcuts may be present.	Uncommon; vegetation is stabilizing the bed and slopes. No signs of active headcuts, nickpoints, or bed erosion.	None. Drainages are represented as natural stable channels; vegetation is common and no signs of erosion.

7. **WIND SCoured, BLOWOUT, AND/OR DEPOSITIONAL AREAS** – In blowout areas, the finer soil particles have blown away, sometimes leaving residual gravel, rock, or exposed roots on the soil surface. For deposition, look for sand accumulation on top of moss.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Extensive.	Common.	Occasionally present.	Infrequent and Few.	None.

8. **LITTER MOVEMENT (by wind or water)** – Look for litter dams, accumulation of other litter under and on the east side of shrubs (away from the wind), or patchy litter distribution that doesn't seem to be related to plant species distribution.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Lots of litter has moved and is concentrated around obstructions. Most size	Litter is loosely concentrated near obstructions. Moderate to small size	Moderate movement of smaller size classes in scattered concentrations around	Slight to moderate amount of litter movement, with only small size	No movement. Fairly uniform distribution of litter.

classes of litter have been displaced.	classes of litter have been displaced.	obstructions and in depressions.	classes of litter being displaced.	
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- 9. SOIL SURFACE LOSS OR DEGRADATION** – This describes soil surface degradation throughout a plot. Signs of degradation are massive or blocky structure; light color; and weak soil aggregates that lack pores. Comparing the surface to the subsurface by digging a shallow hole (>4 cm for Claypan sites, >10 cm for Mountain Loam sites) with a trowel will also help; you should see differences in color and structure. The soil profile description at the pit also contributed to this indicator.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Soil surface horizon absent. Soil structure at surface is similar, or more degraded, than that in subsurface horizons. No distinguishable difference in subsurface organic matter content.	Soil loss or degradation severe throughout the site. Minimal differences in soil organic matter content and structure of surface and subsurface layers.	Moderate soil loss or degradation in plant interspaces with some degradation beneath plant canopies. Soil structure is degraded and soil organic matter content is significantly reduced.	Some soil loss has occurred and/or soil structure shows signs of degradation (massive or angular structure; light color; aggregates weak, lack pores), especially in plant interspaces.	Soil surface layer intact. Soil structure and organic matter content match that expected for site- granular structure, and soil color value/chroma of 3/2 or darker.

- 10. COMPACTION LAYER (below soil surface):** Indicators of compaction are: 1) massive or platy soil structure within the first foot of the soil surface, and 2) large plant roots growing horizontally parallel to the platy structure, with only fine roots growing vertically into the plates. While the soil profile description indicates whether compaction was present at the pit, this indicator focuses on how extensive compaction is in the plot.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Extensive; severely restricts water movement and root penetration (rare vertical	Widespread; greatly restricts water movement and root penetration (many	Moderately widespread, moderately restricts water movement and root penetration	Rarely present or is thin and weakly restrictive to water movement	None to minimal, not restrictive to water movement and root penetration.

roots).	horizontal and few vertical roots).	(still some vertical roots).	and root penetration.	
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11. PLANT MORTALITY/DECADENCE – This is the proportion of dead or decadent (e.g. dying, like a large sagebrush with large sections of dead material) plants relative to young and mature plants at a plot. It is an indicator of plant population dynamics.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Dead and/or decadent plants are common.	Dead plants and/or decadent plants are somewhat common.	Some dead and/or decadent plants are present.	Slight plant mortality and/or decadence.	Little to no plant mortality and decadence.

12. LITTER AMOUNT – Litter is dead plant material that is detached from the base of the plant. Again, this is a judgment call. Given last year's wet weather, you would expect some (1/6-1/8 in thick), but sparse litter cover in Claypan sites. Mountain Loam sites should have more or less continuous litter cover ½ to 1 inch thick.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Largely absent or dominant relative to site potential and weather.	Greatly reduced or increased relative to site potential and weather.	Moderately more or less relative to site potential and weather.	Slightly more or less relative to site potential and weather.	Amount is what is expected for the site potential and weather.

13. INVASIVE PLANTS – Invasive plants are plants that are not part of (if exotic), or are a minor component of (if native), the original plant community or communities that have the potential to become dominant or co-dominant species on the site if their future establishment and growth is not actively controlled by management interventions. Species that become dominant as a short term response to disturbance are not invasive. List species and possible effects on function in the comments.

Extreme-Total (4)	Moderate-Extreme (3)	Moderate (2)	Slight-Moderate (1)	None-Slight (0)
Invasive plants dominate the site.	Invasive plants common throughout the site.	Invasive plants scattered throughout the site.	Invasive plants present primarily in disturbed areas within the site.	If present, composition of non-native species matches that expected for site (e.g. a few

				dandelions, prickly lettuce, etc. present); no invasive plants.
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14. REPRODUCTIVE CAPABILITY OF PERENNIAL PLANTS (native or seeded) –

Specific indicators are seed production for shrubs and forbs and tillering for grasses. The implication is that management or ecosystem processes—i.e. heavy grazing or erosion that reduces water infiltration—have reduced the ability of the plants to reproduce.

Extreme- Total (4)	Moderate- Extreme (3)	Moderate (2)	Slight- Moderate (1)	None-Slight (0)
Seed production or vegetative tillering is severely reduced throughout the entire plot.	Seed production or vegetative tillering is greatly reduced in more than one functional group throughout much of the plot.	Seed production or vegetative tillers are reduced in a functional group or moderate sized areas of the plot.	Seedheads and new tillers are present on most perennial plants. However, small patches of individuals have few tillers and/or seedheads.	Seedheads and new tillers are present on nearly all perennial plants (that you would expect at this time of year).

Appendix 5. Indicators of Rangeland Health ratings for potential states of the Claypan (CP) and Mountain Loam (ML) ecological sites, Elkhead Watershed, NW CO. Indicators were rated on their departure from reference conditions for each ecological site using an evaluation matrix (Appendix 4), from None-Slight (0) to Extreme-Total (4).

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Potential States	N	Rills	Water Flow Patterns	Pedestals	Terracettes	Bare Ground	Gullies	Litter Movement	Soil Surface Loss or Degradation	Compaction	Plant Mortality/Decadence	Litter Reproductive Capability	Litter Amount	Invasive Plants
CP Bluegrass	5	0.6± 0.4	1.4± 0.4	1.2± 0.4	1.6± 0.4	1.8± 0.4	0±0	1.2± 0.2	0.4± 0.2	0.4± 0.2	0±0	0±0	0±0	0.2± 0.2
CP Diverse	3	0.3± 0.3	1.7± 0.7	1.7± 0.9	2.3± 0.9	1.7± 0.7	0±0	1.3± 0.3	0.7± 0.3	0.7± 0.7	0.7± 0.3	0±0	0.3± 0.3	0±0
CP Native Grassland	10	0.8± 0.3	1± 0.4	0.6± 0.2	1.2± 0.2	1.4± 0.3	0.3± 0.2	1.7± 0.2	0.6± 0.2	0±0	0.2± 0.1	0±0	0.3± 0.2	0.2± 0.2
CP Planted Grassland	2	0±0	0±0	0±0	0±0	0±0	0±0	1±0	1±1	1±1	0±0	1±1	0.5± 0.5	1.5± 0.5
CP Sparse	6	0.7± 0.3	3.7± 0.2	3.2± 0.3	4±0	3.3± 0.3	0.5± 0.5	2± 0.3	1.8± 0.3	0.5± 0.3	0.3± 0.2	0.3± 0.3	0.2± 0.2	0.8± 0.7
CP Three-tip	4	0.5± 0.5	2.5± 0.5	2± 0.6	2.5± 0.3	2± 0.4	0±0	2± 0.4	1.3± 0.5	1± 0.6	1.5± 0.9	0.5± 0.5	0.8± 0.5	0.3± 0.3
CP Wheatgrass	11	0.2± 0.1	0.3± 0.2	0.3± 0.1	1.1± 0.2	0.9± 0.1	0.2± 0.2	1.1± 0.2	1.1± 0.3	0.3± 0.1	0.4± 0.2	0±0	0.3± 0.2	0.5± 0.2
ML Dense	5	0±0	0.8± 0.5	0.2± 0.2	0±0	2± 0.6	0±0	1.8± 0.4	0.4± 0.2	1± 0.3	1± 0.8	0±0	1± 0.4	1.4± 0.6
ML Diverse	7	0.4± 0.4	0.1± 0.1	0.7± 0.6	1.3± 0.2	0.3± 0.2	0±0	1.7± 0.4	0.1± 0.1	0±0	0.4± 0.2	0±0	0.4± 0.2	0±0

Potential States	N	Rills	Water Flow Patterns	Pedestals	Terracettes	Bare Ground	Gullies	Litter Movement	Soil Surface Loss or Degradation	Compaction	Plant Mortality/Decadence	Plant Reproductive Capability	Litter Amount	Invasive Plants
ML Planted Grassland	2	0±0	1±1	0.5±0.5	0.5±0.5	1±0	0±0	1±0	0.5±0.5	1.5±0.5	0±0	0±0	1±1	2±0
ML Sparse	5	0±0	1.2±0.5	1.6±0.5	1.8±0.5	1.6±0.8	0±0	1.2±0.4	1±0.5	0.6±0.6	1.6±0.6	0.6±0.6	0.6±0.6	2.6±0.5
ML Three-tip	4	0±0	0.5±0.3	0.5±0.3	1±0	1.3±0.6	0±0	1±0.6	0±0	0.3±0.3	0.3±0.3	0±0	0±0	0±0
ML Wheatgrass	12	0.4±0.2	0.7±0.2	1.2±0.3	1.1±0.3	1.2±0.3	0.2±0.2	1.5±0.2	0.5±0.2	0.2±0.1	0.9±0.3	0.1±0.1	0.4±0.1	0.6±0.2