

THESIS

IMPROVING STATE-AND-TRANSITION MODELS FOR MANAGEMENT OF SAGEBRUSH STEPPE

ECOSYSTEMS

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## ABSTRACT

### IMPROVING STATE-AND-TRANSITION MODELS FOR MANAGEMENT OF SAGEBRUSH STEPPE ECOSYSTEMS

The sagebrush biome was once the most widely-distributed in North America, but has recently experienced range reductions of up to 45% and has been considered one of the most endangered ecosystems in the United States (West 1983, Noss et al. 1995, Miller et al. 2011). Management for multiple land-use goals in this biome is complex, requiring an intricate understanding of biotic and abiotic interactions, their responses to disturbance, and the potential for catastrophic ecosystem shifts in response to stress. State-and-transition models (STMs) illustrate the complex relationships between ecosystem components and convey both equilibrium and non-equilibrium dynamics, in a conceptual, visual framework (Westoby et al. 1989, Walker and Westoby 2011). Recognizing their potential to guide both research and management decision-making, the Natural Resource Conservation Service, U.S. Forest Service, and Bureau of Land Management recently signed an interagency agreement to develop and use STMs to guide rangeland management decision-making nation-wide (Caudle et al. 2013).

The growing popularity of STMs has brought them under increased scrutiny (Knapp et al. 2011, Tidwell et al. 2013). Common criticisms of STMs include: 1) reliance on insufficient empirical datasets or knowledge-based data prone to bias; 2) failure to explicitly identify the spatial and temporal scale of the model and the limitations of its generalizability; 3) dependency on assumptions of linear, reversible succession toward a climax reference

community while ignoring the roles of non-equilibrium change, multiple disturbance types and abiotic gradients in shaping system resilience; 4) focus on the practices associated with structural change, while overlooking the ecological process feedbacks that influence disturbance response; 5) failure to validate STMs by testing model predictions.

Motivated by the need for improved sagebrush-steppe management tools, my thesis addresses these criticisms and challenges by exploring new approaches to build and refine STMs. The first chapter provides a review of sagebrush-steppe ecosystem dynamics, paradigms of vegetation change, and the application of STMs to natural resource management. The second chapter presents work to apply a collaborative, iterative approach proposed by Kachergis et al. (2013c) that integrates knowledge-based and empirical datasets to develop an STM for a Wyoming big sagebrush-steppe ecosystem in Moffat County, Colorado. The third chapter presents a pilot project to revise an existing STM by incorporating the role of specific ecological processes (nitrogen cycling) into a state transition. I conclude that the approaches employed here can address many of the challenges and criticisms of current STMs, but should be coupled with rigorous experimental testing of model assumptions and uncertainties and long-term monitoring of experimental outcomes. In addition, collaborative approaches should take care to carefully balance resource limitations with the desire to include a broad base of stakeholders and research interests, carefully manage stakeholder expectations, and explicitly define success in terms of both the collaborative process and the scientific outcomes.

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## Chapter 1.

### Introduction and Literature Review

#### INTRODUCTION

Once the most widely-distributed in North America, the sagebrush biome has experienced range reductions of up to 45% and has been considered one of the most endangered ecosystems in the United States (West 1983, Noss et al. 1995, Miller et al. 2011). It is home to a number of iconic wildlife species including sage-grouse (*Centrocercus* sp.), pygmy rabbit (*Brachylagus idahoensis*), pronghorn (*Antilocapra americana*), and ferruginous hawk (*Buteo regalis*) in addition to a number of other sagebrush obligate birds, mammals and reptiles. In addition to wildlife habitat conservation, North American sagebrush ecosystems are also managed for livestock production, oil, gas and mineral extraction, and recreation and sportsman's activities. These goals often appear to conflict but may also present potential synergies. However, understanding the roles of trade-offs and synergies in land management decisions requires an intricate understanding of the complex biotic and abiotic interactions of a system and the responses of these components to disturbance. Study of these interactions is further complicated by the vulnerability of (semi-) arid systems like those of the sagebrush biome to catastrophic ecosystem shifts in response to stress (Rietkerk et al. 2004, Bestelmeyer 2006, Scheffer 2012).

State-and-transition models (STMs) illustrate the complex relationships between ecosystem components, and convey both equilibrium and non-equilibrium dynamics, in a conceptual, visual framework to guide both research and management decision-making (Westoby et al. 1989, Walker and Westoby 2011). Adaptive natural resource management is an

“experimental management program” that attempts to address the complexity and uncertainty inherent in natural systems in the context of developing specific management policies (Walters and Holling 1990); management informs learning and learning informs management in an iterative cycle (Williams 2011a). When coupled, STMs and AM can be a powerful approach to improving understanding of ecosystem complexity in a practical framework: STMs can guide adaptive management (AM) projects, and monitoring results can be used to update STMs. Indeed, the Natural Resource Conservation Service, U.S. Forest Service, and Bureau of Land Management recently signed an interagency agreement to develop and use STMs to guide rangeland management decision-making nation-wide (Caudle et al. 2013); these agencies have also embraced adaptive management approaches to land management planning and evaluation (Coelho et al. 2013).

However the growing popularity of STMs has also brought them under increased scrutiny, and limitations in their current form and development and validation methods have been brought to light (Knapp et al. 2011, Tidwell et al. 2013). Common criticisms of STMs include: 1) reliance on insufficient empirical data or on expert- and local- knowledge prone to bias; 2) failure to explicitly identify the spatial and temporal scale of the model and the limitations of its generalizability; 3) dependency on assumptions of linear, reversible succession toward a climax community while ignoring the roles of non-equilibrial change, multiple disturbance types and abiotic gradients in shaping system structure and function ; 4) focus on the practices associated with structural change, while overlooking the ecological process feedbacks that influence disturbance response; 5) failure to validate STMs by testing model predictions.

Motivated by the need for improved sagebrush-steppe management tools, I attempt to address these criticisms and challenges in this thesis by exploring new approaches to build and refine STMs. In so doing, I pursue three primary objectives:

- 1) to develop an STM for a sagebrush-steppe system by following the collaborative, integrative process proposed by (Kachergis et al. 2013c); this process and the resulting STM will address some of the common criticisms of STMs by using both qualitative and quantitative data to define research questions and model resolution and to investigate the roles of abiotic gradients, multiple disturbance types, and functional attributes in influencing vegetation structure.
- 2) to incorporate ecological processes into an existing sagebrush-steppe STM.
- 3) to generate specific, measurable hypotheses concerning the structure-function dynamics of each site that can be experimentally tested using adaptive management.

In this introduction and literature review, I outline important components of the structure, function, and disturbance regime of the sagebrush-steppe ecosystem and review paradigms of vegetation change and disturbance response relevant to rangeland ecosystems. I then present the STM framework as tool for visualizing and investigating the plant association-site-disturbance interactions of a specific site, and discuss common criticisms and challenges of STMs. Finally I briefly outline the adaptive management approach to addressing system uncertainty from a practical perspective. In the chapters that follow, I will present approaches that integrate qualitative and quantitative data sources, rigorous multi-variate data analysis

techniques, consideration of specific belowground ecological processes and adaptive management to improve the credibility and utility of STMs.

## SAGEBRUSH ECOSYSTEMS

### *Occurrence and Assemblages*

The sagebrush biome, characterized by the dominance of woody species of *Artemisia* (sagebrush), was once the most widely distributed semi-desert vegetation type in North America, covering more than 44 million hectares (West 1983). Sagebrush steppe is a sub-type of the biome, characterized by a co-occurrence of *Artemisia* shrub species and a diverse herbaceous vegetation community comprised predominately of perennial bunchgrasses. Composition of herbaceous plant assemblages and the specific species and subspecies of *Artemisia* that make up a sagebrush-steppe system vary across the biome according to climate, topography, elevation, and soils, as well as disturbance history. Of the major sagebrush species, big sagebrush (*Artemisia tridentata*), two subspecies and their assemblages are of interest: Wyoming big sagebrush (*A.t. wyomingensis*) and mountain big sagebrush (*A.t. vaseyana*). The Wyoming big sagebrush-steppe typically occurs in moderately deep aridic-xeric sandy to clay loam soils in foothills and valleys at elevations ranging from 150 – 2150 m that receive 180 – 300 mm precipitation annually. By contrast mountain big sagebrush-steppe is generally found on deeper, loamier, udic soils of plateaus, mountainslopes, and bottomlands of higher elevations (1,200 – 3,200 m) receiving 350 – 450 mm annual precipitation. These differences in soils, topography and climate influence not only the systems' structural differences but also their responses to disturbance (West and Young 2000, Miller et al. 2011). For example, with its

cooler, moister conditions and coarser textured soils mountain big sagebrush tends to grow taller, and its understory tends to be more continuous, diverse and productive, compared to the warmer, drier Wyoming big sagebrush system; this in turn influences fire behavior and return interval, described further below.

In general, big sagebrush-steppe soils tend to be nitrogen-limited, in part due to slower decomposition rates resulting from the semi-arid climate (Smith et al. 1997). Big sagebrush produces long-lived leaves rich in phenolic anti-herbivory compounds, resorbs nitrogen efficiently before senescence, and is associated with arbuscular mycorrhizal fungi that can aid in “mining” of inorganic nitrogen from the soil (Allen et al. 1995, Coyne et al. 1995, Smith et al. 1997). As a result, sagebrush is well-adapted to sites with slow nitrogen turnover and its slow-to-decompose, nitrogen-poor litter may reinforce slow rates of nitrogen cycling (Aerts and Chapin 2000). Compared to sagebrush, the deciduous herbaceous species in the big sagebrush-steppe understory tend to produce foliage that is relatively nitrogen-rich and short-lived (Coyne et al. 1995, Smith et al. 1997). These traits could lead to relatively rapid rates of herbaceous litter decomposition and of recycling of the nitrogen derived from herbaceous litter, which in turn could help sustain the population of relatively fast growing, nitrogen-rich, understory herbs (Hobbie 1992). Thus, microsites beneath sagebrush tend to exhibit higher soil nitrogen concentrations and slower nitrogen cycling rates compared to microsites beneath herbaceous species (Doescher et al 1984, Schlesinger et al. 1990, Chen and Stark 2000). This patchy resource distribution likely both facilitates the coexistence of different functional group types and results from their differing nitrogen use strategies (Wedin and Tilman 1990, Van Cleve et al. 1991, Hobbie 1992, Berendse 1994, Aerts and Chapin 2000).

## *Disturbance Effects on Sagebrush-Steppe Vegetation Structure and Soil Nitrogen Dynamics*

Today, the sagebrush system is estimated to cover just 55% of its historical extent (Miller et al. 2011) and has been considered one of the most endangered ecosystems in the United States (Noss et al. 1995). Disturbance from native herbivory and fire shaped the steppe landscape over millennia. Since Overuse by domestic livestock, invasion by exotic species, especially cheatgrass (*Bromus tectorum*), and changes to historic fire regimes since European settlement and are frequently implicated for degradation, fragmentation and loss of sagebrush ecosystems (West and Young 2000, Miller et al. 2011).

Fire is one of the most dramatic disturbance factors influencing sagebrush ecosystem structure. Big sagebrush is very vulnerable to fire and does not re-sprout after burning, making post-fire regeneration entirely dependent on the surviving seed bank and seed sourced from unburned sagebrush stands. Due to a less-continuous understory of fine fuels, the pre-historic fire regime in Wyoming big sagebrush-steppe is believed to have been one of infrequent (> 100 year fire return interval) but expansive fires, while mountain big sagebrush experienced more frequent, patchier burns. Ignitions in both cases would have been from summer lightning strikes as well as spring and fall ignitions by aboriginal groups, likely used to drive game and encourage desirable herbaceous species (Reid et al. 1989, Kimmerer and Lake 2001, McAdoo et al. 2013). In Wyoming big sagebrush-steppe, these fire patterns are expected to have created large, continuous expanses of similar-aged sagebrush in various stages of regeneration; in mountain big sagebrush the pattern would likely have been a more intricate mosaic of

sagebrush stands and herbaceous patches (Baker 2006, Gruell and Swanson 2012, Bukowski and Baker 2013).

Fire transforms organic and mineral matter through oxidation and heat stress. These transformations alter the structure, volatility, and mobility of nitrogen compounds (Boerner 1982). The immediate effect of fire on semi-arid shrub land systems appears to be an increase in ammonium concentrations in the upper soil horizons. However, nitrogen fixation rates tend to decline immediately after fire, indicating that the increase in ammonium comes largely from ash deposits of partially-combusted organic matter, rather than microbial mineralization of organic nitrogen. Over the next few years, ammonium concentrations gradually decline while nitrate concentrations increase. Enhanced nitrification is likely facilitated not only by increased ammonium deposits available to nitrifiers, but also by deactivation of secondary metabolites (which tend to slow decomposition) via sorption with charcoal deposits (DeLuca et al. 2002, 2006). Elevated levels of nitrate have been observed to remain four years after fire in sagebrush (Rau et al. 2007). Indeed, the first few years after fire, shrub lands typically exhibit a widespread flush of herbaceous cover (Bates et al. 2009, Davies et al. 2009a, 2012) and enhanced foliar N concentrations (Rundel and Parsons 1980), indicating plants are accessing newly available, more homogeneously distributed nitrogen pools.

In arid and semi-arid landscapes where nitrogen is limiting, grazing has been observed to reduce soil resource homogeneity, facilitating resource patchiness and “islands of fertility” (Schlesinger et al. 1990, Allington et al. 2014). Grazed plants in resource-poor locales may be unable to access sufficient nitrogen for adequate compensatory regrowth, reducing their vigor

as well as the region over which they access and influence belowground resources, sometimes referred to as their “ecological field” (Walker et al. 1989); the result may be competitive release of soil nitrogen pools which may then be usurped by neighboring plants (Davies et al. 2007, Eilts et al. 2011). If nitrogen-use efficient species, such as sagebrush, were to acquire a greater share of soil nitrogen due to competitive release of nitrogen pools from neighboring grazed herbaceous species, this might increase the spatial extent of resource-poor patches in the landscape via the litter feedbacks described above. But not all nitrogen-poor environments experience herbaceous species loss in the face of grazing. The extent to which compensatory growth is limited in nitrogen poor environments depends on the timing, intensity, and duration of grazing. Resources may be adequate for regrowth of grazed plants even in nitrogen-limited environments if grazing intensity is low, short-term, or occurs during a time of year when plant resource demands are small (Archer and Smeins 1991). The extent to which plant associations evolved with large herbivores can also affect compensatory growth responses to herbivory.

The sagebrush-steppe in Northern Colorado probably co-evolved to some extent with large prehistoric browsing mammals, but major climatic changes during the late Pleistocene (12,000 years ago) interrupted this coevolution and drove the extinction of many large ungulates (Grayson 1991). After the Late Pleistocene, populations of large grazing ungulates in the intermountain valleys of the Rocky Mountains were relatively small compared to the large numbers of bison grazing rhizomatous and sod-forming grasses to the east (Mack and

Thompson 1982 )<sup>1</sup>. Thus, coevolution of intermountain sagebrush-steppe plant associations with intense grazing by large native ungulates was likely very limited.

European settlement in the 19<sup>th</sup> and 20<sup>th</sup> centuries introduced domestic livestock grazers (sheep, cattle, and horses) at high intensities. East of the Rockies where bison had once been abundant, “one bovid essentially replaced another” and native grasses tended to persist despite high stocking rates. By contrast, in many areas of the Intermountain West, including sagebrush-steppe systems of northwestern Colorado, unprecedented high grazing pressure from domestic ungulates (sheep, cattle, and horses) in the 19<sup>th</sup> and 20<sup>th</sup> centuries drastically altered the composition of native plant assemblages and altered the fire regime by reducing fine fuel loads (Mack and Thomspson 1982). Reductions in fire frequency, especially in the already sparse understory of Wyoming big sagebrush, allowed sagebrush to grow older and more “decadent” above a depauperate overgrazed understory (West 2000, Allington and Valone 2011). West (2000) estimated 25% of all sagebrush stands exist in this “stagnant” or “brush-choked” form.

Livestock managers often apply mechanical shrub control measures to reduce sagebrush cover and provide herbaceous species access to resources, with the intent of improving the quality and cover of herbaceous understory. However studies testing the efficacy of mechanical

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<sup>1</sup> Historical and paleontological records provide evidence that large ungulates, especially bison, were rare west of the Rocky Mountains. Examination of common close associates, such as the dung beetle genus *Onthophagus*, also provides evidence to this effect. There are 34 species of *Onthophagus* on the sod-forming grasslands east of the Rocky Mountains, but none in the bunchgrass-dominated regions of the Rockies and western slope. Bison, elk, and deer co-occurrence in the Intermountain West may have been restricted by a dis-synchrony between grass phenology and the timing of calving and peak milk-production. While C3 bunchgrasses which predominate to the west of the Rockies mature relatively early, the mixture of C3 and C4 species to the east would offer forage throughout the spring and summer to support calves and milk production (Mack and Thompson 1982).

shrub treatment have yielded mixed results (Davies et al. 2011, Davies et al. 2012b, Davies et al. 2012c, Hess and Beck 2014). In some cases mechanical sagebrush control also has been advocated for improving wildlife habitat (Connelly et al. 2004, Archer et al. 2011), but long-term alterations in sagebrush structure resulting from mowing can be detrimental to sagebrush facultative and obligate wildlife species (Davies et al. 2009, Beck et al. 2012, Hess and Beck 2014).

In many areas where herbaceous understory competition has been reduced by heavy grazing, invasion by exotic annual grasses such as cheatgrass (*Bromus tectorum*) has increased. Cheatgrass invasion appears to be especially successful in Wyoming big sagebrush-steppe systems. Cheatgrass is one of the first species to emerge in spring, quickly setting seed and drying, resulting in increased fuel continuity and flammability of the understory during most of the growing season. This increases both the frequency and extent of wildfire where once a sparse understory had kept fires relatively infrequent. After fire, cheatgrass appears to be a superior competitor for nutrients and water compared to native species (Reisner et al. 2013, Chambers et al. 2014). The result can be a reduction in fire return intervals from more than one hundred years to less than five and the conversion of sagebrush shrublands to persistent, monotypic exotic annual grasslands (Balch et al. 2013). Post-fire seeding has been advocated to improve competition success of native grasses against cheatgrass and thereby reduce fire frequency, but research testing this method have been mixed and inconclusive (Eiswerth and Scott Shonkwiler 2006, Jessop and Anderson 2007, Eiswerth et al. 2009, Shinneman and Baker 2009).

## *Sagebrush-Steppe Conservation Concerns*

Deterioration and loss of sagebrush habitats can negatively affect both livestock producers and wildlife that rely on sagebrush rangelands for forage and shelter year-round. Both monotypic cheatgrass grasslands and sagebrush-dominated depauperate shrublands provide insufficient high-quality forage for both livestock and large ungulates such as mule deer, pronghorn, and elk. Sagebrush avifauna may be especially vulnerable to habitat loss, as a number of bird species rely on sagebrush for forage, nesting, and shelter either partially or entirely (Braun et al. 1976). Perhaps one of the most iconic sagebrush obligate species is the greater sage-grouse (*C. urophasianus*), which was recently a candidate species for protection under the Endangered Species Act (U.S. Fish and Wildlife Service, 2010). Greater sage-grouse are completely dependent on the sagebrush system in every season and every stage of its lifecycle: adult diet consists entirely of sagebrush foliage during winter, while broods as well as adults depend on the insects and forbs that abound in a diverse herbaceous understory; nesting occurs beneath sagebrush with high annual site fidelity; winter shelter requires tall, contiguous sagebrush stands (Connelly et al. 2004). As a result, greater sage-grouse is considered an umbrella species for many other sagebrush wildlife, including passerine birds (Hanser and Knick 2011), songbirds (Timmer et al. 2015), and pygmy rabbit (Rowland et al. 2006). This means that habitat management that conserves greater sage-grouse will likely benefit many other wildlife species of conservation concern (Rowland et al. 2006). Wildlife conservationists and ranchers also share many common goals and management strategies that may mutually benefit both producers and sagebrush obligate wildlife (Beall and Zeoli 2008, Essen 2010). However, to successfully manage sagebrush habitat to the benefit of multiple land-users, it is necessary to

understand the specific patterns and mechanisms of vegetation change in response to disturbance and environmental variability.

#### PARADIGMS OF VEGETATION ASSOCIATION AND DISTURBANCE-RESPONSE

For much of the 20<sup>th</sup> century, vegetation change was described as following a gradual succession of plant associations over time toward some “climax” association characterized by dominance of slow-growing, long-lived species; succession might be halted or temporarily reversed by a disturbance (e.g., livestock grazing), but would resume along its original trajectory once the disturbance was removed (Clements 1916). These assumptions underlie the “range condition model” of pasture management, developed by Dyksterhuis (1949) and still used by many to guide rangeland vegetation management practices. Under this model, current range condition is assessed in terms of the extent to which plant species composition deviates from that of some pre-defined climax association or “reference condition”; restoration of reference conditions on a pasture can be achieved simply by limiting or excluding grazing for some period of time. Thus rangelands were considered to exist in a “dynamic equilibrium” (Connell and Sousa 1983), tending to maintain a stable condition unless disturbed, and then only to deviate only temporarily. This property of returning to prior condition with removal of a disturbance is often termed the “resilience” of a system (Holling 1973)<sup>2</sup>.

However, mounting evidence at the end of the 20<sup>th</sup> century began to demonstrate that while linear successional trends and equilibrial dynamics can and do exist in rangelands, they

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<sup>2</sup> A number of terms to describe stability dynamics have been presented and developed in the literature: *persistence* (Margalef 1969, Holling 1973), *resistance* (Boesch 1974), and *inertia* (Murdoch 1970, Orians 1975) describe a system’s tendency to remain in a particular state, while *adjustment* (Margalef 1969) and *resilience* (Holling 1973) describe the extent to which it can to return to a prior state after disturbance.

are by no means sufficient to describe all aspects of vegetation association and change, especially in (semi-)arid systems (e.g., Ellis and Swift 1988, Laycock 1991, Fernandez-Gimenez and Allen-Diaz 1999). Patterns in plant association change over time may have one central tendency, but can vary significantly in specific composition as a result of interactions between biotic and abiotic characteristics that vary across landscapes (Gleason 1939, Jenny 1941, Whittaker 1967, Pierson et al. 2011). Moreover, the trajectory of structural plant community change is not necessarily unidirectional; rather thresholds can exist beyond which removal of disturbance pressures does not restore previous associations (Holling 1973, West et al. 1984, Laycock 1991, Rietkerk and Van de Koppel 1997).

To understand threshold dynamics, it is important to recognize that the structure and function of a system are fundamentally linked. Functional ecosystem properties that reciprocally influence plant community structure include soil attributes (Jenny 1941, Farley et al. 2004, Bestelmeyer et al. 2006), hydrology (Petersen et al. 2009, Pierson et al. 2011), fire regime (Balch et al. 2012), and climate (Bates et al. 2006, Tietjen 2015). In stable systems, structure and function reinforce one another via ecological process feedbacks which serve to dampen changes to one or both elements induced by disturbances (Briske et al. 2006). Thus system resilience can be described as the measure of its ability to maintain structure-function relationships despite disturbances to one or both properties (Holling 1973).

However, the resilience of a system is finite. Sufficient disturbance of structure and/or function can alter ecosystem processes to such an extent that the negative feedbacks that resisted change become positive feedbacks that amplify it; as functional change progresses,

structure changes follow until the state of the system no longer resembles the original (Briske et al. 2006). This switch from negative to positive ecological process feedbacks can be considered the threshold of the system; change progresses until a new stable state is created, maintained by a new set of negative structural-functional ecological process feedbacks, and thus a new resilience regime (Holling 1973, Briske et al. 2006). To return to the previous state requires substantial inputs of energy and/or time to restore altered ecological processes, and thus a transition across thresholds is often considered irreversible, at least on management timescales (Friedel 1991, Bestelmeyer et al. 2003). Transitions across thresholds may be triggered by chronic, low-intensity disturbances (e.g., long-term livestock grazing; extended drought), acute, high-intensity disruptions (e.g., strip-mining; wildfire), or interactions among multiple disturbances across time and/or space (e.g., multiple wildfires; regional drought and heavy winds coupled with local deforestation driving major soil loss) (Peters et al. 2006, Barnosky et al. 2012)

## THE STATE-AND-TRANSITION MODEL

### *STM Framework*

The State-and-Transition model of vegetation change proposed by Westoby et al. (1989) is an alternative to the range condition model that incorporates both equilibrium and non-equilibrium dynamics. 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). Fluctuations among communities within a state represent the structural range of dynamic equilibrium; transition between states conveys

non-equilibrial change in both ecological processes and structure across some functional threshold (Westoby et al. 1989, Friedel 1991, López et al. 2011).

Compared to the old range condition model, STMs can more broadly and accurately convey the influence of soil, climate, spatial and temporal scale, and historic and current management actions on ecosystem structure and function (Bestelmeyer et al. 2004, Knapp et al. 2011); they also provide a framework in which to evaluate the potential ecological and economic costs and benefits of various management strategies in a given system (Bestelmeyer et al. 2004, Hemstrom et al. 2001, Ritten et al. 2011). This framework also allows STMs to integrate multiple sources and types of information about the system into a single model, and can help make uncertainties and assumptions about ecosystem dynamics more explicit (Bestelmeyer et al. 2009). STMs can also be used effectively as outreach and education tools. By visually conveying ecological dynamics in a simple form, they make complex ecological topics accessible to a variety of audiences and lend themselves well to hands-on learning modules (Crimmins et al. 2007, Escamilla 2012, Pritchett et al. 2012). When constructed collaboratively with stakeholders of diverse interests, STMs can help establish common ground and improve participants' understanding of not only the ecological dynamics of a given system, but also the sociological, ecological, and political ramifications of management decisions and vegetation change (Knapp and Fernandez-Gimenez 2009, Knapp et al. 2011, Peters et al. 2012).

STMs have been developed for a wide range of spatial scales from continental (e.g., Staver et al. 2011), to watershed (e.g., Provencher et al. 2007), to management district (e.g., Forbis et al. 2006), to soil type (e.g., Holmes and Miller 2010). The U.S. Department of

Agriculture Natural Resources Conservation Service (NRCS) advocates the “ecological site” concept to bound descriptions of plant association dynamics. An ecological site is a specific, high-resolution (1:12,000) complex of associated climate, topography, and soils that bound the ecological potential (composition and production) of a site and govern plant community responses to disturbance, time, and management actions. Ecological Site Descriptions (ESDs), originally developed by NRCS, detail the specific biotic and abiotic components of each ecological site and include an STM to convey the ecological dynamics of their interactions. In 2010, the NRCS, United States Forest Service, and Bureau of Land Management formalized an interagency collaboration to develop and use ESDs and STMs to guide rangeland management decision-making nation-wide (Caudle et al. 2013). As a result, thousands of STMs are being developed for rangelands across the U.S., covering an area of more than 300 million hectares (Tidwell et al. 2013).

#### *Conceptual vs. Simulation STMs*

STMs may take the form of conceptual models or quantitative simulations. Conceptual models describe patterns in vegetation and associated disturbances on a landscape, but do not make specific predictions about the likelihood of transitions over time or space. They are usually accessible to a wide range of stakeholders, are useful for revealing assumptions about system dynamics, and can guide development of goals and objectives for management planning. However, conceptual models have limited utility for predicting specific management outcomes and do not provide quantitative, falsifiable hypotheses for model testing. As a result,

model validation tends to center on producing circumstantial case histories rather than empirically tested experiments (Lockwood and Lockwood 1993, Bestelmeyer et al. 2009).

By contrast, simulation models are well suited for scenario planning and evaluating specific alternative management actions in terms of both ecological and economic outcomes (Daniel and Frid 2011). Simulation models are parameterized with transition probabilities associated with management actions and stochastic events, then run iteratively over some time period given a suite of starting conditions, management actions, and constraints to provide a probability distribution of potential outcomes. Simulation outcomes are typically expressed in terms of land area resulting in different states over time (Frid et al. 2013), but may also compute the associated cost versus benefit of treatment or an index of some desired ecological service associated with each state. (Hemstrom et al. 2001, Ritten et al. 2011, Provencher et al. 2013). When sufficient datasets are available, simulation models may also account for the influence of stochastic events, spatially-explicit phenomena, and cross-scale interactions on vegetation dynamics (e.g., Provencher et al. 2007, Price et al. 2011, Frid et al. 2013). Because they provide quantitative outputs, simulation models can be calibrated and tested against empirical data (Frid et al. 2013, Hill et al. 2005). However, as models grow more complex, they may become less accessible to stakeholders who lack sufficient expertise to properly use and interpret them.

### *Types of Knowledge in STMs*

STMs may incorporate knowledge derived from experts (e.g., land managers, scientists) or locals (e.g., producers, aboriginal groups), quantitative datasets (e.g., field data), the literature, or a combination of these. Each approach presents benefits and challenges.

Data-driven STMs identify the communities, states, and transition drivers present in a system from the results of statistical analysis of quantitative datasets describing the structural and functional attributes of a system. These datasets may be collected via experiments (e.g., Jackson and Bartolome 2002) or observational methods using long-term datasets (Allen-Diaz and Bartolome 1998, Hill 2005, Bagchi et al. 2012) or data representing only current conditions (e.g., Stringham et al. 2001, Peterson et al. 2009, Kachergis et al. 2012). While potential thresholds may be inferred from observational datasets, experiments, especially those that consider interactions between biotic and abiotic attributes across various spatial and temporal scales, are necessary to determine the specific mechanisms which drive a system across a threshold (Peters et al. 2004, Scheffer 2012). Long-term studies provide information about the probability, frequency, magnitude, and reversibility of transitions that is difficult to determine from short-term datasets (Bagchi et al. 2012, Kachergis et al. 2013b), and can also be used to validate and revise existing models (Thacker et al. 2008). However, long-term datasets are often unavailable or impossible to collect given available resources and timelines. As a result, STM modelers may look to space-for-time substitution to infer effects of past management on current vegetation structure. However, retrospective approaches make many assumptions about the conditions under which treatments and structural change developed that may not be

correct. For example the results of past treatments may have been affected by climate variability or microsites whose influence is unaccounted for in a retrospective study (Johnson and Miyanishi 2008).

Some approaches attempt to overcome shortfalls in available data by using published quantitative results from the literature to parameterize models (e.g., Spooner and Allcock 2006, Provencher et al. 2013). However application of data from one geographic area and sampling design may not be truly representative of the area or conditions for which an STM is being developed. As a result, many STMs are based entirely on expert and/or local knowledge about the study area (Walker et al. 2002, Raymond et al. 2010, Reisner 2010, Knapp et al. 2011). In addition to filling knowledge gaps and providing a long-term perspective on a study area, local and expert knowledge can provide social, economic and regional land-use context (Knapp and Fernandez-Gimenez 2009, Price et al. 2012). By incorporating a variety of perspectives and addressing scenarios of interest to stakeholders, knowledge-driven approaches may also improve stakeholder buy-in and cooperation with policies imposed as a result of model outcomes (Johnston and Soulsby 2006, Strager and Rosenberger 2006, Knapp and Fernandez-Gimenez 2009, Knapp et al. 2011, Price et al. 2012)

However, knowledge-driven models have a significant potential for bias, may overlook indicator species, trends, and thresholds present, and ultimately may be valid only for the local areas to which incorporated knowledge applies (Bagchi et al. 2012, Knapp and Fernandez-Gimenez 2009, Price et al. 2012). This may result in perpetuation of long-held assumptions that have not been rigorously tested (Knapp et al. 2011, Tidwell et al. 2013). In addition, estimates

of uncertainty are difficult to accurately quantify in knowledge-driven models (Price et al. 2012), and thus often are omitted all together, making models misleading (Suding and Hobbs 2009).

Collaborative, data-driven research projects that integrate local/expert knowledge with field data are gaining momentum in the field of STM development (Knapp and Fernandez-Gimenez 2009, Kachergis et al. 2013c, Knapp et al. 2013, Johanson and Fernandez-Gimenez 2015). This process may take two basic forms: 1) Use data to test hypotheses and update knowledge-driven models (Stringham et al. 2001, Bagchi et al. 2012, Kachergis et al. 2013c); 2) Use local and expert knowledge to parameterize unknowns in data-driven models (Hemstrom et al. 2007, Price et al. 2012, Frid et al. 2013, Provencher et al. 2013). Incorporating multiple knowledge types can improve the generalizability of STMs and make uncertainties more explicit. When model uncertainties are directly tested via adaptive management or simulation experiments, models can be iteratively updated and re-evaluated to improve accuracy and further reduce bias.

Kachergis et al. (2013c) propose an STM development process that integrates different types of knowledge via collaboration between researchers and expert and local knowledge-holders. This process integrates the participatory STM-development process outlined by Knapp and Fernandez-Gimenez (2009) with the data-driven STM development methods of Kachergis et al. (2011, 2013a) and incorporates active adaptive management experiments to test uncertainties and update the resulting integrated STM (Figure 1.1). The process is as follows:

- 1) Identify ecological site(s) of interest and assemble draft STM(s) based on existing data.

- 2) Iteratively revise this draft model to integrate both local knowledge and field data:
  - a. Local knowledge holders critique and revise the latest draft STM in workshops;
  - b. Project participants identify remaining key uncertainties and devise research questions and hypotheses;
  - c. Researchers conduct observational field research studies to quantitatively characterize the study area with respect to uncertainties and research questions;
  - d. Researchers analyze empirical data and use the results to revise the draft STM;
  - e. Steps 2(a-d) are repeated until participants settle on the final integrated STM.
- 3) Devise, implement and monitor adaptive management experiments to test remaining uncertainties; further revise the draft STM with new quantitative data (Step 2).

This process alleviates many of the challenges associated with a using only knowledge-based or only empirical datasets. By integrating both types of data, this approach reduces bias associated with relying entirely on knowledge-based data while providing access to long-term ecological data when quantitative datasets are lacking. The iterative process of revising STMs and refining research questions and hypotheses ensures that uncertainties are explicitly identified and addressed. At the same time, the collaborative approach facilitates valuable relationships between researchers, managers, and producers; this improves the utility and relevance of the resulting model and may strengthen collaborators' willingness to use it to guide decision-making.

In Chapter 2 I present my work as part of an interdisciplinary team of wildlife and plant ecologists, agricultural economists, and producers to apply the Kachergis et al. (2013c)

approach to develop an STM for the Wyoming big sagebrush-steppe ecosystem in eastern Moffat County, Colorado. I describe the collaborative process by which the scope, research focus, and sampling design were developed, present an STM derived from empirical field data collected over two field seasons, and discuss the role of expert and local knowledge in revising the data-driven model and guiding additional sampling to address remaining uncertainties. This STM will provide a framework for examining the effects of disturbances on not only rangeland production and structure but also wildlife habitat and producer economics.

### *Criticisms and Limitations of STMs*

While STMs are growing in popularity for both research and management applications, a number of challenges continue to limit their utility and acceptance. My thesis attempts to address some of the most common criticisms of STMs. In addition to the challenges described above associated with the source of data from which STMs are derived (i.e., knowledge- vs. empirical data), matters of scale, continued adherence to the old “range-condition” paradigm, omission of the ecological processes influencing vegetation structure and disturbance response, and lack of rigorous validation and revision all complicate STM development and hamper their widespread acceptance (Tidwell et al. 2013).

Equilibrial and nonequilibrial dynamics may exist within the same system at different spatial and temporal scales (Connell and Sousa 1983, Fernandez-Gimenez and Allen-Diaz 1999, Jackson and Bartolome 2002) and these dynamics may interact (Peters 2004). The reversibility of state-changes also depends on the timescale over which it is observed, the life-spans of the species involved, and the rate at which ecological processes occur. As a result, the spatial and

temporal scales of any model should be relevant to the needs of those who will be using the model to make decisions, and the bounds of certainty should be explicitly communicated. The scale of relevance to a livestock producer may be different from that relevant to a federal land manager, urban planning department or a researcher studying elemental cycling. The scale chosen will limit the degree to which certain ecological processes and structural components can be accurately portrayed. Thus the generalizability of an STM is limited: it is typically relevant only at the scale for which it is developed and the application for which it was intended. In Chapter 2 I discuss how to integrate both qualitative knowledge and quantitative data to explicitly define the spatial extent of our STM to be ecologically justifiable as well as relevant to managers and producers. I also discuss the temporal limits of the inferences that can be drawn from the data used and ways to address remaining uncertainties using future adaptive management projects.

Another common criticism of STMs is that although the state-transition concept was developed to incorporate non-equilibrial dynamics and the influence of abiotic gradients on vegetation associations, many STMs differ little from the old range-condition paradigm: state-changes are still presented as linear structural change, caused by a disturbance (e.g., grazing) and reversed by removal of that disturbance (e.g., rest from grazing) without regard to changes to state function; a single historic climax community defines the expected or “desirable” association, without regard to heterogeneity across the landscapes influenced by environmental gradients and stochastic events (Bagchi et al. 2013, Tidwell et al. 2013). In Chapter 2 I present a rigorous, quantitative approach to identify the influence of both known

and unknown environmental gradients and disturbances on structural and functional patterns in an ecosystem, and how to incorporate these into an STM.

In addition, many STMs are criticized for focusing primarily on management *practices* as the drivers of vegetation change, rather than on the ecological *processes* involved in maintaining resilience or carrying a system across a threshold (Bestelmeyer 2006, Briske et al. 2006). This likely stems in part from inconsistent and imprecise definition, quantification and application of concepts central to the STM framework, such as resilience, reversibility, trigger, and especially threshold (Knapp et al. 2011, Tidwell et al. 2013). Many STMs assume the existence of thresholds when changes in vegetation structure persist for a long time, without consideration of the life-histories of the organisms involved nor their relationships to abiotic attributes of the system. Failure to consider the structural-functional relationships underlying system dynamics inhibits efforts to prevent or reverse undesirable state-transitions (Bestelmeyer 2006, Bagchi et al. 2012, Tidwell et al. 2013). In Chapter 3 I present a case study to incorporate ecological process mechanisms into STM descriptions of states and transitions. Specifically, I propose and evaluate evidence for a nitrogen-cycling mechanism to explain the loss of herbaceous understory from old-growth sagebrush stands in a mountain big sagebrush ecosystem in western Routt County, Colorado.

Finally, although STMs are designed to make uncertainties explicit and thus testable, in practice these uncertainties and the state, transition, and threshold assumptions of STMs are infrequently validated and revised with rigor (Tidwell 2013, Bagchi et al. 2012; but see Oliva et al. 2008, Thacker et al. 2008). Validation that does occur often constitutes informal review by

experts and local knowledge-holders (Knapp et al. 2011) or comparison of model conclusions to published literature regarding similar sites (Hill et al. 2005, Standish et al. 2009, Frid et al. 2013) rather than field testing of hypotheses. Resource constraints, inadequate coordination, and shifting organizational priorities can hamper rigorous validation of STMs (Provencher et al. 2008, Evers et al. 2013). Yet STMs are ideally suited for informing adaptive management projects which can, in turn, inform and refine models (Bestelmeyer et al. 2003, 2004, Zweig and Kitchens 2009, Rumpff et al. 2011). At the end of Chapter 2 I propose several adaptive management “next steps” to address uncertainties remaining in the STM. Types of adaptive management and their potential synergies with STMs are described below.

#### ADAPTIVE MANAGEMENT

Adaptive management (AM) is a method of “learning by doing” that monitors and evaluates the results of management actions within the context of the socio-ecological system in question (Walters and Holling 1990, Williams 2011a). AM is an iterative cycle in which the outcomes of alternative management actions are monitored and evaluated in light of management objectives, models are refined based on what is learned from monitoring, and future management actions are chosen based on improved understanding of the social-ecological system at hand (Murray and Marmorek 2004). In this way AM seeks to: reduce system uncertainty by testing assumptions and alternative models; facilitate management concurrently with learning and creative problem-solving; inform evidence-based management policies; improve stakeholder and policy-maker buy-in to management objectives (Walters and

Holling 1990, Brunner and Clark 1997, Hardesty et al. 2000, Murray and Marmorek 2004, Fernandez-Gimenez et al. 2008).

Often AM is collaborative between management agencies, local stakeholders, researchers, and political bodies. Collaboration can greatly improve project efficacy in practice, by leveraging additional resources (financial, human, infrastructural, Coelho et al. 2013), deepening initial understanding of systems and the breadth and depth of future learning (McLain and Lee 1996, Cheng and Sturtevant 2012), improving oversight and accountability (Brunner and Clark 1997, Failing et al. 2004, Schultz and Nie 2012), empowering local communities to take ownership of the project long-term (Fraser et al. 2006, Reed 2008), and improving implementation, acceptance, and enforcement of conservation/management policies stemming from project results (Danielsen et al. 2005, Danielsen et al. 2007). Successful collaborative adaptive management (CAM) projects include explicit goals with measurable objectives, a strong rooting in the scientific literature, a clear decision-making process that incorporates new information, and a learning process that engages stakeholders in improving not only management but also the CAM process itself (Caves et al. 2013). Collaboration requires additional skills from investigators beyond research expertise, including the ability to recruit stakeholders and keep them engaged, build organizational infrastructure and partnerships for long-term monitoring and hypothesis revision, and disseminate project outcomes to the community at large (Fernandez-Gimenez et al. 2008).

While its acceptance is growing across many fields of natural resource management, AM still faces substantial challenges. Perhaps most widespread is the problem that different parties

often have different expectations of the process and outcomes which result in discord if unmet. When designing AM projects agencies must be transparent about expectations and build accountability into the project, for example by clarifying experimental design, monitoring protocols, and decision-making frameworks early in the process (Brunner and Clark 1997, Aldridge et al. 2004, Coelho et al. 2013). Other common challenges to effective AM projects include: demonstrating to policy-makers that AM is needed, especially when alternative management actions are more expensive or perceived to bring higher short-term risk; developing creative and rigorous management experiments that can discern management effects from stochastic effects or other environmental factors; maintaining a commitment to long-term experiments and monitoring, despite limited resources or changing political winds; implementing and maintaining a successful decision-making framework by which monitoring continues to inform future management through an iterative process (Walters and Holling 1990, Nichols et al. 1995, Moir and Block 2001, Aldridge et al. 2004, Walters 2007, Coelho et al. 2013).

Adaptive management may be retrospective, passive, or active (Walters and Holling 1990). Retrospective AM examines the present results of past management actions. No new treatments are initiated, and monitoring may use historical datasets and/or space-for-time substitution approaches to field sampling. The extent to which statistical inference can be drawn from retrospective analyses is limited, since past treatments are often not implemented with experimental rigor and long-term, multi-scale datasets may be lacking (Nichols et al. 1995, Marmorek et al. 2004). Thus, relationships inferred from retrospective AM are best used to

develop initial models that can inform rigorous future passive or active AM projects to test remaining uncertainties (Marmorek et al. 2004).

In passive AM, a single “best” management option is chosen for implementation based on current understanding of the system, and the results are monitored to determine whether objectives were accomplished. Passive AM is a simple process and can be conducted with limited upfront resources, making it easy for policy-makers and stakeholders to accept; however, because only one management strategy is tested a time, it may not be cheaper in the long run, learning is slower, and systems may suffer longer until successful management strategies are uncovered (Walters and Holling 1990, Murray and Marmorek 2004).

Active AM uses current understanding of the system to determine a number of possible management actions, and selects several management actions to test concurrently, using a scientifically-rigorous experimental design (Walters and Holling 1990). Actions may be selected according to both expected performance toward management objectives and associated learning potential (Walters and Holling 1990, Williams 2011b). While testing multiple strategies can improve learning and better inform management policy, it often also means implementing management approaches that are expensive or have undesirable short-term outcomes for the sake of experimental rigor and long-term gains in knowledge. Such “risks” may be difficult for policy-makers and other stakeholders to accept or to justify to their constituents (Walters and Holling 1990).

In the work presented here, I use a retrospective AM approach to: 1) infer the results of past burn and mechanical shrub control treatments on Wyoming big sagebrush-steppe

structure (Chapter 2) and 2) infer the role of nitrogen-cycling and soil properties on vulnerability of mountain big sagebrush plant associations to understory loss given summer grazing and lack of shrub disturbance (Chapter 3). At the end of each chapter I recommend a number of passive and active AM projects to reduce remaining uncertainties and understanding of system dynamics to improve STMs.

#### IMPROVING STMs AND ADAPTIVE MANAGEMENT OF SAGEBRUSH STEPPE ECOSYSTEMS

The need to improve sagebrush-steppe conservation for the benefit of multiple land uses and goals is apparent, and this requires a strong understanding of the interaction of ecosystem structure and function with disturbances and environmental gradients. However common criticisms of STMs make apparent the need to refine the ways in which STM creators identify uncertainty, collect and analyze data, and test model predictions. Motivated by the need for improved sagebrush-steppe management tools and guided by these challenges my thesis addresses three objectives:

- 1) to develop an STM for a sagebrush-steppe system by following the collaborative, integrative process proposed by (Kachergis et al. 2013c); this process and the resulting STM will address some of the common criticisms of STMs by using both qualitative and quantitative data to define research questions and model resolution and to investigate the roles of abiotic gradients, multiple disturbance types, and functional attributes in influencing vegetation structure.
- 2) to incorporate ecological processes into an existing sagebrush-steppe STM.

- 3) to generate specific, measurable hypotheses concerning the structure-function dynamics of each site that can be experimentally tested using adaptive management.

I address these objectives with two observational studies. One in a Wyoming big sagebrush-steppe system eastern Moffat County, Colorado integrates local knowledge and empirical soil and vegetation data collected from sites with different management histories but similar abiotic characteristics to infer the effects of burns and mechanical shrub control on sagebrush-steppe structure and to explain these relationships in an STM. The other is a pilot study using soil properties and nitrogen-transformation data derived from an *in situ* soil incubation to investigate evidence for a nitrogen-cycling based mechanism of understory loss from a mountain big sagebrush shrubland system in the Elkhead watershed of northwest Colorado. Below I introduce the specific ecological and methodological questions that motivate each chapter and briefly describe how they are addressed.

*Chapter 2: A Conceptual, Collaborative, Knowledge-Integrative STM for a Wyoming Big Sagebrush-Steppe Ecosystem in Eastern Moffat County, Colorado*

STMs have been criticized for being drawn from insufficient or biased data and for failing to make associated uncertainties explicit (Knapp et al. 2011, Tidwell et al. 2013). The generalizability and credibility of many STMs is also limited by inexplicit spatial and temporal scales and for failing to consider interactions between disturbances and environmental gradients (Bestelmeyer 2006, Tidwell et al. 2013). To address these concerns, we applied the STM development approach proposed by (Kachergis et al. 2013c) to integrate empirical data, derived from field sampling of areas with different management histories, with local and expert

knowledge via a collaborative approach that iteratively identifies and addresses uncertainties through workshops, field sampling, and quantitative multivariate data analysis. Spatial and temporal scope were based on practical relevance to land managers and producers and qualitative NRCS land classifications, coupled with quantitative analysis of the range of abiotic variability in the study area (e.g., soils, topography) likely to influence plant association structure, function and disturbance response. Potential interactions between environmental factors and disturbances that may influence plant association structure and function were identified using a suite of multivariate techniques. Chapter 2 describes in detail the collaborative process, quantitative data-analysis approaches, their results, and their implications for constructing an STM for Wyoming big sagebrush-steppe eastern Moffat County. The final STM is also presented and discussed.

### *Chapter 3: Nitrogen-Cycling in a Mountain Big Sagebrush Ecosystem: An Ecological Process-Based Approach to State-Transition-Model Development*

A central assumption of STMs is that many ecosystems exhibit both equilibril and non-equibril change dynamics. Equibril change occurs when a system absorbs perturbations (e.g., management actions, weather variability) so that they do not fundamentally alter the fundamental structural-functional feedback relationships that define the system; this property of a system to resist change over some range of variability is its “resilience” (Holling 1973). Non-equibril change occurs when disturbances are acute or long-term enough to switch the negative structural-functional feedbacks that once maintained the system to positive feedbacks that amplify change. Eventually some threshold of change is crossed beyond which structure-

function relationships are inextricably altered, and simple removal of the disturbance does not restore previous relationships; at this point a new state has been established, maintained by a new set of negative feedbacks (Briske et al. 2006). Thus state-transitions in an STM can be described in terms of the structural-functional feedbacks that maintain or alter states. However STMs have been criticized for focusing on practices rather than processes; that is, for describing primarily the management practices correlated to changes in vegetation structure while overlooking the ecological processes involved in maintaining or altering resilience dynamics (Tidwell et al. 2013).

The purpose of the third chapter is to revise an existing STM state transition, presented by Kachergis et al. (2012), to include ecological processes. Kachergis et al. (2012) observed a loss of herbaceous understory cover and diversity and concomitant increase in sagebrush height and canopy cover to be correlated with long-term lack of shrub disturbance (e.g., via mechanical or chemical control, or fire) and long-term medium- to high-intensity summer livestock grazing. I hypothesize that each state is maintained by feedbacks between litter pool quality and nitrogen cycling, and predict that the Diverse state, with its extensive, fast-growing herbaceous understory, should exhibit a high quality (low C:N), readily decomposable litter and faster nitrogen cycling; the Depauperate state, dominated by nitrogen efficient sagebrush, should exhibit poor quality (high C:N) litter pool and slower nitrogen cycling.

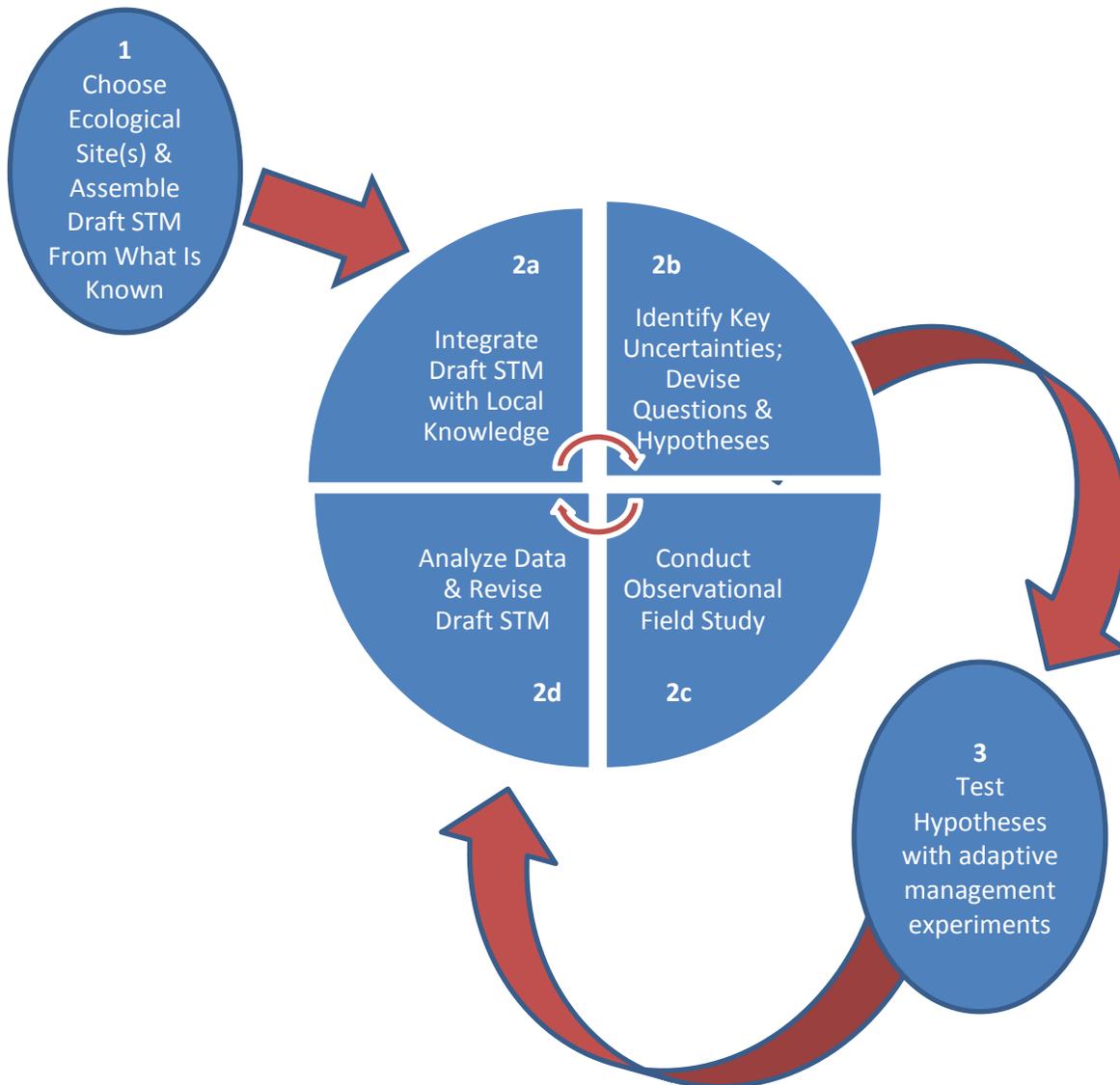
I compare the soil nitrogen transformation rates, derived from a series of *in situ* soil incubations conducted over the 2014 growing season, as well as soil and litter pool properties between the two states and discuss whether there is sufficient evidence to support this hypothesis. I also

discuss how long-term summer grazing and lack of shrub disturbance may trigger the switch from fast to slow rates, and propose adaptive management experiments to test this mechanism.

## CONCLUSION

State-and-Transition models are a valuable tool for presenting what is known and unknown about the equilibrial and non-equibrial dynamics of a system and for guiding management decision-making. As a result, STMs are now being developed by a wide range of federal, state, and private land management agencies. However, remaining challenges to the development of STMs limit their utility and widespread acceptance: 1) Long-term quantitative datasets from which to derive data-driven inferences about structural change and thresholds are often unavailable or insufficient, while STMs that rely on expert or local knowledge for long-term data risk bias and often fail to make uncertainties explicit; 2) The generalizability of an STM is limited to the specific system at the specific spatial and temporal resolution it describes, yet often neither these bounds nor their rationale are made explicit in the model; 3) Many STMs describe all vegetation associations as following linear succession toward some climax community, and all disturbance-induced changes as readily reversible; this approach ignores the intention of STMs as a tool to incorporate non-equibrial dynamics into the old succession-based range-condition paradigm (Dyksterhuis 1949, Westoby et al. 1989), and overlooks the interactions of environmental gradients and multiple disturbances on plant association assembly and response to disturbance; 4) STMs tend to focus on the practices correlated with structural change, while failing to describe the ecological processes that

influence the resilience and disturbance response of a system; 5) The predictions of STMs often are not rigorously tested. The following two chapters attempt to address these criticisms and challenges by exploring new approaches to build and refine STMs.



**Figure 1.1** Conceptual Diagram of Streamlined Collaborative STM Development Process adapted from that proposed by Kachergis et al. (2013). The process is iterative over the following steps: 1) Choose ecological site(s) of interest and assemble a draft model based on what is known about that site (e.g., from literature, existing monitoring and remote sensing data, historical records). In an iterative fashion over several field seasons: 2a) Present the draft model to local and expert knowledge holders in a workshop setting in which participants critique and revise the model draft based on their knowledge and experience, 2b) Identify key uncertainties remaining in the model and develop hypotheses that address them, 2d) Update the model draft with quantitative results gleaned from field study; present this revised integrated model to workshop participants to further critique (2a). Concurrently, devise adaptive management experiments to actively test hypotheses and use these to further revise the hybrid model with quantitative data (3).

## **Chapter 2.**

A Conceptual, Collaborative, Knowledge-Integrative STM for a Wyoming Big Sagebrush-Steppe Ecosystem in Eastern Moffat County, Colorado

### INTRODUCTION

Successful management and conservation of ecosystems depends on having and communicating a solid understanding of the relationships between plant community structure, ecological function, and natural and human-caused disturbance. Conceptual state-and-transition models can be used to summarize what is known and unknown about these relationships in order to inform and guide future management and scientific investigation. State-and-transition models (STMs) may be developed from expert or local knowledge, observational field studies, or published literature. The benefits of integrating quantitative data with local and expert knowledge have been increasingly recognized (Walker et al. 2002, Raymond et al. 2010, Reisner 2010, Knapp et al. 2011). Kachergis et al. (2013c) proposed a streamlined approach to participatory STM development that integrates local and expert knowledge with quantitative datasets in an iterative process. We implemented this approach to build and refine an STM for the Wyoming big sagebrush-steppe ecosystem in eastern Moffat County, Colorado.

### STATE-AND-TRANSITION MODELS

The STM framework was proposed by Westoby et al. (1989) as an alternative to the succession-based range condition model of Dyksterhuis (1949) to characterize vegetation associations and their relationships to disturbance patterns. Instead of assuming that all vegetation change follows a linear, readily reversible trajectory toward some climax plant

community, STMs incorporate both equilibril and non-equibril dynamics. An STM 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). A state is maintained by negative ecological process feedbacks that reinforce these structural-functional relationships over some range of variability; this variability is represented by plant communities within states. Fluctuations among plant communities within a state tend to be readily reversible with removal of the driving disturbance (e.g., short-term weather changes or herbivory patterns) (Briske et al. 2006).

State transitions arise when triggering events (e.g., anthropogenic or environmental disturbances) alter state structure and/or function to such an extent that it can no longer be maintained by the same ecological processes; instead, positive feedbacks amplify structural-functional change until a new state is created, maintained by a new set of structural-ecological process feedbacks (Briske et al. 2006). The switch from negative to positive ecological process feedbacks is often described as a “threshold” of change in ecological function; beyond this threshold, the system is no longer resilient, structural-functional change is accelerated rather than resisted, and significant energy investment (e.g., management intervention) is necessary to restore the original state (Friedel 1991, Laycock 1991, Lockwood and Lockwood 1993, Briske et al. 2006, Scheffer 2012).

STMs have been developed for a wide range of spatial scales from continental (e.g., Staver et al. 2011), to regional watershed (e.g., Provencher et al. 2007), to management district (e.g., Forbis et al. 2006), to groups of similar soil types (e.g., Holmes and Miller 2010). The US

Department of Agriculture Natural Resources Conservation Service (NRCS) advocates the “ecological site” concept to bound descriptions of plant association dynamics, and is currently developing thousands of STMs to describe vegetation change at the ecological site scale across the United States (Bestelmeyer 2015). The ecological site concept attempts to classify sites based on the specific climate, topographic, and soil relationships that limit their ecological potential (e.g., productivity, species composition, response to disturbance) (Caudle et al. 2013). Abiotic characteristics of an ecological site limit the outer bounds of vegetation type, association, and production expected to occur on the site. Individual ecological sites are not uniform, however, and can contain internal abiotic gradients (e.g., variation in hillslope position or soil properties) which can affect different plant responses to similar stimuli (Charley and West 1975, Lane et al. 1998, Bestelmeyer et al. 2009, Kachergis et al. 2012, Tietjen 2015). These internal gradients should be considered when developing and interpreting STMs and the scale over which an STM is applied should be relevant to the management context in which it is applied.

Long-term high-resolution quantitative datasets derived from observational and experimental studies, while providing objective evidence of vegetation change dynamics in an area, are rarely available (but see Bagchi et al. 2012, 2013, Kachergis et al. 2014). Some approaches attempt to overcome this shortfall by using published quantitative results from the literature (e.g., Spooner and Allcock 2006, Provencher et al. 2013), but the published study area and design may not be truly representative of the area or conditions for which an STM is developed. As a result, many STMs are based entirely on expert and/or local knowledge (Walker et al. 2002, Raymond et al. 2010, Reisner 2010, Knapp et al. 2011). In addition to filling

knowledge gaps and providing a long-term perspective on a study area, local and expert knowledge can provide social, economic and regional land-use context (Knapp and Fernandez-Gimenez 2009, Price et al. 2012). By incorporating a variety of perspectives and addressing scenarios of interest to stakeholders, knowledge-driven approaches may also improve stakeholder support and cooperation with policies imposed as a result of model outcomes (Knapp and Fernandez-Gimenez 2009, Knapp et al. 2011, Price et al. 2012, Strager and Rosenberger 2006, Johnston and Soulsby 2006).

However, knowledge-driven models have a significant potential for bias, may overlook indicator species, trends, and thresholds present, and ultimately may be valid only for the local areas to which incorporated knowledge applies (Bagchi et al. 2012, Knapp and Fernandez-Gimenez 2009, Price et al. 2012). This may result in perpetuation of long-held assumptions that have not been rigorously tested (Knapp et al. 2011, Tidwell et al. 2013). In addition, estimates of uncertainty are difficult to accurately quantify in knowledge-driven models (Price et al. 2012), and thus often are omitted all together, making models misleading (Suding and Hobbs 2009).

Collaborative, data-driven research projects that integrate local/expert knowledge with field data are gaining momentum in the field of STM development (Knapp and Fernandez-Gimenez 2009, Kachergis et al. 2013c, Knapp et al. 2013, Johanson and Fernandez-Gimenez 2015). This process may take two basic forms: 1) Use data to test hypotheses and update knowledge-driven models (Stringham et al. 2001, Bagchi et al. 2012, Kachergis et al. 2013c); or 2) Use local and expert knowledge to parameterize unknowns in data-driven models (Frid et al.

2013, Hemstrom et al. 2001, Price et al. 2012, Provencher et al. 2013). Incorporating multiple knowledge types can improve the generalizability of STMs and make uncertainties more explicit. When model uncertainties are directly tested via adaptive management or simulation experiments, models can be iteratively updated and re-evaluated to improve accuracy and further reduce bias.

The integrative model-building process proposed by Kachergis et al. (2013c) provides an avenue to integrate existing field datasets, access long-term ecological knowledge about the study area when quantitative field data is lacking, explicitly identify and address model uncertainties, and reduce bias while educating and building relationships between researchers, managers, and producers. Ultimately, this process has the potential to both improve the utility and accuracy of STMs and strengthen producer and manager willingness to use the models to guide short- and long-term decision-making. The end result should be management guidance that better integrates management, production, and conservation goals to the mutual benefit of all stakeholders.

## THE SAGEBRUSH STEPPE ECOSYSTEM

The sagebrush system was once the most widely distributed semi-desert vegetation type in North America, covering more than 44 million hectares (West 1983), but has experienced range reductions of up to 45% (Miller et al. 2011) and has been considered among the United States most endangered ecosystems (Noss et al. 1995). Alterations to fire regime, invasion by exotic annual grasses such as cheatgrass (*Bromus tectorum*), and overuse by domestic livestock are frequently implicated for degradation, fragmentation and loss of

sagebrush ecosystems (West and Young 2000, Miller et al. 2011). The majority of the sagebrush biome (70%) is publicly owned and managed for a variety of uses including resource extraction, sheep and cattle production, recreation, sportsman's activities and wildlife habitat protection (Knick et al. 2003). These multiple land use goals present challenges for conservation and sustainable land management.

Sagebrush steppe is a sub-type of the biome, found primarily in northern and higher elevation reaches of its range. Steppe is characterized by a co-occurrence of *Artemisia* shrub species and a diverse herbaceous vegetation community comprised predominately of perennial bunchgrasses. The dominant subspecies of *Artemisia* and the structure and composition of herbaceous plant assemblages vary across the biome according to temperature and precipitation regime, topography, elevation and soils, as well as disturbance history. The steppe system of the Wyoming big sagebrush subspecies (*Artemisia tridentata* spp. *wyomingensis*) typically occurs in mesic, aridic sandy to clay loam soils in foothills and valleys at elevations ranging from 150-2150 m (West and Young 2000, Miller et al. 2011).

Fire is one of the most dramatic disturbance factors influencing sagebrush ecosystem structure. Big sagebrush is very vulnerable to fire and does not re-sprout after burning, making post-fire regeneration entirely dependent on the surviving seed bank and seed sourced from unburned sagebrush stands. The pre-historic fire regime in Wyoming big sagebrush-steppe is believed to have been one of infrequent (> 100 year fire return interval) but expansive fires ignited by mid-summer lightning strikes; aboriginal groups also appear to have regularly ignited fires in spring and fall, likely to drive game and encourage desirable herbaceous species (Reid et

al. 1989, Kimmerer and Lake 2001, McAdoo et al. 2013). These fire patterns are expected to have created large expanses of similar-aged stands of sagebrush in various stages of regeneration (Baker 2006, Gruell and Swanson 2012, Bukowski and Baker 2013).

Historic overgrazing by sheep, cattle, and horses during European settlement of the west in the 19<sup>th</sup> and early 20<sup>th</sup> centuries greatly reduced herbaceous cover and thereby fine fuels in the sagebrush biome, reducing fire frequency and allowing sagebrush to grow older and more “decadent” above a depauperate understory (West 2000, Allington and Valone 2011). West (2000) estimated 25% of all sagebrush stands exist in this structure. Livestock managers often apply mechanical shrub control measures to reduce sagebrush cover and provide herbaceous species access to resources, with the intent of improving the quality and cover of herbaceous understory. However studies testing the efficacy of mechanical shrub treatment have yielded mixed results (Davies et al. 2011, Davies et al. 2012b, Davies et al. 2012c, Hess and Beck 2014). In some cases mechanical sagebrush control has also been advocated for improving wildlife habitat (Scifres 1980, Archer et al. 2011), but long-term alterations in sagebrush structure resulting from mowing can be detrimental to sagebrush facultative and obligate wildlife species (Davies et al. 2009, Beck et al. 2012, Hess and Beck 2014).

In many areas where herbaceous understory competition has been reduced by heavy grazing, invasion by exotic annual grasses such as cheatgrass (*Bromus tectorum*) has increased. Cheatgrass increases fuel continuity and flammability, increasing the risk of expansive fire where once understory loss had reduced fire. Fire in cheatgrass-dominated stands tends to further favor cheatgrass where native grasses are insufficient competitors for water and

nutrients (Reisner et al. 2013, Chambers et al. 2014). The result can be very frequent fire return intervals and the conversion of sagebrush shrublands to persistent exotic annual grasslands (Balch et al. 2013). Post-fire seeding has been advocated to improve competition success of native grasses against cheatgrass and to reduce fire frequency, but results of research to test this method have been mixed and inconclusive (Eiswerth and Scott Shonkwiler 2006, Jessop and Anderson 2007, Eiswerth et al. 2009, Shinneman and Baker 2009).

Here I present work to develop an STM for a Wyoming big sagebrush-steppe system that integrates local and expert knowledge with empirical observational data in a collaborative, iterative process proposed by (Kachergis et al. 2013c). This process and the resulting STM will address some of the common criticisms of STMs described in Chapter 1 by using both qualitative and quantitative data to define research questions and model resolution and to investigate the roles of abiotic gradients, multiple disturbance types, and functional attributes in influencing vegetation structure.

## METHODS

Our STM building effort incorporated different types of knowledge following the proposed streamlined multi-disciplinary process outlined by Kachergis et al. (2013c). This process integrates the participatory STM-development process outlined by Knapp and Fernandez-Gimenez (2009) with the data-driven STM development methods of Kachergis et al. (2011, 2013a) and incorporates active adaptive management experiments to test uncertainties and update the resulting integrated STM (Figure 1.1).

The primary steps in this process are:

- 1) Identify ecological site(s) of interest and assemble draft STM(s) based on existing data.
- 2) Iteratively revise this draft model to integrate both local knowledge and field data:
  - a. Local knowledge holders critique and revise the latest draft STM in workshops;
  - b. Project participants identify remaining key uncertainties and devise research questions and hypotheses;
  - c. Researchers conduct observational field research studies to quantitatively characterize the study area with respect to uncertainties and research questions;
  - d. Researchers analyze empirical data and use the results to revise the draft STM;
  - e. Steps 2(a-d) are repeated until participants settle on the final integrated STM.
- 3) Devise, implement and monitor adaptive management experiments to test remaining uncertainties; further revise the draft STM with new quantitative data (Step 2).

We followed steps 1) and 2) above to develop an STM that integrates local and expert knowledge with observational data to convey the relationships of plant communities to past disturbances (mechanical shrub treatment and wildfire) in the Wyoming big sagebrush-steppe of eastern Moffat County, Colorado. This model will be used to develop future adaptive management experiments (Step 3) to test remaining model uncertainties and update the STM.

*Step 1: Choose Ecological Site(s) and Assemble Initial Draft STM*

A large proportion of Moffat County, Colorado exists as open sagebrush rangeland and is managed for a wide variety of land uses important to regional stakeholders. A gradient of increasing elevation and precipitation runs generally west to east through the county, resulting in very different ecological site designations in the west, which tends to resemble the arid Great

Basin sagebrush type, compared to the east, best described as Wyoming big sagebrush-steppe. As a result, Moffat County stakeholders chose to study eastern and western regions of their county separately. The work of the eastern Moffat (EM) group is described here.

EM stakeholders chose to focus STM development efforts on the Sandy Land and Rolling Loam ecological sites. These sites comprise a substantial proportion of the area and tend to intergrade across the landscape, provide important ecosystem services, including livestock forage and wildlife habitat, and appear to stakeholders to respond similarly to disturbance (USDA-NRCS 2009). ESDs for the two sites describe very similar vegetation structure, although specific species composition may differ, and they are found nearly identical abiotic situations: sandstone-derived parent materials at elevations ranging from 1828 m – 2225 m, slopes ranging from 0-25%, hill, plateau, and piedmont landforms, and hillslope positions ranging from summit to toe-slope (USDA-NRCS 1975, 1987, 2009). As their names suggest, there are slight soil textural differences between the two ecological sites, with Rolling Loam dominated by horizons of loam, sandy loam, and sandy clay loam textures, while the Sandy Land pedon tends to consist of sand or loamy sand (USDA-NRCS 2009). Because of their similarity, stakeholders questioned whether the two sites really are distinct, or could be adequately described by a single STM.

NRCS partners provided initial draft STMs developed for similar loamy ecological sites in western Colorado and southern Wyoming. These initial models had been devised based on expert knowledge, literature review, and field sampling.

*Step 2a,b: Revise Draft Model Based on Participant Knowledge (a); Determine Key Uncertainties (b)*

The eastern Moffat (EM) stakeholder group included representatives from local sheep and cattle producers (6), Colorado State University (CSU) Extension (5), USDA Natural Resources Conservation Service(4), USDA Agricultural Research Service (1), Bureau of Land Management (1), Colorado Parks and Wildlife (1), United States Forest Service (1), and members of the public (3), in addition to CSU researchers. This group applied their knowledge and experience of vegetation change resulting from past management and natural disturbances to revise the initial draft models and create a single draft STM for the combined Sandy Land and Rolling Loam ecological sites. The roles of fire, post-fire seeding, and mechanical brush control (either mowing or “dragging”, the latter considered a less destructive method that topples sagebrush without cutting or uprooting it) were identified as key areas of remaining uncertainty. To address these uncertainties and guide sampling design and analyses, the following research questions and hypotheses were devised:

- R1. Are the Rolling Loam and Sandy Land ecological sites sampled sufficiently similar in abiotic properties, plant composition and structure to comprise a single STM?
- R2. Which plant associations in the study area represent compositionally distinct, functionally similar communities (expected to exhibit equilibril dynamics)?
- R3. Which plant associations in the study area represent compositionally and functionally distinct states (expected to exhibit non-equibril, difficult to reverse “threshold” dynamics)?

R4. To what extent do static abiotic environmental gradients versus dynamic site attributes and management history within the study area explain the differentiation of plant associations?

H4(a) Static abiotic gradients alone will be insufficient to explain patterns of plant association patterns.

H4(b) Each of the treatment groups (burned/not seeded, burned + seeded, mowed, dragged, and no treatment) will exhibit significantly distinct species compositions.

H4(c) Areas treated with mechanical treatments (mow or drag) in the past will exhibit less shrub cover, greater herbaceous, grass and forb cover, and greater species richness and forb diversity, compared to untreated areas (controls).

H4(d) Past drag treated areas will exhibit greater herbaceous cover, grass cover, forb diversity and cover, and shrub cover compared to mow treatment plots.

H4(e) There exists a “decadent” (high shrub cover) and “depauperate” (low herbaceous cover and species richness) sagebrush shrubland state; this state is associated with long-term lack of shrub disturbance.

H4(f) Burned plots will have greater *Bromus tectorum* cover than unburned plots; burned plots seeded with native grasses will have greater *Bromus tectorum* cover than unseeded burned plots.

## *Step 2c: Conduct Observational Field Study to Address Research Questions*

### **Sampling Design**

The sampling design uses space-for-time substitution to examine the effects of past management treatments (fire and mechanical shrub control) on the structure, composition, and function of plant associations on 101,400 ha of private and public rangelands in eastern Moffat County, Colorado (latitude 40.7°N, longitude 108°W). All areas were currently and historically grazed by livestock (cattle and/or sheep) and were observed to also be utilized by large wild ungulates (mule deer, pronghorn and elk). Site management history and the boundaries of past treatment areas were provided by private landowners and public land agencies.

For the 2013 and 2014 sampling seasons, fifty-nine field sampling points were randomly generated in ArcGIS 10.0 within treatment areas and undisturbed “control” areas on our target ecological sites, Rolling Loam and Sandy Land, as identified in Web Soil Survey (USDA-NRCS 2009) (Figure 2.1). The number of sampling points per treatment depended on its area and extent of variability (Herrick et al. 2005). Treatment areas consisted of a mowed area (174 ha in 1996), two dragged areas (28.8 ha in 1997 and 15.2 ha in 1998), two wildfires with no post-fire seeding (1,505 ha in September 2008; 2,679 ha in August 2010), and a portion of the 2010 wildfire seeded with native species (506 ha in 2011); additional “control” plots were generated in undisturbed regions across the entire study area (Table 2.1). Livestock grazing resumed on all wildfires within two years of the fire. We later learned that some areas of the seeded and

unseeded burns had been old homestead properties seeded with the exotic bunchgrass crested wheatgrass (*Agropyron cristatum*) in the 1940's and 50's.

We did not stratify sampling by livestock type or grazing intensity, since the primary research questions centered on treatments and not treatment grazing interactions. However, as discussed below, we later learned that changes in winter elk use and historical livestock use patterns may have a stronger influence on current vegetation patterns than initially anticipated. Sampling points were randomly selected using the following criteria: points were at least 50 m from a fence line, two-track road, water source (e.g., stock tank, stream) or drainage bottom. Slopes greater than 25% were not sampled. No more than two sampling points were allowed within 400 m of each other in order to better ensure sampling across the range of landscape-scale variability within the target ecological sites.

### **Data Collection**

High-resolution sampling occurred on 59 50 m x 50 m plots (31 in July and August 2013; 28 in July 2014). Each plot was described in terms of site, soil, and vegetation characteristics (Table 2.2). Site characteristics of each plot were described by elevation, aspect, hillslope position, distance to water (a proxy for grazing intensity), distance to sagebrush (a proxy for sage-grouse habitat suitability), and distance to the closest road. Soils at each plot were characterized from a soil pit or augur hole dug in the center of each plot to at least 50 cm depth. Soils were described following NRCS protocols (Schoeneberger et al. 1998), recording the thickness, color, structure, and field texture in each horizon. Soil value (lightness) was also

used as an indicator of soil organic matter in the first two horizons (indicated by low values) and of coarser soil textures and thus drainage in the third horizon (indicated by high color values).

Soil and site characterizations at each plot were compared to the soil complex component descriptions for those complexes associated with the Rolling Loam and Sandy Land ecological sites to confirm that plots were located one of these two target ecological sites. To simplify comparisons by horizon, plots exhibiting at least 50% of the pedon depth in horizons of loam, sandy loam, or sandy clay loam were classified as Rolling Loam, while those exhibiting at least 50% of pedon depth in sandy or loamy sand horizons were classified as Sandy Land. Five plots sampled did not fit either description, with soil pedons dominated by at least 90% of depth in clay loam or clay horizons; these were classified as Claypan. Because the Claypan sites occurred on otherwise very similar situations, and because field observations of plant community composition and structure did not reveal any clear distinctions between the Claypan, Rolling Loam, and Sandy Land plots, all three ecological sites were included in initial analysis. As described below, data analysis proceeded to explore how similar the abiotic (soil and site) and biotic (species composition and structure) attributes of the three ecological site types are, in order to determine whether to include all three in a single STM.

Species richness at each plot was determined via a 15-minute timed search through the plot during which each unique species was identified and noted; this list was amended if additional species were discovered through the course of remaining sampling. Relative species composition by mass was estimated using the Dry Weight Rank method (Jones and Hargreaves 1979); 15 40 cm x 40 cm quadrats were ranked per plot in 2013 sampling, but only 5 per plot in

2014 in order to reduce field sampling time per plot and increase the number of sample units achievable given the time available. Total standing crop of all current-year plant growth was determined per plot by clipping quadrats (3 quadrats per plot in 2013; 5 quadrats per plot in 2014), and extrapolating the mean quadrat production to the plot area. Per plot production by species was then estimated by multiplying dry weight rank composition by total standing crop per plot.

Plant cover by species was determined using the line-point-intercept (LPI) method (Bonham 1989) at 1-meter intervals (points) along five 50-meter transects spaced 12.5 meters apart; vascular plant foliar and basal hits were recorded by species in addition to hits of litter, rocks, dung, and bare ground. Absolute cover by species was determined from the proportion of LPI “hits” per cover type out total LPI points per plot (250); top and middle canopy cover was determined separately from basal cover. Plant cover by species was used to describe plant association structure.

LPI data also were used to describe ecological function via several aggregate metrics. These functional indicators were used to describe ecological function in two ways: 1) in terms of implications for soil and belowground function (i.e., soil erosion potential, soil temperature, and nutrient deposition) via perennial basal cover, litter cover, and bare ground cover along with additional functional indicators described below; 2) in terms of plant functional differentiation by functional group (grass, forb, and shrub cover, stratified by native/exotic status and perennial/annual habit, as well as legume cover and bunchgrass/rhizomatous grass cover).

To further assess ecological function, the continuous gap intercept method (Herrick et al. 2005b, c) was used to measure the length of gaps between plant bases (perennial plants and cheatgrass, minimum gap size 25 cm). This method has been promoted as an important tool for functional assessment of rangelands because it describes exposed soil (and thus the extent of erosion potential) in terms of the *arrangement of plant bases* (Herrick et al. 2006) rather than merely the total proportion of uncovered soil in an area. Large basal gaps have been correlated with decreased soil stability in a Chihuahuan Desert rangeland in Arizona (Bestelmeyer et al. 2006). Soil surface stability was rated qualitatively according to Resource Retention and Soil Redistribution Classes (RRC, and SRC respectively). RRC describes the extent of vegetation patch fragmentation (related to nutrient and water retention and erosion prevention) and SRC describes the degree of surface erosion and deposition (Burkett et al. 2011).

In addition to recording distance to water and LPI dung hits, we also conducted interviews with producers to determine historic and current grazing/browsing intensity and timing of livestock and wildlife. These data are still being processed and will be used to further refine the results described here.

### **Data Manipulation**

Each treatment was treated as a unique binary variable. Aspect was transformed following Beers et al. (1966) into a continuous variable where the largest values are associated with most productive northeastern slopes and lowest values for southwestern slopes. Hillslope position was given a score from 1-5 (1 = summit, 5 = toe-slope). Soil attributes in the first three horizons were used for analysis, as at least three horizons were present in all soils. Field texture

groups were assigned a numerical value according to the median percent clay value associated with that group. Structure was given a score from 1-4 (1 = single grain, 2 = granular, 3 = blocky, and 4 = subangular blocky). Hue was excluded from analysis, since all soils exhibited the same hue; chroma was excluded due to difficult interpretation. Qualitative field textures were given the median percent clay value associated with that texture type (e.g., clay loam soils range from 27-40% clay, and were given a texture value of 33.5 % clay). Basal gap data were binned at 25-50 cm, 50-100 cm, 100-200 cm, and 200+ cm gaps. A correlation matrix of soil and site characteristics, treatment, and functional indicator variables was created and highly correlated variables ( $r > 0.75$ ) removed from the suite of explanatory co-variates (although they were examined explicitly in sub-analyses to describe plant association structure). The following variables were removed: shrub cover, and sagebrush cover (each correlated with the Burn treatment), percent rock fragments in the 3<sup>rd</sup> soil horizon (correlated with fragments in 2<sup>nd</sup> horizon), gaps size 50-100 mean gap size (correlated with gaps size 100-200); Pedoderm Class and Year were almost perfectly correlated ( $r = 0.9$ ) and both were eliminated. The remaining variables were standardized as z-scores. LPI percent cover values were square root transformed to reduce the influence of very common species, and species occurring in fewer than 5% of plots (i.e., those found in a single plot) were omitted to reduce noise (McCune and Grace 2002, Kachergis et al. 2012).

#### *Step 2d: Analyze Empirical Data and Revise Draft STM with Quantitative Results*

All analyses were performed in R (version 0.98.1028, The R Foundation for Statistical Computing) using the packages cluster (Maechler et al. 2015), indicpecies (De Caceres and

Jansen 2015), vegan (Oksanen et al. 2011), and glmnet (Friedman et al. 2015). Data analysis and STM creation involved four stages:

#### Analysis Stage 1)

Determine the major abiotic gradients in the study area and appropriate ecological resolution (R1).

*This step identifies the extent of abiotic variation across study area, and clarifies whether this variation is adequately described by one or multiple STMs.*

#### Analysis Stage 2)

Determine what compositionally distinct plant associations exist in the study area.

*This step identifies the structural patterns that exist across the study area.*

#### Analysis Stage 3)

Determine which associations are functionally distinct states (R3) and which are functionally similar communities within states (R2).

*This step classifies plant associations as either states or communities for the STM.*

#### Analysis Stage 4)

Determine the relative extent to which static versus dynamic site attributes and past disturbances explain structural patterns (H4(a));

*This step reveals changing patterns in ecological function (dynamic abiotic attributes) and triggers (natural and management disturbances) which may influence state-transitions; it also reveals whether environmental gradients alone (static abiotic attributes) can explain structural patterns.*

#### Analysis Stage 5)

Explore the specific effects of management treatments on association structure (H4(b-f)). *This step elucidates the specific structural effects of past management actions.*

### **Analysis Stage 1: Determine Major Abiotic Gradients and Appropriate Ecological**

#### **Resolution (R1)**

Nonmetric Multidimensional Scaling (NMS; Kruskal 1964) using Euclidian distance was used to qualitatively explore the primary abiotic gradients that exist across the plots sampled, and the extent to which these gradients differentiate ecological sites. NMS is an indirect, unconstrained ordination method that proceeds from ranked distances between sample units to generate a rank linear relationship between distances in the original data space (in this case soil and site attributes) and distances in ordination space. Sample units plotted closer to each other in ordination space thus exhibit similar soil and site attributes. The significance of correlation between these attributes and the NMS axes was determined using a permutation test (1,000 permutations) using p-values adjusted according to the modified Bonferroni method of Hommel (1988) ( $\alpha = 0.05$ ). Correlated attributes were plotted as vectors whose length and direction describe the magnitude and direction of relationship to sample units, allowing the distribution of sample units along the primary abiotic gradients in the study area to be portrayed. When sample units in NMS are identified by ecological site, it is possible to qualitatively assess the extent to which these gradients differentiate ecological sites.

NMS runs were performed from random starts and convergent solutions identified by comparing Procrustes residual mean square errors to a convergence criterion of 0.005. To determine the number of dimensions to use for the NMS ordination, first a Monte Carlo test was performed using 100 runs each on observed and randomized data for each number of dimensions from 6 to 1, and the minimum stress for each run at each dimension determined. A p-value was computed for each dimension as the proportion of randomized runs resulting in minimum stress equal to or lower than the minimum stress observed in the true dataset for that dimension. The dimensionality selected was that a) which resulted in the lowest MC p-value, b) beyond which reductions in stress were < 5%, and c) at which the minimum stress in observed data was less than the minimum stress in all randomized runs at that dimension (McCune and Grace 2002).

Multiple Response Permutation Procedure (MRPP) was used to determine whether ecological sites differ significantly in terms of static site and soil attributes, species cover, and species composition by mass. MRPP is a non-parametric test of the null hypothesis of no difference between groups, similar to multiple analysis of variance (MANOVA). MRPP proceeds from a distance matrix and computes the sum of the mean distances within each group weighted by the proportion of sample units in that group. This observed weighted mean within-group distance ( $\delta_{\text{observed}}$ ), is smaller the more tightly clustered a group is. Next the distribution of the expected weighted mean within-group distance ( $\delta_{\text{expected}}$ ) is determined by iterative permutations of the sample units among the number of groups. The probability of a Type I error (analogous to a p-value) is computed based on the proportion of permutations yielding  $\delta_{\text{expected}} < \delta_{\text{observed}}$ . As with parametric tests, the likelihood of a significant p-value increases with

sample size, so an n-independent measure of effect size is also necessary. For MRPP, the effect size A can be computed as:  $1 - (\delta_{\text{observed}} / \delta_{\text{expected}})$ ; when  $\delta_{\text{observed}}$  is small (indicating tight clustering of groups), the effect size is large. Significance was evaluated at  $\alpha = 0.05$  using Hommel (1988) adjusted p-values.

## **Analysis Stage 2: Determine Compositionally Distinct Plant Associations**

Agglomerative Hierarchical Cluster Analysis (AHCA; Bray-Curtis distance measure and the flexible beta linkage method,  $\beta = -0.25$ ) was used to determine plant associations based on absolute cover by species using the LPI cover dataset. ACHA begins with n groups, where n is the number of sample units (plots), and iteratively combines (“agglomerates”) them into fewer, larger groups based on their dissimilarity to one another. Each time the number of groups is reduced, the distances between groups increase and the amount of information remaining decreases. At each iteration, attributes associated with sample units in a group are merged and used to compute a new distance matrix, which is then used to further merge groups. This process continues until all groups are merged. This process can be displayed as a dendrogram, illustrating the nested (“hierarchical”) groups and distances at each iteration. This diagram then must be “pruned” to select the appropriate number of groups.

The distance measure used to determine dissimilarity between sample units and the linkage method employed to merge groups greatly influence the resulting dendrogram. Some linkages tend to contract the space between groups (e.g., single linkage or “nearest neighbor”) others tend to be space expanding (e.g., complete linkage or “farthest neighbor”). One of the few space conserving linkage methods is Ward’s method which merges groups so as to

minimize the increase in variance within the new group after merging. However, Ward's method is not compatible with Bray-Curtis distance measures, which are often used to create the distance matrix for vegetation data because it avoids the "double-zero" problem (that is, inability to quantify extent of dissimilarity between sample units associated with absent species) common with Euclidian distance measures. The flexible beta method allows the user to define the linkage parameter somewhere between complete and single linkages, and  $\beta = -0.25$  has been shown to give results similar to Ward's method (Lance and Williams 1967). Thus, ACHA was performed using the Bray-Curtis distance measure and the flexible beta linkage method at  $\beta = -0.25$ .

Indicator Species Analysis (ISA) was used to prune the cluster dendrogram, such that the resulting groups contained the maximum number of significant indicator species (Dufrene and Legendre 1997). ISA aims to quantify the extent of species' faithfulness and exclusivity to groups. A species which is a perfect indicator of a group will be both faithful (always present in plots in that group) and exclusive (not present in plots in any other groups). Exclusivity (A) of a species to a group is computed as the relative abundance (or concentration of abundance) of a species in that group; faithfulness (B) is computed as the proportion of sample units within a group that contain the species. An indicator value (IV) for each species in each group is computed as the product of  $A \times B$  expressed as a percentage. The greater the indicator score for a given species in a given group, the more indicative that species is of that group, where 100% is a perfect indicator. Species are then assigned as indicators to the group for which they hold the highest indicator value (IV<sub>max</sub>); thus a species may only be an indicator of a single group. The significance of these assignments is then tested using a Monte Carlo permutation test,

whereby sample units are randomly assigned to groups and the IVmax for each species computed over 1,000 permutations. The probability of a Type I error for species assignment as an indicator species to a group is computed as the proportion of times that the IVmax for that species in that group in the randomized datasets is greater than its IVmax in the true dataset. If this proportion was less than  $\alpha = 0.05$  the observed IVmax was considered significant.

IVmax value (and thus the significance of a given species as a group indicator) is strongly influenced by the number of groups used. IVmax values computed from many, small groups will tend to be low because exclusivity of species to any given group is unlikely; likewise, IVmax values computed from a few large groups will be low as a result of high within-group heterogeneity in species abundances (i.e., low fidelity scores). Dufrene and Legendre (1997) demonstrated that IVmax values peak at some intermediate number of clusters. Thus, ISA results can be used to prune the AHCA dendrogram such that the number of clusters (groups) is that which returns the greatest number of significant indicator species, the highest mean p-value, or both (McCune and Grace 2002).

### **Analysis Stage 3: Determine Functionally Distinct States and Functionally Similar Communities**

MRPP was used to determine 1) which AHCA clusters chosen using ISA differ significantly in species composition and 2) which compositionally distinct plant communities differ significantly in functional attributes. Two suites of functional attributes were used over two MRPP tests: 1) belowground functional attributes (perennial basal cover, litter cover, bare ground cover, resource retention class, soil redistribution class, extent of basal gaps by sizes 25-

50 cm, 100-200 cm, and 200+cm, soil color value, and percent clay in the first three horizons) and 2) percent cover by plant functional groups (shrub, perennial forbs (all are native), native annual forbs, exotic annual forbs, legumes, exotic perennial grasses (only one species, *Agropyron cristatum*), native perennial bunchgrasses, native rhizomatous grasses, and annual grasses (only one species, *Bromus tectorum*, after rare species were removed). Clusters that significantly differed in both function (one or both suites of variables) and composition were considered states, while those that differed only compositionally were considered equilibril communities within a state.

#### **Analysis Stage 4: Determine the Relative Roles of Static versus Dynamic Attributes in Differentiating Plant Associations (H4(a))**

NMS was used to illustrate the dissimilarity of plots and communities/states with respect to plant species composition and the extent to which this dissimilarity is related to explanatory variables (i.e., site characteristics and management history). Because NMS does not require any assumptions about the distribution of cover data relative to the explanatory variables measured and preserves distances in species and ordination space, it avoids the “zero truncation problem” whereby we lack information on the extent of un-favorability of environmental variables beyond a species’ range. In addition, because it is not constrained to the environmental variables measured, NMS will allow us to identify any trends in species composition not explained by site variables collected (McCune and Grace 2002). The Bray-Curtis distance measure was used because it avoids the double-zero problem and because it has been used successfully by others in community ecology analyses (McCune and Grace 2002). NMS

runs and dimensionality selection proceeded as described above. To identify potential transition drivers and site characteristics influencing plant association, site attributes and management history significantly correlated with NMS were plotted as vectors whose length and direction describe the strength and direction of relationship to NMS axes.

Multinomial Logistic Regression performed with a Least Absolute Shrinkage and Selection Operator (LASSO) was used to determine the relative explanatory power of static abiotic soil (horizon characteristics) and site attributes (e.g., Elevation, Slope, Landform) versus management history (past burns, seeding, mechanical treatments) and dynamic site attributes (distance to road, distance to sagebrush, distance to water, soil redistribution class). LASSO selects the best predictor variables to include in the regression model by constraining the sum of the magnitudes of the model coefficients while minimizing sums of squares. K-factor cross validation was used to select the shrinkage factor that produced a cross-validated model with mean squared prediction error within one standard error of all predictions. If static abiotic attribute coefficients in the final models are the strongest (i.e., greatest magnitude) predictors of a state, it is possible that data were collected at too broad a spatial scale to inform a single STM; that is, sites with very different potentials are being inappropriately assumed to exhibit the same plant community dynamics. However, if management and/or dynamic site attributes are strong predictors of states, other factors such as management actions or competitive interactions have a greater influence on plant association than environmental gradients, in which case the sampling scale is probably appropriate.

## **Analysis Stage 5: Explore Effects of Past Treatments on Association Structure (H4(b-f))**

Treatment effects on plant association composition and structure were explored using one-way ANOVA or the nonparametric Kruskal-Wallis rank sum test for univariate tests and MRPP for multivariate tests; significance was assessed at the 0.05 level using p-values adjusted according to Hommel (1988).

### EMPIRICAL RESULTS

Results presented here focus on quantitative analysis of empirical field data (Step 2c in Figure 1.1).

#### *Environmental Gradients and Ecological Resolution (R1)*

Of the 59 plots sampled, 39 were determined to be Rolling Loam and 15 were determined to be Sandy Land; 5 plots did not fit either ecological site and were determined to be Claypan, characterized by the existence of clay or clay loam textures throughout the entire soil pedon. The site and soil attributes associated with each ecological site sampled are summarized in Table 2.3.

NMS explained differences in site and soil attributes along three axes (59 plots, 19 attributes; final stress = 14.8, two convergent solutions found after three tries, Procrustes rmse < 0.001). The proportion of variation in dissimilarity explained by ordination distance was 0.98. Figure 2.2 plots the Soil/Site NMS results on three axes, with plots identified by plant association; significantly correlated site and management history attributes are overlaid as

vectors whose direction and length indicate the direction and magnitude of relationship with NMS axes. The  $p$  and  $R^2$  values for these correlations are provided in Table 2.4.

Not surprisingly, given how ecological sites were distinguished, ecological site distribution across the study area follows a strong texture gradient, with Rolling Loam and Claypan plots generally exhibiting greater clay in all three soil horizons than Sandy Land plots (all horizons:  $p = 0.003$ ,  $R^2 > 0.5$ ); a gradient in structure parallels this texture gradient (all horizons:  $p < 0.005$ ,  $R^2 \sim 0.3$ ). The texture/structure distinction between sites is not complete, however: Rolling Loam plots are intermixed with Sandy Land plots at the low end of the texture gradient and with Claypan at the upper end. Ecological sites do not appear to be well distinguished in terms of topography. There is a strong elevation gradient across the plots sampled ( $p = 0.003$ ,  $R^2 = 0.61$ ), which appears to correspond positively with slope ( $p = 0.004$ ,  $R^2 = 0.32$ ), soil rockiness (Frag1 and Frag2;  $p = 0.003$ ,  $R^2 > 0.44$ ), and third horizon thickness ( $p = 0.003$ ,  $R^2 = 0.51$ ) and negatively with downslope landform ( $p = 0.003$ ,  $R^2 = 0.34$ ). However, all three ecological sites are relatively evenly distributed along these gradients. There also exists a gradient of lower hillslope positions with darker soils (larger hillslope value, low color value) to higher hillslope positions with whiter soils (lower hillslope value, higher color values); this gradient makes pedologic sense, since one would expect more pedogenic clay development and greater deposition of clay and organic matter on lower hillslope positions. However, all the three ecological sites are distributed across the hillslope/value gradient, and thus it does not explain differences in ecological sites.

Results of MRPP tests for differences among ecological sites with respect to soil and site attributes, cover composition, and composition by mass are shown in Table 2.5. In all three tests, all three sites were statistically significant ( $p \leq 0.05$ ); however, all effect sizes were very small ( $< 0.07$ ).

#### *Plant Communities and States (R2, R3)*

Four clusters provide the maximum number of significant indicator species (20) and the minimum mean p-value (0.1). Figure 2.4 shows the AHCA cluster dendrogram pruned to 4 clusters and the resulting ISA groupings. Table 2.6 shows the significant Indicator Species, their Exclusivity (A) and Fidelity (B) scores, and p values. Figure 2.3 shows species composition of each state; only those species comprising at least 5% cover in at least one of the four states are shown.

Vegetative cover in Cluster 1 (12 plots) is dominated by *A.t. wyomingensis*, native bunchgrass *Hesperostipa comata*, and exotic annual *Bromus tectorum*. Every plot in Cluster 1 has *H. comata* (A = 0.37, B = 1.00) and *Bromus tectorum* (A = 0.33, B = 1.00) present, and nearly every plot had animal dung LPI hits (A = 0.51, B = 0.92). Other indicators of Cluster 1 include native bunchgrasses *Achnatherum hymenoides* (A = 0.74, B = 0.67), *Elymus elymoides* (A = 0.46, B = 0.83), and native forbs *Comandra umbellata* (A = 0.61, B = 0.67) and *Epilobium brachycarpum* (A = 0.87, B = 0.33).

Cluster 2 (15 plots) lacks a minimum of 5% cover for any shrubs and has very little *B. tectorum* cover (mean cover 4%) and thus can be considered a native grassland. Always present in Cluster 2 are the native rhizomatous grass *Pascopyrum smithii* (A = 0.54, B = 1) and native

bunchgrass *Poa secunda* (A = 0.33, B = 1), and together with *H. comata* these three grasses are the primary cover species in Cluster 2. Other indicators in Cluster 2 are the native forbs *Sphaeralcea coccinea*, also perfectly faithful (A = 0.46, B = 1) and *Trifolium gymnocarpon* (A = 0.76, B = 0.33).

The exotic bunchgrass, *Agropyron cristatum*, is a nearly perfect indicator of Cluster 3 (6 plots) (A = 0.91, B = 1) and provides 41% cover. The remaining vegetative cover is provided primarily by *A.t. wyomingensis* (16% cover). *Astragalus drummondii* is a significant indicator of Cluster 3 (A = 0.6996, B = 0.3333) but exhibits < 5% cover.

Cluster 4 (26 plots) has nine significant indicator species and is the only cluster to contain shrubs as indicator species. The highly-palatable native shrub *Purshia tridentata* is a near perfect indicator of Cluster 4, occurring in no other clusters and nearly all Cluster 4 plots (A = 1, B = 0.92), and provides 8% cover; *Artemisia tridentata* is the dominant shrub and primary cover species (A = 0.39, B = 0.96, 25% cover); *Chrysothamnus viscidiflorus* is also a significant indicator species with near perfect fidelity to Cluster 4 (A = 0.50, B = 0.92) but provides less than 5% cover. Five additional indicator species are present at less than 5% cover: native bunchgrasses *Komandra macrantha* (A = 5.1, B = 0.88) and *Pseudoroegneria spicata* (A = 0.78, B = 0.54), native forbs *Eriogonum corymbosum* (A = 0.55, B = 0.77), *Allium acuminatum* (A = 1, B = 0.27), and the exotic annual forb *Alyssum desertorum* (A = 0.35, B = 1). A variety of native bunchgrasses also contribute substantial cover, including *H. comata* (20%), *P. secunda* (14%) and *P. smithii* (8%); *B. tectorum* is also present at 12% cover.

All clusters are significantly different with respect to absolute cover by species (in all cases  $p = 0.001$ ) at a moderate effect size ( $A$  ranges from 0.10 to 0.22) (Table 2.7); thus, we may regard all four clusters as compositionally distinct plant associations. With respect to soil and site functional variables, only the comparison of Cluster 4 with Clusters 1 and 3 were significant at the 0.05 level ( $p = 0.005$ ); however all other comparisons gave a  $p$ -value of 0.06, which is nearly significant; all effect sizes for the soil function comparisons were very small ( $A < 0.08$ ) (Table 2.8). With respect to plant functional groups, all clusters are significantly different at  $p = 0.001$  (Table 2.8); all cluster comparisons exhibit moderately high effect sizes for differences in functional group composition (all  $A > 0.2$ ) except for Cluster 1 vs. 4 ( $A = 0.08$ ).

#### *The Roles of Static and Dynamic Attributes in Differentiating Plant Associations (R4)*

Other than Cluster 3 (the cluster indicated by crested wheatgrass dominance), which only appears on plots keyed as “Rolling Loam”, no cluster is exclusive to any single site, suggesting that the Rolling Loam site may explain a tendency for crested wheatgrass persistence (Figure 2.9). However, the overall lack of distinction among ecological sites with respect to clusters suggests that differences in abiotic features between keyed ecological sites do not result in differences in plant association.

NMS explained differences in cover by species along three axes (59 plots, 49 species; final stress = 13.2, two convergent solutions found after three tries, Procrustes  $rmse < 0.001$ ) (Figure 2.5). The primary treatments explaining cover by species in NMS space were Burning ( $R^2 = 0.81$ ), which primarily explained Cluster 2, the presence of old Homesteads ( $r^2 = 0.48$ ), which primarily explained Cluster 3 plots, and post-burn Seeding ( $R^2 = 0.35$ ), the lack of which

primarily explained Cluster 4. No mechanical treatments were significantly correlated to NMS axes at the 0.05 level (drag  $p = 0.8$ , mow  $p = 0.3$ , Mechanical (any)  $p = 0.4$ ) (Table 2.9).

Several aggregate metrics derived from LPI were included to better understand structural trends in plant associations. Cluster 4 exhibits the greatest foliar cover ( $R^2 = 0.51$ ) while Cluster 3 is associated with greater bare ground ( $R^2 = 0.33$ ) and more extensive coverage of relatively large basal gaps in the 100-200 cm size range ( $R^2 = 0.32$ ).

LASSO and k-factor cross-validation for the multinomial logistic regression of plant association against site attributes and management history selected the model providing MSPE within one standard error using a shrinkage factor of  $\lambda = 0.05$ . Cluster 1 was primarily predicted by Landform (2.3) and by mow treatment (0.8), with very small contributions by Elevation (-0.01) and Distance to Road (0.003). Burn treatment alone was the best predictor of Cluster 2 (4.0). Cluster 3 was predicted entirely by the existence of old Homesteads (5.9). The predictors of Cluster 4 were all static properties with relatively low coefficient magnitudes: Horizon 1 Rock Fragments was the strongest predictor (0.2), with some contribution from Elevation (0.01), Distance to Road (-0.004) and Horizon 2 Rock Fragments (0.007) (Table 2.10).

#### *Treatment Effects on Association Structure (H4 b-f)*

Each of the five treatments resulted in significantly different species composition, both by cover and by mass (Table 2.11). The effect sizes for contrasts against the control and for the contrast between burned/seeded and burned/not seeded treatments were very small ( $A < 0.1$ ). Contrasts including the drag treatment exhibited the strongest effect sizes.

No statistically significant differences were observed between mechanically treated and control plots with respect to herbaceous cover, grass cover, shrub cover, forb count, or species richness, although herbaceous cover was significant at the  $\alpha = 0.1$  level; forb cover was actually lower in the mechanically treated plots compared to controls ( $p = 0.02$ ,  $\mu_{\text{mechanical}} = 12\%$ ,  $\mu_{\text{control}} = 22\%$ ) (Figure 2.7). Mow and drag treatments did differ significantly however: drag treatments had greater forb cover ( $p = 0.01$ ,  $\mu_{\text{drag}} = 19\%$ ,  $\mu_{\text{mow}} = 7\%$ ), forb diversity ( $p = 0.01$ ,  $\mu_{\text{drag}} = 9$ ,  $\mu_{\text{mow}} = 6$ ), species richness ( $p = 0.02$ ,  $\mu_{\text{drag}} = 33$ ,  $\mu_{\text{mow}} = 27$ ) and shrub cover ( $p = 0.01$ ,  $\mu_{\text{drag}} = 40$ ,  $\mu_{\text{mow}} = 20$ ); there was no difference in total herbaceous or grass cover between mow and drag treatments (Figure 2.6).

To determine whether one of the two shrublands represents a depauperate, decadent state, the Clusters 1 and 4 were compared in terms of herbaceous, grass, forb and sagebrush cover, shrub height, forb count and species richness (Figure 2.7). Cluster 4 exhibits significantly greater mean shrub height ( $p = 0.02$ ,  $\mu_{\text{CIG}} = 42$  cm,  $\mu_{\text{DS}} = 50$  cm) but also greater total herbaceous cover ( $p = 0.05$ ,  $\mu_{\text{CIG}} = 136\%$ ,  $\mu_{\text{DS}} = 153\%$ ), and forb cover ( $p \ll 0.001$ ,  $\mu_{\text{CIG}} = 9\%$ ,  $\mu_{\text{DS}} = 21\%$ ). There were no significant differences in sagebrush cover, grass cover, forb count or species richness between the two states.

*Bromus tectorum* cover was higher in unburned plots compared to burned plots ( $p = 0.005$ ,  $\mu_{\text{burned}} = 6\%$ ,  $\mu_{\text{unburned}} = 11\%$ ); there was no difference detected in *B. tectorum* cover between seeded and unseeded plots ( $p = 0.4$ ) (Figure 2.8).

## DISCUSSION

### *Major Abiotic Gradients and Ecological Resolution (R1)*

The Interagency Ecological Site Handbook for Rangelands, which provides official guidance for ESD development, defines an ecological site as “a distinctive kind of land based on recurring soil, landform, geological, and climate characteristics that differs from other kinds of land in its ability to produce distinctive kinds and amounts of vegetation and in its ability to respond similarly to management actions and natural disturbances” (Caudle et al. 2013). Thus distinct ecological sites are expected to differ distinctly in terms of: a) soil, landform, geology, and climate; b) the species present and their abundance (i.e., in terms of cover, density, and/or mass); c) response to management and disturbance.

While the Monte Carlo tests performed found statistically significant differences among the three keyed ecological site types in terms of soil and site attributes and species cover (Table 2.5), the effect sizes of these differences are so slight as to make the differences indistinct. The Cluster 3 (Crested Wheatgrass state) plots were found to be exclusive to the Rolling Loam ecological site (Figure 2.9), but this may not reflect an influence of the Rolling Loam site characteristics. All Cluster 3 plots occurred on old homesteads, and all old homesteads sampled happen to have occurred on the Rolling Loam ecological site. The relationship between site and state may thus be coincidental: we cannot conclude that the ecological site is responsible for the persistence of crested wheatgrass. Indeed, crested wheatgrass has been found to be very persistent on a variety of ecological sites (Fansler and Mangold 2011).

There is also little evidence that ecological site influenced disturbance response. Burns tended to result in the Grassland state, while all mowed plots presented as Cheatgrass-Invaded Shrubland and dragged plots as Sagebrush-Bitterbrush Shrubland (Table 2.6), yet in all cases these states existed across two or more ecological sites (Figure 2.9).

Thus, the soil, site, and vegetation attributes, and disturbance responses of the study area are sufficiently similar to reasonably represent these dynamics in a single STM (Figure 2.20). This decision is consistent not only with the ecological site literature, but also with the needs and perspectives of land managers and producers, who make decisions at broader scales than those at which subtle variations in soil texture, elevation, slope, and landform occur within the study area. These small-scale “meso-gradients” appear to influence plant community composition and disturbance response at very local scales within the study area, and similar dynamics have been observed by others (e.g., Kachergis et al. 2012, Bestelmeyer et al. 2006). By making these relationships explicit, we highlight areas of remaining uncertainty that can be investigated in future sampling efforts, adaptive management experiments, and targeted interviews with knowledge-holders.

### *Communities (R2) and States (R3)*

Plant composition of the study area can be described in terms of four compositionally distinct plant associations (Tables 2.6 and 2.7): Cheatgrass-Invaded Shrubland (Cluster 1), Native Grassland (Cluster 2), Crested Wheatgrass association (Cluster 3), and a Sagebrush-Bitterbrush Shrubland (Cluster 4).

Soil functional attributes failed to fully distinguish all four associations, and the effect sizes of any differences were very slight. That plant functional group composition produced both statistically significant differences and large effect sizes for all but one of the comparisons suggests that the groups do function differently; however the quantitative metrics used did not fully capture all functional differences, especially in terms of specific abiotic functional attributes. The low effect size for the plant functional group difference between the Cheatgrass-Invaded and Sagebrush-Bitterbrush Shrublands suggests that the two communities function very similarly and represent two communities within a single state (Table 2.8).

One alternative to the quantitative soil functional metrics used may have been the qualitative Indicators of Rangeland Health. Kachergis et al. (2011) found that IRH were significantly correlated with many of the quantitative attributes used here and significantly distinguished plant associations in a mesic Claypan ecological site, although they do not report effect sizes for these differences. IRH define rangeland health in terms of soil and site stability, hydrologic function, and biotic integrity, and relate these to 17 qualitative structural attributes evaluated in the field according to their extent of deviation from reference conditions (Pellant et al. 2005). IRH can be faster to conduct in the field than direct functional measurements, but IRH can also be very subjective and thus should be conducted by one consistent observer (Pellant et al. 2005), which may ultimately limit sampling team efficiency. In addition, IRH are not intended for long-term monitoring because they are not necessarily repeatable, providing only a snapshot of functional characteristics of a site at a given time (Pellant et al. 2005). It is for this reason we chose not to use IRH, opting to quantify function more directly (i.e., via basal gap size distribution, bare ground percentage, soil texture and value, perennial basal cover) because

these metrics can be used for ongoing monitoring, are more objective, were (with the exception of basal gap) already being collected in the course of determining ecological site and LPI cover, and are useful for investigating other responses, including wildlife patterns. However, these metrics do not address the full suite of functional attributes considered by IRH, and thus may have made it more difficult to distinguish functional differences among communities.

#### *Influences of Static vs Dynamic Environmental Attributes and Past Management on Associations (R4)*

Logistic regression with LASSO revealed that both past management and static abiotic variables were necessary to predict plant associations (H4(a); Table 2.10). The texture/structure/horizon-thickness gradient distinguishing Sandy Land from Rolling Loam/Claypan ecological sites (Figure 2.2) did not significantly predict any plant community associations (Table 2.10). This supports the decision to include all ecological site types encountered in a single STM. Past treatment alone was sufficient to predict both Native Grassland (predicted by past burns) and Crested Wheatgrass (predicted by past homesteads), demonstrating that management actions can override the influence of meso-gradients. The elevation/landform gradient, which does not distinguish ecological sites but remains a strong a meso-gradient within the STM (Figure 2.1), is the primary influence distinguishing the two shrublands. Sagebrush-Bitterbrush Shrublands were exclusively found on steep, rocky hills and hillslopes, typically at higher elevations, while the Cheatgrass-Invaded Shrubland was limited to lower elevations and could be found on piedmont landforms in addition to hills and hillslopes (Figure 2.5, Table 2.9).

Is the differentiation of the two shrubland types truly driven by differences in elevation and slope, or does their correlation with this gradient indicate some unmeasured driver? *P. tridentata* is exclusive to the higher-elevation Sagebrush-Bitterbrush Shrubland (Table 2.6), yet it is known to occur over a range of elevations much wider than that of our study area (1,219 m – 2,590 m). Model revision workshops with project participants in 2015 revealed that *P. tridentata* once existed in low elevation shrublands, dramatically declined over the past 50+ years, and is now absent. Thus, something other than elevation must be driving the persistent loss of *P. tridentata* from the areas characterized as Cheatgrass-Invaded Shrubland. Two proposed drivers of *P. tridentata* loss are 1) historical long-term, intensive grazing by sheep and 2) increased elk browsing pressure. Project stakeholders report that both of these factors appear to have been present on the low-elevation shrubland plots sampled, while most of the higher elevation plots sampled were historically grazed by cattle and have not experienced increases in elk browsing pressure. Interestingly, indicator species analysis of LPI cover data, which included animal dung as a soil surface hit, revealed animal dung cover to be a significant indicator of the Cheatgrass-Invaded Shrubland sites, with a fidelity score of 0.92 indicating animal dung was almost always found in this shrubland type. The project is currently working to process and analyze specific historic and current livestock use data from producer stakeholders and elk use pattern data from the Colorado Department of Parks and Wildlife to improve our understanding of the factors differentiating the two shrubland types.

### *Treatment Effects (H4 b-f)*

All treatments appeared to have a significant effect on species composition both by cover and by mass (H4(b)), although in several cases the effect size was so small ( $A < 0.1$ ) as to render these differences negligible (Table 2.11). Small samples sizes and an unbalanced sampling design mean that any trends in treatment differences should be interpreted as preliminary. Small effect sizes for differences between the burn-no-seed and burn + seed treatments may suggest that seeding after burning makes no difference 15+ years later. Likewise, small effect sizes for comparison of the control to the mow and drag areas, along with the lack of strong differences in understory cover between the control and mechanical group as a whole, suggest that community composition recovers within 15 years after these treatments.

More compelling are the structural differences between the drag and mow treatments (H4(c); Figure 2.6). The drag treatment has been advocated as an alternative to mowing sagebrush that is less destructive of sagebrush while also improving forb cover and diversity, both of which could benefit sage-grouse brood rearing success while also improving herbaceous cover to benefit livestock producers. Dragged areas did indeed exhibit greater forb diversity and overall species richness and double the forb and shrub cover compared to mowed areas, with no difference in grass or overall herbaceous cover. Thus dragging may be a promising less-destructive shrub treatment for improving both the quantity and variety of herbaceous species. However, these patterns are only preliminary and may not be due only to treatment effects, as the two treatments also occur on ranches with different management histories. All mow plots occurred on a single ranch found in the lower end of the elevation range of the study area

(1,962-2,003 m) that has historically run sheep and recently experienced a dramatic increase in winter use by elk; all drag plots occurred on a single higher elevation ranch (2,123-2,152m) that has historically run cattle and has not experienced the same increase in elk use.

At the initial STM building workshop, participants had proposed the existence of a sagebrush shrubland state consisting of “decadent” sagebrush and a “depauperate” understory that developed in the absence of shrub control or fire. They described this state as exhibiting the tallest, most expansive sagebrush and a sparse herbaceous understory. However, none of the distinct plant associations revealed in our analyses meet this description. Of the two shrubland associations identified, the Sagebrush/Bitterbrush shrubland has taller shrubs on average than the Cheatgrass-Invaded Shrubland, but is no different in terms of sagebrush cover and presents significantly greater total herbaceous and forb cover (Figure 2.7).

Moreover, it is worth noting that ISA revealed that the Sagebrush/Bitterbrush Shrubland contains more native indicator species than any other association, including three species with exclusivity scores greater than 0.75, suggesting that this association supports species rarely found elsewhere in the study area. This state is also not associated with any particular past treatment. Thus, the Sagebrush/Bitterbrush shrubland may bear a closer resemblance to an historical reference community than any other (Table 2.6).

Contrary to initial expectation, unburned plots exhibited more cheatgrass cover than burned plots (Figure 2.8). If we assume that the shrubland associations identified here represent the associations that existed prior to the burns studied, then it would appear that burning cheatgrass actually reduced, rather than perpetuated, cheatgrass cover. This is possible

given sufficient abundance and distribution of native perennial grasses after fire to deny cheatgrass access to soil resources (Chambers et al. 2007, Reisner et al. 2013, Chambers et al. 2014). Thus resistance of a sagebrush ecosystem to increased cheatgrass invasion after fire may depend on plant community composition prior to fire, as well as fire conditions (e.g., season, temperature, duration) which affect plant survival and thus post-fire plant community composition. Some studies suggested that overgrazing by domestic livestock, especially on coarser-textured soils, may limit the resistance of sagebrush shrublands to cheatgrass invasion by reducing native grass cover and biological soil crusts and increasing connectivity of plant interspaces in which cheatgrass can establish (Reisner et al. 2013, Chambers et al. 2014). We hypothesized that an increase in post-fire native seedbank may also improve resistance to cheatgrass invasion. However, no effect on cheatgrass cover was found for seeding with native grass species (Figure 2.8). It may be that intact native grasses and the existing seedbank were sufficient to outcompete cheatgrass seedlings, making additional seeding unnecessary, or it may simply be that low sample size for the seeding treatment ( $n = 6$ ) provided insufficient power to detect an effect.

## REVISED STM AND REMAINING UNCERTAINTY

### (Step 2d)

Results of analysis of empirical field data were integrated with knowledge-based model drafts to produce an STM (Figure 2.20). Black lines indicate transitions revealed in the above analysis, while red lines and text indicate remaining areas of uncertainty. Additional attributes and ecological services are summarized by plant association in Table 2.12.

A potential sagebrush shrubland reference state is proposed, comprised of two primary plant communities: a Sagebrush/Antelope Bitterbrush Shrubland that tends to occur on steeper, rockier hills and hillslopes at higher elevations and a Diverse Sagebrush Shrubland that lacks bitterbrush and tends to be found on gentler hillslopes and piedmonts at lower elevations. Because the effect sizes for soil and plant functional differences between these two communities were very small ( $A < 0.1$ ; Table 2.8) they are considered functionally similar communities which may occur within a single state. However, given the extent of current sampling, the two communities appear to occur at almost exclusive elevations, which would prevent them from intergrading. We suspect that elevation is correlated with livestock management and differences in elk grazing, and that long-term intensive sheep grazing and/or increases in winter use by elk may be responsible for the loss of antelope bitterbrush from the Sagebrush/Bitterbrush Shrubland. Thus, the two shrubland communities may not actually be separated by elevation differences but rather by differences in long-term domestic and wild animal use. Information about historic and current livestock and wildlife use patterns, derived from interviews with producers and managers, will be used to update the analyses described above and determine what role of animal type and use intensity may play in the differentiation of the two shrubland associations observed.

All plots mowed in the late 1990's were found to be the Cheatgrass-Invaded Shrubland state while all dragged plots are now Sagebrush/Bitterbrush Shrubland. Since, according to project stakeholders, the presence/absence of antelope bitterbush in the two shrublands predates the mechanical treatments applied, it appears that each shrubland has recovered from its respective mechanical treatment in fifteen years or less; whether this recovery time is

typical for mechanical treatments remains uncertain. However, due to the retrospective nature of the study no inferences can be drawn about the structure or function of plant communities in the first years after treatment; nor are there data regarding the effects of dragging on the Cheatgrass-Invaded Shrubland or mowing on the Sagebrush/Bitterbrush Shrubland. These uncertainties can be addressed with adaptive management experiments to directly study the effects of mow and drag treatments on understory composition and shrubland structure; long-term monitoring of such experiments can elucidate the recovery time and trajectory of each treatment. These treatments should be performed with sufficient replicates across the dominant gradients of the study area (i.e., the elevation-slope gradient and the texture-structure gradient) to eliminate confounding effects of abiotic situation on treatment response and recovery.

A Native Grassland State largely devoid of non-native species, including very low cheatgrass cover, appears to be associated with large wildfire. Workshop participants have confirmed that grassland areas were shrublands before fire, but are uncertain about the pre-fire cheatgrass cover. It is unclear whether cheatgrass was uncommon in the shrublands prior to fire, or whether wildfire actually reduced cheatgrass cover. This question could be addressed with adaptive management experiments that implement proscribed burns in sagebrush shrublands with and without extensive cheatgrass cover and monitor the short- and long-term cheatgrass response.

The conditions and time necessary to return post-fire grasslands to shrubland are uncertain, but because sagebrush recruitment depends on seed dispersal, regeneration time

will likely depend on proximity to unburned islands or the burn perimeter. Immediate post-fire seeding with *Artemisia tridentata* may increase sagebrush regeneration time (Eiswerth et al. 2009). The post-fire recovery time for sagebrush might be determined from active adaptive management experiments that implement prescribed burns coupled with seeding/non-seeding with sagebrush followed by long-term monitoring. An alternative approach might be retrospective monitoring of a chronosequence of past burns of different sizes and ages to determine the role of burn patch size on sagebrush recruitment and recovery, although the challenges of assumptions associated with chronosequences might limit the inference possible from such an approach (Johnson and Miyanishi 2008).

A state dominated by Crested Wheatgrass cover is associated with areas previously homesteaded and seeded to crested wheatgrass for pasture or reclamation. It is assumed that these areas had resembled the shrubland state prior to homesteading, but it is uncertain whether they can return to that state. Two of the six crested wheatgrass plots surveyed had burned in 2010 and were seeded with native grasses in 2011 but remained a crested wheatgrass monoculture. This may suggest that the crested wheatgrass state is very resistant and not easily restored to the assumed reference state. Work by others suggests this to be the case. Fansler and Mangold (2011) tested a variety of methods to suppress crested wheatgrass and revegetate with a mix of native species, but found them all to be largely ineffective at reducing crested wheatgrass cover and density. Wilson and Pärtel (2003) found that continued suppression of crested wheatgrass with herbicide or clipping after seeding reduced but did not eliminate crested wheatgrass cover. Adaptive management experiments could test the effectiveness of such treatments under the conditions specific to our eastern Moffat study area.

## CONCLUSION

The primary objective of this project was to apply the streamlined participatory STM-development approach proposed by Kachergis et al. (2013c) on Wyoming sagebrush-steppe in northwestern Colorado. Primary research questions identified by participants through this process centered on determining the effects of mechanical control, fire, and post-fire seeding on vegetation dynamics on the Rolling Loam and Sandy Land ecological sites in eastern Moffat County, CO. The data-driven STM presented here largely complements the states proposed in the original knowledge-driven draft STMs. This included the presence of a potential reference shrubland state comprised of multiple shrubland community types, a transition to grassland on large burned areas, and a persistent non-native grassland on old homestead lands. However, overall small sample sizes resulted in insufficient power to make many inferences about specific treatment effects based on field data alone, resulting in several areas of remaining uncertainty after two field seasons of data collection. However, by continuing to integrate local knowledge into successive data-driven STM drafts, we have been able to update project hypotheses and refine future sampling efforts to address these remaining uncertainties. For example, local knowledge of trends in increased elk winter use of sagebrush communities at lower elevations over the last four decades may help explain the existence of bitterbrush only at high-elevation sites in the study area, and elk tracking data provided by the Colorado Department of Wildlife may provide a data-driven approach to testing this hypothesis.

Some uncertainties can only be addressed with active adaptive management approaches, however. For example, we will need to implement new drag treatments in order to

understand their short-term effect on plant community structure. Continuous involvement of project stakeholders in STM critique and evaluation can facilitate implementation of successful adaptive management experiments that engage stakeholders in study design, treatment application and data collection. This has been the case for the planned drag experiment, which, as a result of stakeholder interest in the link between herbaceous diversity and insect populations available to sage-grouse brood, will investigate the effects of the drag on both the plant and insect community. Stakeholders were involved with planning this study and baseline data collection and will implement the drag treatment.

While involving a wide variety of project stakeholders and knowledge sources in STM development can ensure research questions and approaches are relevant to management, it also introduces some challenges to project logistics and statistical power. Hidden differences in short- and long-term management histories across a study area can confound sources of variation in treatment effects, making it difficult to produce a representative sampling design with sufficient power to answer all research questions raised by study participants. This challenge is made more difficult by a retrospective sampling design which necessarily fails to address varied and confounding climate and environmental conditions between treatment application and sampling time. Thus, to successfully answer stakeholder questions a participatory approach to research must also have a well-defined and narrow scope which proceeds iteratively, rather than with a single broad effort, to answer questions of interest.

STMs are conceptual tools for understanding and communicating plant community dynamics. As such, there is no single “correct” model. Rather, the utility of STMs lies in their

ability to reflect the management questions and values for which they are designed. This makes STMs well suited for a collaborative, multiple-knowledge based development process. The key to success of this process, then, is ensuring that field sampling efforts are focused enough and have sufficient power to provide substantial insights of interest to project stakeholders. This requires a balance between incorporating a variety of stakeholder perspectives and interests and targeting field activities to the most critical and logistically feasible research questions given limited resources.

**Table 2.1** Summary of treatment areas sampled in 2013 and 2014 in eastern Moffat County, Colorado.

Treatment	Treatment Area (ha.)	Treatment Year(s)	# Plots Sampled	Notes
Mow	174	1996	4	
Drag	44	1997, 1998	3	Two areas: 28.2 ha (1997), 15.2 ha (1998)
Burned, not seeded	4,184	2008, 2010	14	Part of the 2008 burn also burned in 1996 or 1997. Livestock grazing resumed within 2 years of fire.
Burned, seeded	506	Burned 2010, Seeded 2011	6	Livestock grazing resumed within 2 years of fire. Native Seed mix: <ul style="list-style-type: none"> <li>• Wyoming big sagebrush (<i>Artemisia tridentata wyomingensis</i>)</li> <li>• antelope bitterbrush (<i>Purshia tridentata</i>)</li> <li>• western wheatgrass (<i>Pascopyrum smithii</i>)</li> <li>• thickspike wheatgrass (<i>Elymus lanceolatus</i>)</li> <li>• indian ricegrass (<i>Achnatherum hymenoides</i>)</li> <li>• bluebunch wheatgrass (<i>Pseudoroegneria spicata</i>)</li> <li>• needle-and-thread grass (<i>Hesperostipa comata</i>)</li> </ul>
Control	NA	NA	32	

**Table 2.2** Attributes sampled in 2013 and 2014 in each 50 m x 50 m plot in eastern Moffat County, Colorado. Site and soil variables are split into two groups: static variables which are generally unchanging over long time-frames, and dynamic variables which are influenced by short-term management actions and disturbances.

<b>Site and Soil</b>	<b>Plant Species &amp; Production</b>	<b>Functional</b>
Static Elevation Slope Aspect Hillslope Position Thickness Texture† Structure Hue Value† Chroma % Rock Fragments Dynamic Distance to Water Distance to Sagebrush Distance to Road Soil Redistribution Class†	Species Richness Cover (Line Point Intercept) Composition by Mass (Dry Weight Rank) Total Standing Crops	<u>Soil Functional</u> Perennial Basal Cover* Litter Cover* Bare ground Cover* Basal Gap Length Resource Retention Class  <u>Functional Group Cover*</u> Shrub Perennial Forb (all native) Native Annual Forb Exotic Annual Forb Native Bunchgrass Native Rhizomatous Grass Exotic Bunchgrass Exotic Annual Grass
* Derived from LPI † Also a Functional Attribute		

**Table 2.3** Summary of site and soil characteristics of Sandy Land, Rolling Loam, and Claypan ecological sites sampled in eastern Moffat County, Colorado in 2013 and 2014. Structure rank: 1 = single grain, 2 = granular, 3 = blocky, 4 = subangular blocky

Attribute	Horizon	Sandy Land	Rolling Loam	Claypan
Elevation (m) (range)	--	1922 – 2155	1921 – 2165	1905 – 2119
% Slope (range)	--	2 – 18	2 – 19	2-10
Aspect (°) (range)	--	7 – 293	0 – 360	69 - 350
Thickness (cm) (mean ± SE)	1	6.8 ± 0.7	8.1 ± 0.6	4.6 ± 0.7
	2	41.5 ± 4.9	36.5 ± 2.1	37.8 ± 3.5
	3	38.1 ± 5.6	35.7 ± 1.8	35.2 ± 9.4
% Clay (mean ± SE)	1	9.5 ± 1.3	12.5 ± 1.3	14.3 ± 4.7
	2	15.8 ± 2.5	22.9 ± 1.8	42.3 ± 8.8
	3	10.5 ± 1.8	27.3 ± 2.2	42.3 ± 8.8
Structure (median)	1	2	4	4
	2	4	4	4
	3	4	4	4
Value (median, range)	1	4	4	4
	2	4	4	4
	3	4	4	4
% Rock Fragments (mean ± SE)	1	2.0 ± 1.0	4.5 ± 0.7	0.4 ± 0.24
	2	3.4 ± 1.6	4.6 ± 1.0	0.2 ± 0.20
	3	6.7 ± 3.6	6.2 ± 1.7	0.2 ± 0.20

**Table 2.4** Significance and  $R^2$  for correlation between NMS axes ordinated on soil and site attributes and those soil and site attributes sampled in 2013 and 2014 in eastern Moffat County, Colorado. P values are significant after Hommel (1988) adjustment ( $\alpha = 0.05$ ).

<b>Attribute</b>	<b>p</b>	<b>R<sup>2</sup></b>
Elevation	<0.01	0.61
Slope	<0.01	0.32
Aspect	<0.01	0.23
Hillslope	<0.01	0.27
Landform	<0.01	0.34
Thickness		
Horizon 1	<0.01	0.13
Horizon 2	<0.01	0.32
Horizon 3	<0.01	0.51
% Clay		
Horizon 1	<0.01	0.60
Horizon 2	<0.01	0.59
Horizon 3	<0.01	0.51
Structure		
Horizon 1	<0.01	0.29
Horizon 2	<0.01	0.38
Horizon 3	<0.01	0.34
Value		
Horizon 1	<0.01	0.46
Horizon 2	<0.01	0.35
Horizon 3	<0.01	0.43
% Rock		
Horizon 1	<0.01	0.54
Horizon 2	<0.01	0.44

**Table 2.5** Probabilities that abiotic and biotic differences between ecological sites in the study area in eastern Moffat County, Colorado in 2013 and 2014 are due to chance. Multiple response permutation procedure (MRPP) was used to test of the null hypothesis of no differences between groups with respect to in static soil and site attributes, absolute cover by species, and species composition by mass. P values in bold are significant after Hommel (1988) adjustment ( $\alpha = 0.05$ ). A represents chance-corrected within-group agreement and is considered a measure of effect size on a scale from 0 to 1.

Ecological Site	Sandy Land		Rolling Loam	
	<i>p</i>	<i>A</i>	<i>p</i>	<i>A</i>
<b>Static Soil and Site Attributes</b>				
Rolling Loam	0.004	0.02		
Claypan	0.003	0.06	0.02	0.02
<b>Absolute Cover by Species</b>				
Rolling Loam	0.03	0.01		
Claypan	0.02	0.05	0.02	0.02
<b>Species Composition by Mass</b>				
Rolling Loam	0.02	0.02		
Claypan	0.02	0.05	0.01	0.03

**Table 2.6** Plant associations ,treatments , number of plots, significant indicator species, exclusivity (A) and fidelity (B) scores, p-values for indicator species analysis, and mean percent cover for each of the clusters identified in the study area in eastern Moffat County, Colorado in 2013 and 2014. Plant associations were identified using hierarchical cluster analysis of plant cover by species for 59 plots (49 species). Indicator species were significant according to indicator species analysis at  $\alpha = 0.05$ . Species names and codes are from the USDA PLANTS database (USDA-NRCS 2011). Treatment codes are as follows: BNS = Burned, not seeded; BS = Burned, seeded; CL = Control; DR = Drag; MW = Mow.

Plant Association and Notable Characteristics	Associated Treatments		Significant Indicator Species	A	B	IVmax	p	% Cover
	Tmt	N						
<b>Cluster 1 (Cheatgrass-Invaded Shrubland)</b>  <ul style="list-style-type: none"> <li>Mountain big sagebrush shrubland with native bunchgrass understory.</li> <li>Shrub cover: 4-36%</li> <li>Cheatgrass cover: 2-25% but <u>always</u> present</li> <li>Elevation Range: 1905-2046m</li> </ul>	BNS	0	Hesperostipa comata (HECO26)	0.37	1.00	0.61	0.005	30
	BS	2	Bromus tectorum (BRTE)	0.34	1.00	0.58	0.045	13
	CL	6	Achnatherum hymenoides (ACHY)	0.74	0.67	0.70	0.005	2
	DR	0	Comandra umbellata (COUM)	0.61	0.67	0.64	0.005	< 1
	MW	4	dung	0.51	0.92	0.68	0.005	< 1
				Elymus elymoides (ELEL5)	0.46	0.83	0.61	0.025
			Epilobium brachycarpum (EPBR3)	0.87	0.33	0.54	0.010	< 1
<b>Cluster 2 (Native Grassland)</b>	BNS	13	Pascopyrum smithii (PASM)	0.54	1.00	0.74	0.005	33
	BS	2	Poa secunda (POSE)	0.33	1.00	0.58	0.010	16
	CL	0	Sphaeralcea coccinea (SPCO)	0.46	1.00	0.68	0.010	3
	DR	0	Trifolium gymnocarpum (TRGY)	0.76	0.33	0.50	0.015	< 1
	MW	0						
<b>Cluster 3 (Crested Wheatgrass)</b>	BNS	0	Agropyron cristatum (AGCR)	0.92	1.00	0.96	0.005	41
	BS	2	Astragalus drummondii (ASDR3)	0.70	0.33	0.48	0.036	< 1
	CL	4						
	DR	0						
	MW	0						
<b>Cluster 4 (Sagebrush/Bitterbrush Shrubland)</b>  <ul style="list-style-type: none"> <li>Mountain big sagebrush shrubland</li> <li>Antelope Bitterbrush <u>exclusively</u> found here</li> <li>Green rabbit brush <u>always</u> present</li> <li>Shrub cover 5-66%</li> <li>Elevation range: 2025-2165m</li> </ul>	BNS	1	Artemisia tridentata spp.	0.39	0.96	0.61	0.010	25
	BS	0	wyomingensis (ARTRW8)					
	CL	22	Alyssum desertorum (ALDE)	0.35	1.00	0.59	0.025	11
	DR	3	Purshia tridentata (PUTR2)	1.00	0.02	0.96	0.005	8
	MW	0	Pseudoroegneria spicata (PSSPS)	0.78	0.54	0.65	0.005	5
			Komandra macrantha (KOMA)	0.51	0.88	0.67	0.006	4
			Chrysothamnus viscidiflorus (CHVI8)	0.50	0.92	0.68	0.006	2
			Allium sp. (ALLIU)	0.45	0.85	0.62	0.025	2
			Eriogonum corymbosum (ERCO14)	0.55	0.77	0.65	0.010	1
			Allium acuminatum (ALAC4)	1.00	0.27	0.52	0.025	< 1

**Table 2.7** Probabilities that differences in absolute cover by species between plant associations in the study area in eastern Moffat County, Colorado in 2013 and 2014 are due to chance. Multiple Response Permutation Procedure (MRPP) was used to test the null hypothesis of no difference between groups. P values in bold are significant after Hommel (1988) adjustment ( $\alpha = 0.05$ ). A represents the chance-corrected within-group agreement and is considered a measure of effect size on a scale from 0 to 1.

Plant Association	Cluster 1 (Cheatgrass Shrubland)		Cluster 2 (Native Grassland)		Cluster 3 (Crested Wheatgrass)	
	p	A	p	A	p	A
Cluster 2 (Native Grassland)	0.001	0.17				
Cluster 3 (Crested Wheatgrass)	0.001	0.21	0.001	0.22		
Cluster 4 (Sagebrush/Bitterbrush Shrubland)	0.001	0.10	0.001	0.17	0.001	0.16

**Table 2.8** Probabilities that differences in soil functional attributes and plant functional group composition between plant associations in the study area in eastern Moffat County in 2013 and 2014 are due to chance, based on multiple response permutation procedure (MRPP) test of the null hypothesis of no differences between groups. P values in bold are significant after Hommel (1988) adjustment ( $\alpha = 0.05$ ). A represents the chance-corrected within-group agreement and is considered a measure of effect size on a scale from 0 to 1.

Plant Association	Cluster 1 (Cheatgrass Shrubland)		Cluster 2 (Native Grassland)		Cluster 3 (Crested Wheatgrass)	
	p	A	p	A	p	A
<b>Soil Functional Attributes</b>						
Cluster 2 (Native Grassland)	<b>0.06</b>	<b>0.02</b>				
Cluster 3 (Crested Wheatgrass)	<b>0.06</b>	<b>0.02</b>	<b>0.06</b>	<b>0.03</b>		
Cluster 4 (Sagebrush/Bitterbrush Shrubland)	<b>0.005</b>	<b>0.04</b>	<b>0.06</b>	<b>0.01</b>	<b>0.005</b>	<b>0.06</b>
<b>Plant Functional Group Composition</b>						
Cluster 2 (Native Grassland)	<b>0.001</b>	0.25				
Cluster 3 (Crested Wheatgrass)	<b>0.001</b>	0.29	<b>0.001</b>	0.31		
Cluster 4 (Sagebrush/Bitterbrush Shrubland)	<b>0.001</b>	<b>0.08</b>	<b>0.001</b>	0.23	<b>0.001</b>	0.25
<p>Notes: Soil functional attributes considered: Soil Redistribution and Resource Retention classes; percent cover of bare ground, perennial plant bases, and litter; extent of basal gaps of sizes 25-50cm, 100-200cm and 200+cm; percent clay and soil value in the first three soil horizons.</p> <p>Plant functional group cover considered: shrubs, perennial forbs (all were native), native annual forbs, exotic annual forbs, legumes, rhizomatous grasses (all were native), native perennial bunchgrasses, exotic perennial bunchgrasses, annual grasses (all were exotic).</p>						

**Table 2.9** Significance and  $R^2$  for correlation of NMS axes ordinated on species cover with soil and site attributes and management history sampled in eastern Moffat County, Colorado in 2013 and 2014. P values are significant after Hommel (1988) adjustment ( $\alpha = 0.05$ ).

<b>Attribute</b>	<b>p</b>	<b>R<sup>2</sup></b>
Burn	0.03	0.81
Seed	0.03	0.35
Homestead	0.03	0.66
Elevation	0.03	0.63
Slope	0.03	0.32
Resource Retention Class	0.03	0.28
Soil Redistribution Class	0.03	0.34
Value, First Horizon (Value1)	0.04	0.24
% Rock Fragments, First Horizon (Frag1)	0.03	0.37
% Foliar Cover	0.03	0.51
% Bareground Cover	0.03	0.33
Number of Basal Gaps size 100-200 cm	0.03	0.32

**Table 2.10** Important predictors of plant associations identified in the eastern Moffat County study area in 2013 and 2014, along with their coefficients, as identified by multinomial logistic regression performed with the least absolute shrinkage and selection operator (LASSO) and cross-validation model selection. The selected shrinkage factor ( $\lambda = 0.08$ ) produces a MSPE within one standard error of all cross-validation predictions. Bolded coefficients represent the greatest single predictor of that plant association.

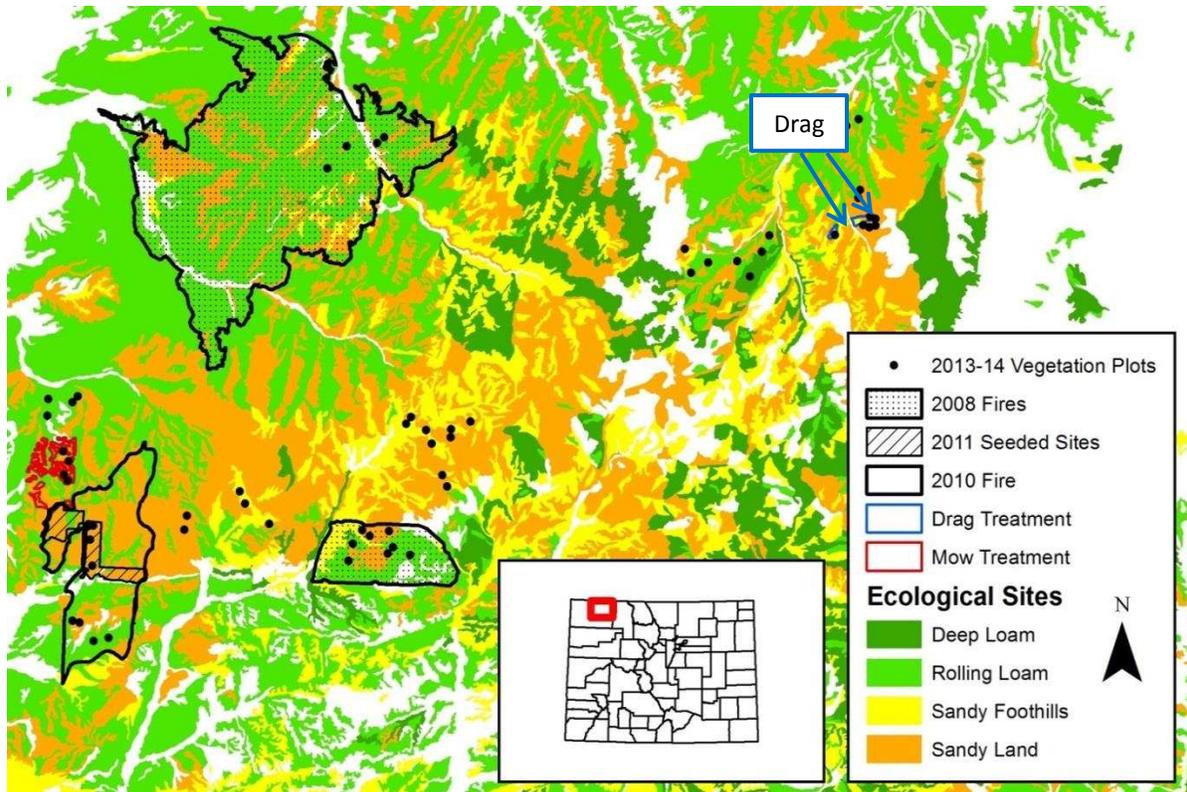
Attribute	Cluster 1 (Cheatgrass Shrubland)	Cluster 2 (Native Grassland)	Cluster 3 (Crested Wheatgrass)	Cluster 4 (Sagebrush/ Bitterbrush Shrubland)
	<b>Regression Coefficient</b>			
<i>Intercept</i>	20.7	0.6	-0.04	-21.1
<b>Management History and Dynamic Site Attributes</b>				
<i>Burn</i>		4.0		
<i>Homestead</i>			5.9	
<i>Mow</i>	0.8			
<i>Distance to Road</i>	0.003			-0.004
<b>Static Soil and Site Attributes</b>				
<i>Elevation</i>	-0.01			0.01
<i>Landform</i>	2.3			
<i>% Rock Fragments, Horizon 1</i>				0.2
<i>% Rock Fragments, Horizon 2</i>				0.007

**Table 2.11** Probabilities that differences in plant community structure (cover by species and composition by mass) between treatments in the study area in eastern Moffat County, Colorado in 2013 and 2014 are due to chance, based on multiple response permutation procedure (MRPP) test of the null hypothesis of no difference between groups. P values in bold are significant after Hommel (1988) adjustment ( $\alpha = 0.05$ ). A represents chance-corrected within-group agreement and is considered a measure of effect size on a scale from 0 to 1.

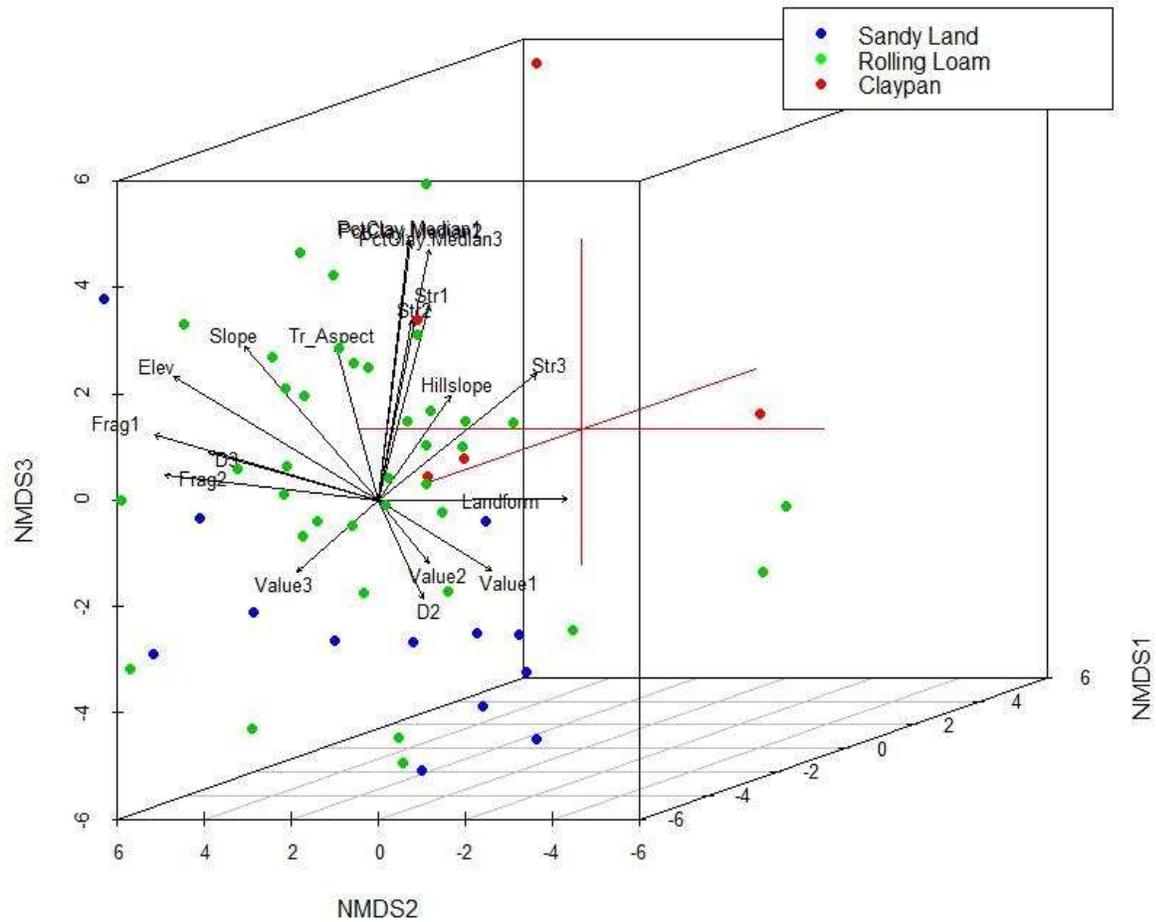
	Mow		Drag		Burn – No Seed		Burn + Seed	
	<i>p</i>	<i>A</i>	<i>p</i>	<i>A</i>	<i>p</i>	<i>A</i>	<i>p</i>	<i>A</i>
<b>Absolute Cover by Species</b>								
Drag	0.04	0.23						
Burn – No Seed	0.01	0.14	0.02	0.17				
Burn + Seed	0.04	0.12	0.04	0.20	0.03	0.05		
Control	0.01	0.04	0.03	0.03	0.01	0.13	0.01	0.08
<b>Species Composition by Mass</b>								
Drag	0.03	0.24						
Burn – No Seed	0.01	0.10	0.01	0.13				
Burn + Seed	0.02	0.15	0.03	0.24	0.01	0.06		
Control	0.02	0.06	0.01	0.05	0.01	0.07	0.01	0.08

**Table 2.12** Summary of ecological services provided by each of the plant associations sampled in the eastern Moffat County, CO study area in 2013 and 2014.

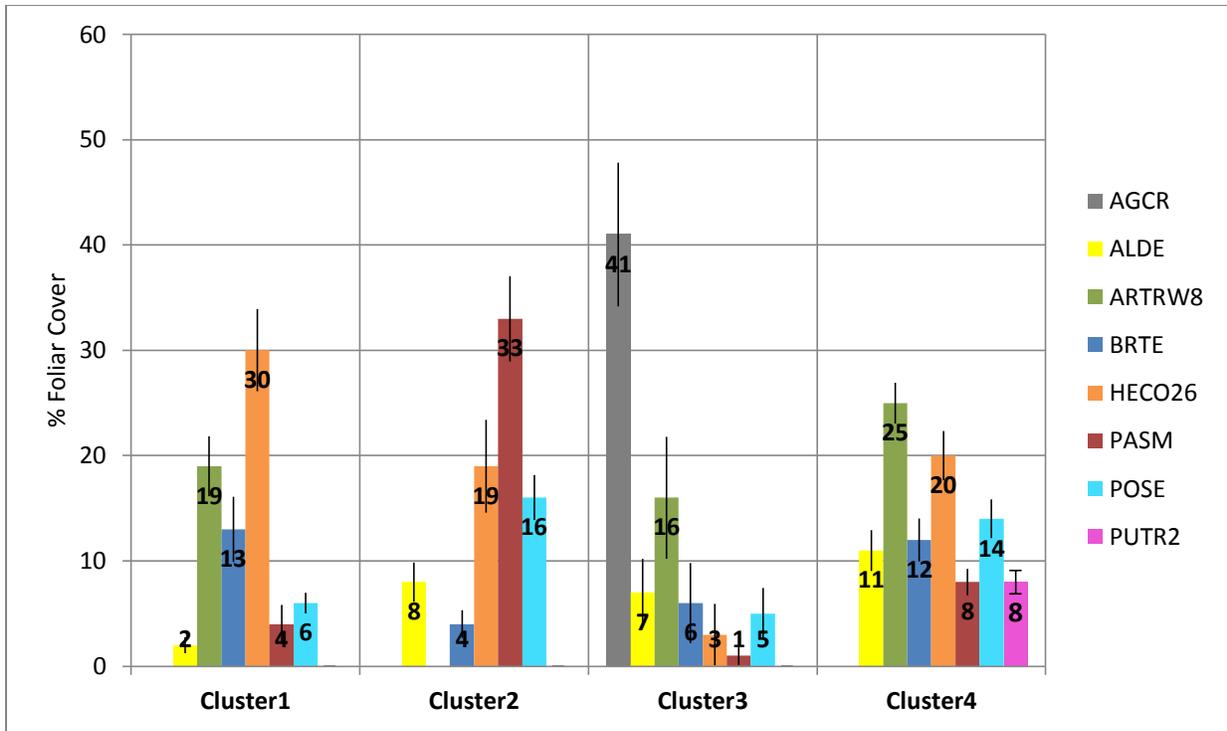
<b>Attribute</b>	<b>Cheatgrass-Invaded Shrubland</b>	<b>Native Grassland</b>	<b>Crested Wheatgrass</b>	<b>Sagebrush-Bitterbrush Shrubland</b>
Species Richness (count) (mean ± SE)	26 ± 2.1	25 ± 1.6	14 ± 1.8	28 ± 1.0
Exotic Species Cover (%) (mean ± SE)	15 ± 3.3	13 ± 2.8	55 ± 3.0	23 ± 3.9
Cheatgrass Cover (%) (mean ± SE)	13 ± 3.2	4 ± 1.3	6 ± 4.2	12 ± 2.1
Bareground Cover (%) (mean ± SE)	10 ± 2.0	6 ± 1.4	9 ± 1.6	5 ± 0.6
Standing Crop (kg/ha) (mean ± SE)	438 ± 199	564 ± 159	628 ± 231	799 ± 305



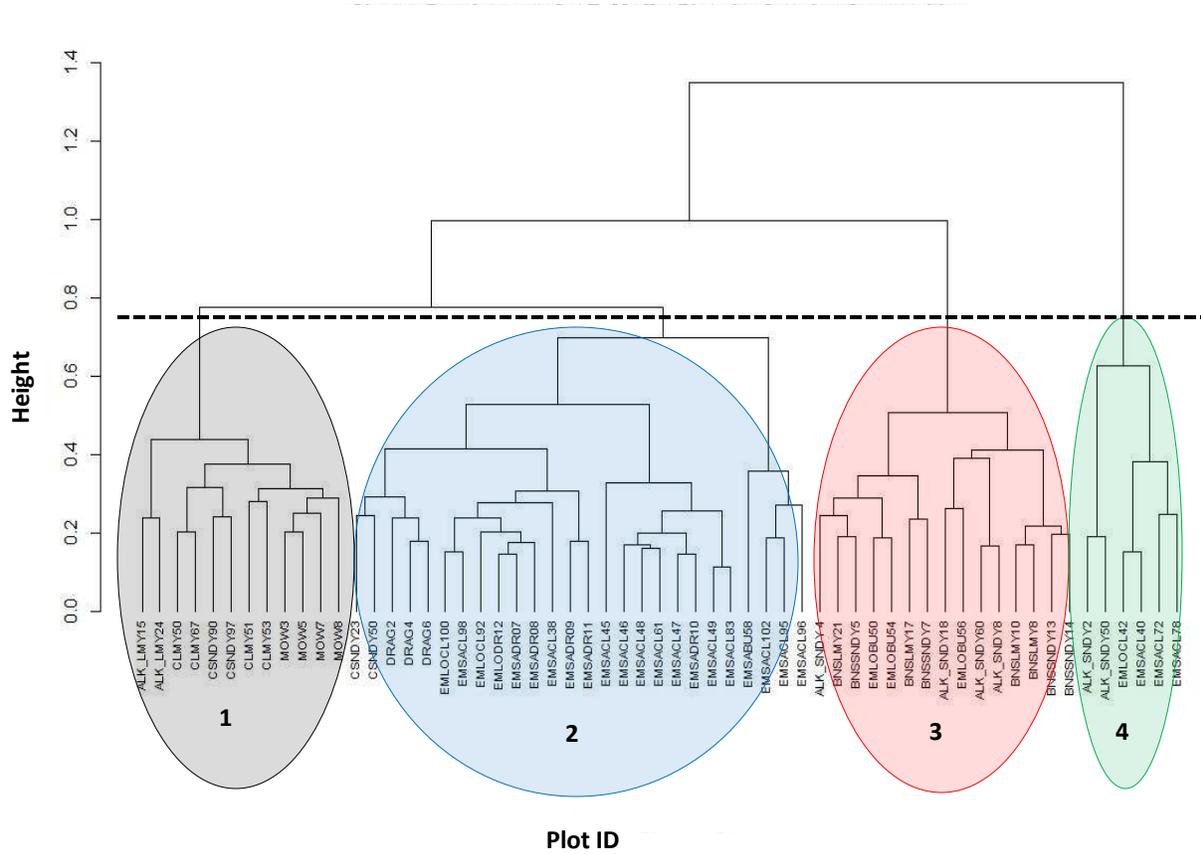
**Figure 2.1** Map of eastern Moffat County study area, showing Web Soil Survey ecological site designations (USDA-NRCS 2009), plots sampled in 2013 and 2014, and treatment areas. Treatment areas consisted of a mowed area (174 ha in 1996), two dragged areas (28.8 ha in 1997 and 15.2 ha in 1998), two wildfires with no post-fire seeding (1,505 ha in September 2008; 2,679 ha in August 2010), and a portion of the 2010 wildfire seeded with native species (506 ha in 2011); additional “control” plots were generated in undisturbed regions across the entire study area.



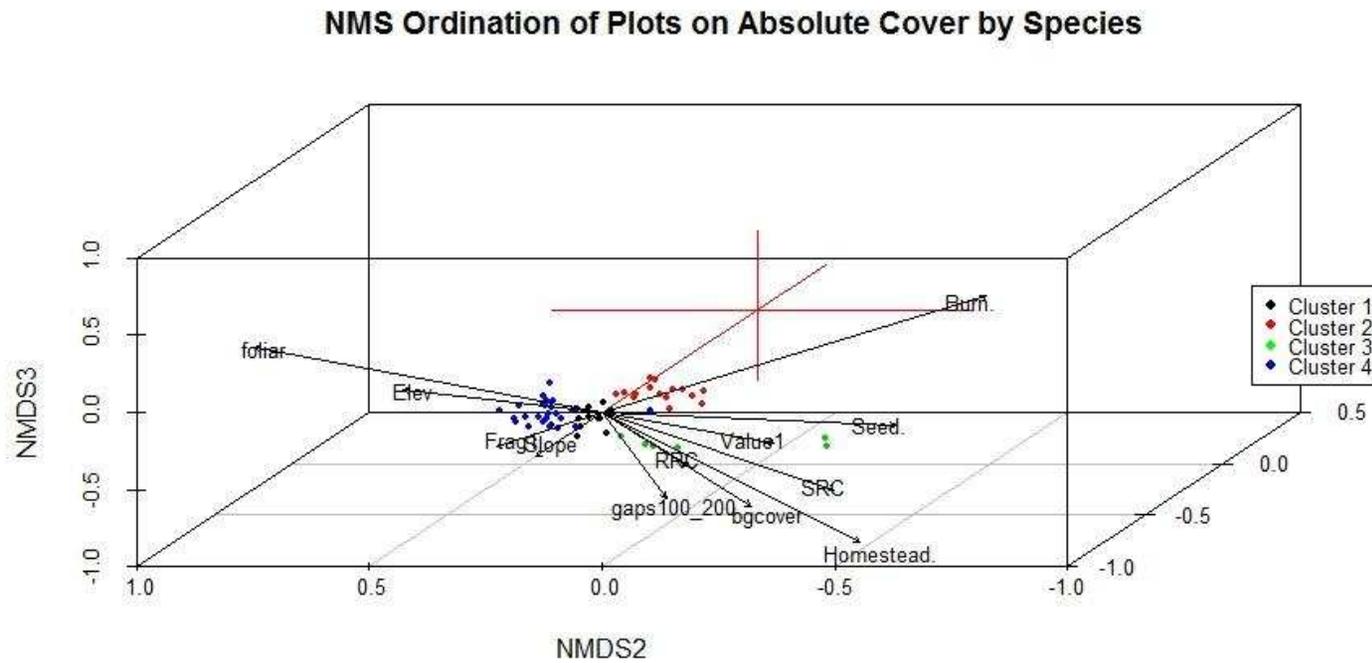
**Figure 2.2** Differences in soil and site attributes between the three ecological sites detected in the study area in eastern Moffat County, Colorado in 2013 and 2014. Nonmetric multidimensional scaling results show differences in scaled attributes for each plot, grouped by ecological site. Distances between plots (colored points) are related to magnitude of differences in soil and site attributes. Vectors represent the direction and magnitude of correlation between individual soil and site variables and the NMS axes (Hommel (1988) corrected  $p < 0.05$ ), thereby representing the dominant environmental gradients in the study site.



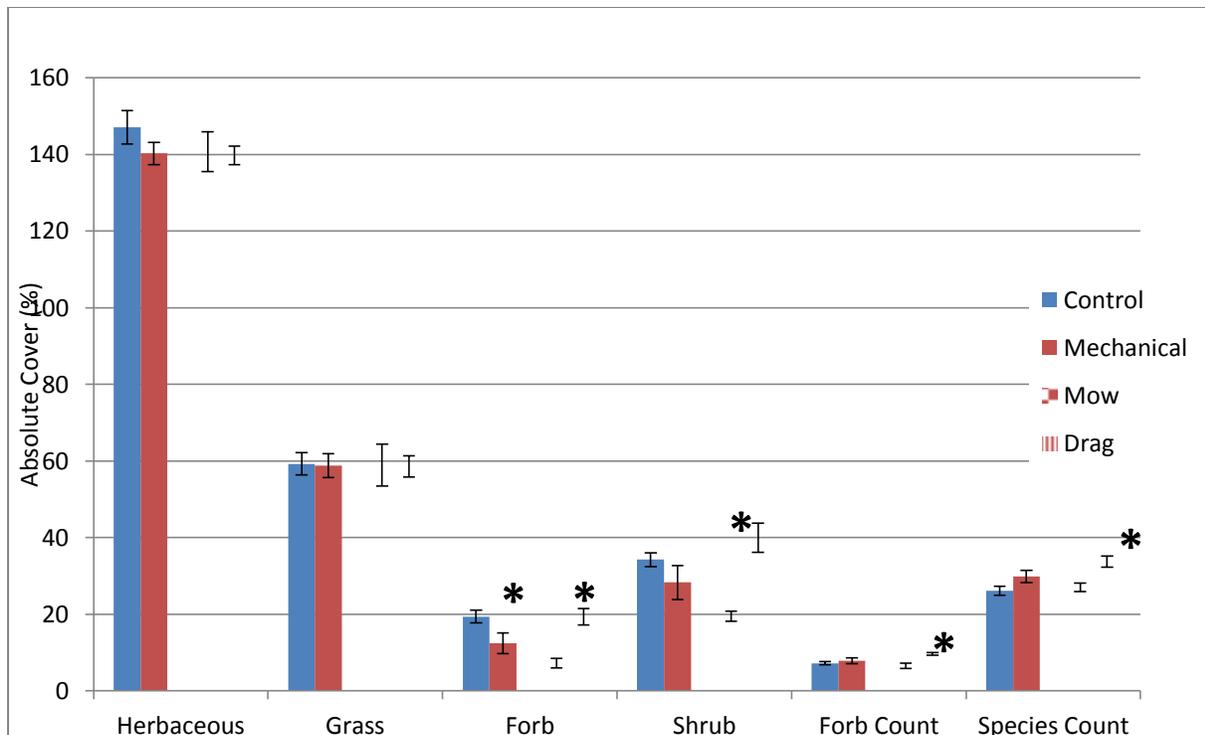
**Figure 2.3** Percent foliar cover by species for each plant association identified in the study area in eastern Moffat County, Colorado in 2013 and 2014. Only those species presenting at least 5% cover in at least one association are shown. Error bars represent one standard error. Species codes are from the USDA Plants Database (USDA-NRCS 2011).



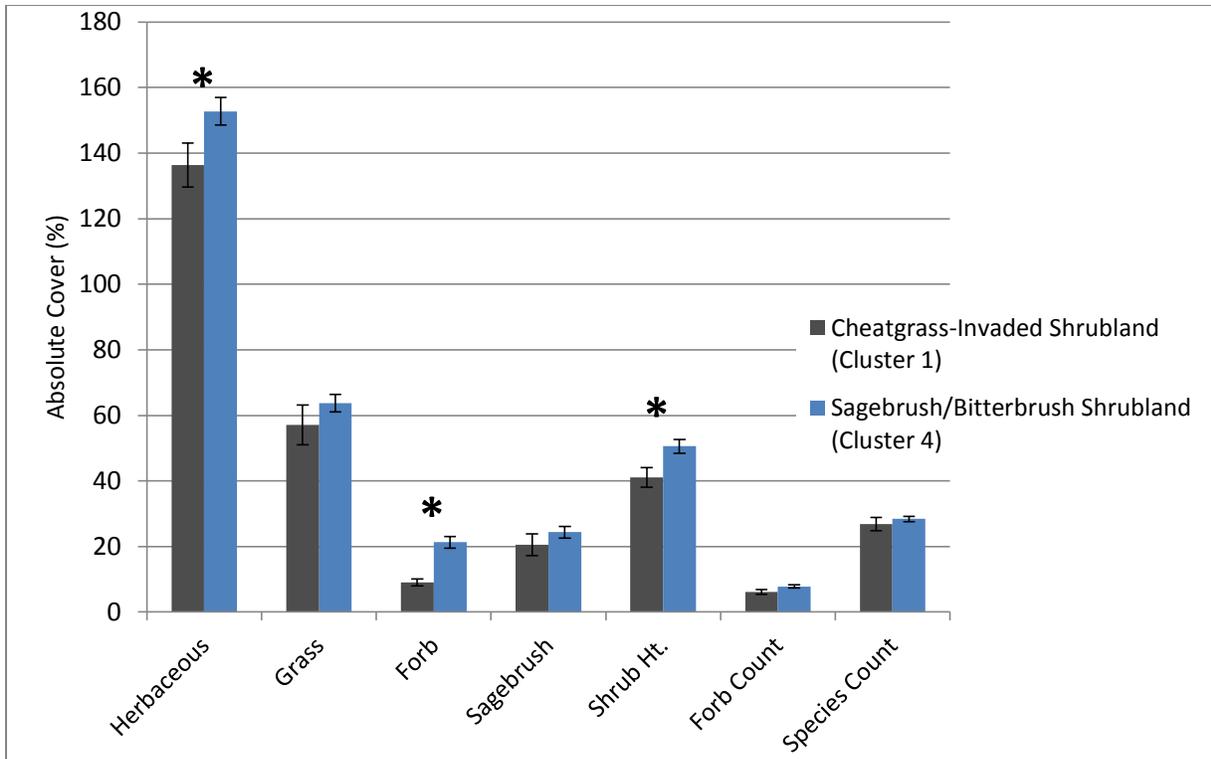
**Figure 2.4** Cluster dendrogram of plots sampled in 2013 and 2014 in eastern Moffat County, Colorado, produced by agglomerative hierarchical cluster analysis on absolute cover by species (Bray-Curtis distance measure; flexible beta linkage method, beta = -0.25). Indicator species analysis was used to prune the dendrogram to the number of clusters that produces the greatest number of significant indicator species, resulting in four clusters. These clusters thus represent the four primary plant associations in the study area.



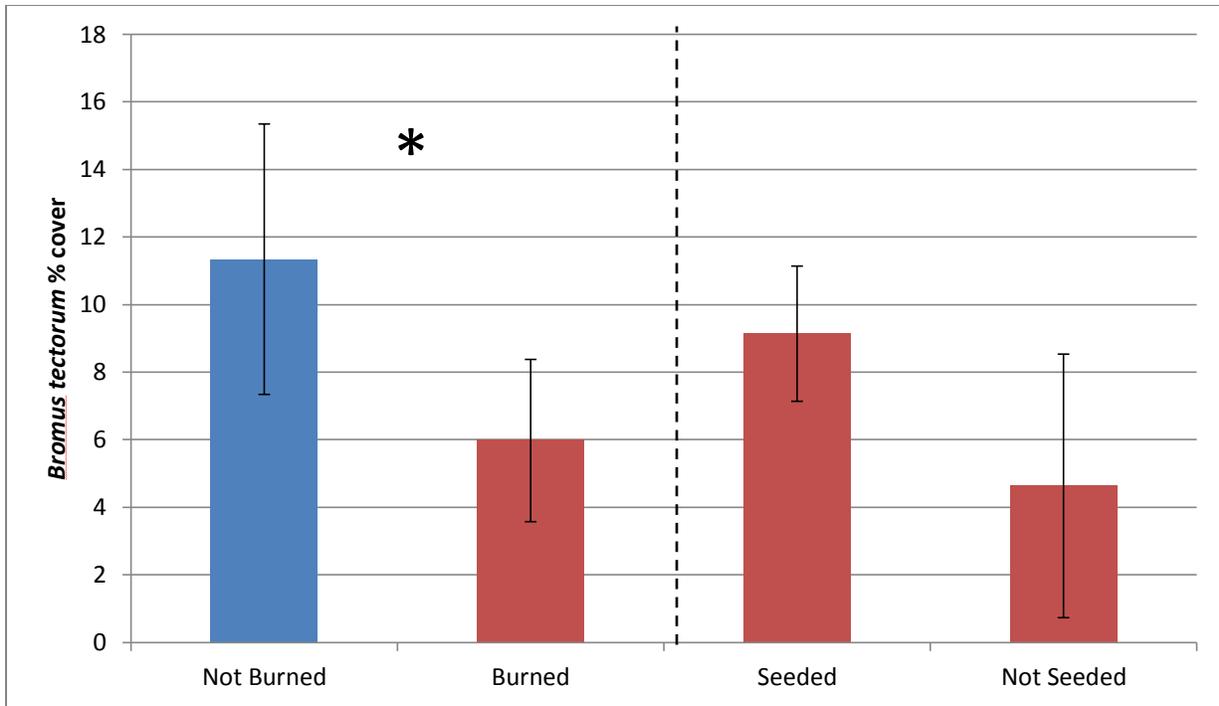
**Figure 2.5** Differences in absolute cover by species and environmental variables between the four plant associations identified in the study area in eastern Moffat County, Colorado in 2013 and 2014. Nonmetric multidimensional scaling results show differences in square root transformed plant species foliar cover for each plot, grouped by plant association. Distances between plots (colored points) are related to magnitude of differences in cover. Vectors represent the direction and magnitude of correlations of other variables with cover (Hommel (1988) corrected  $p < 0.05$ ).



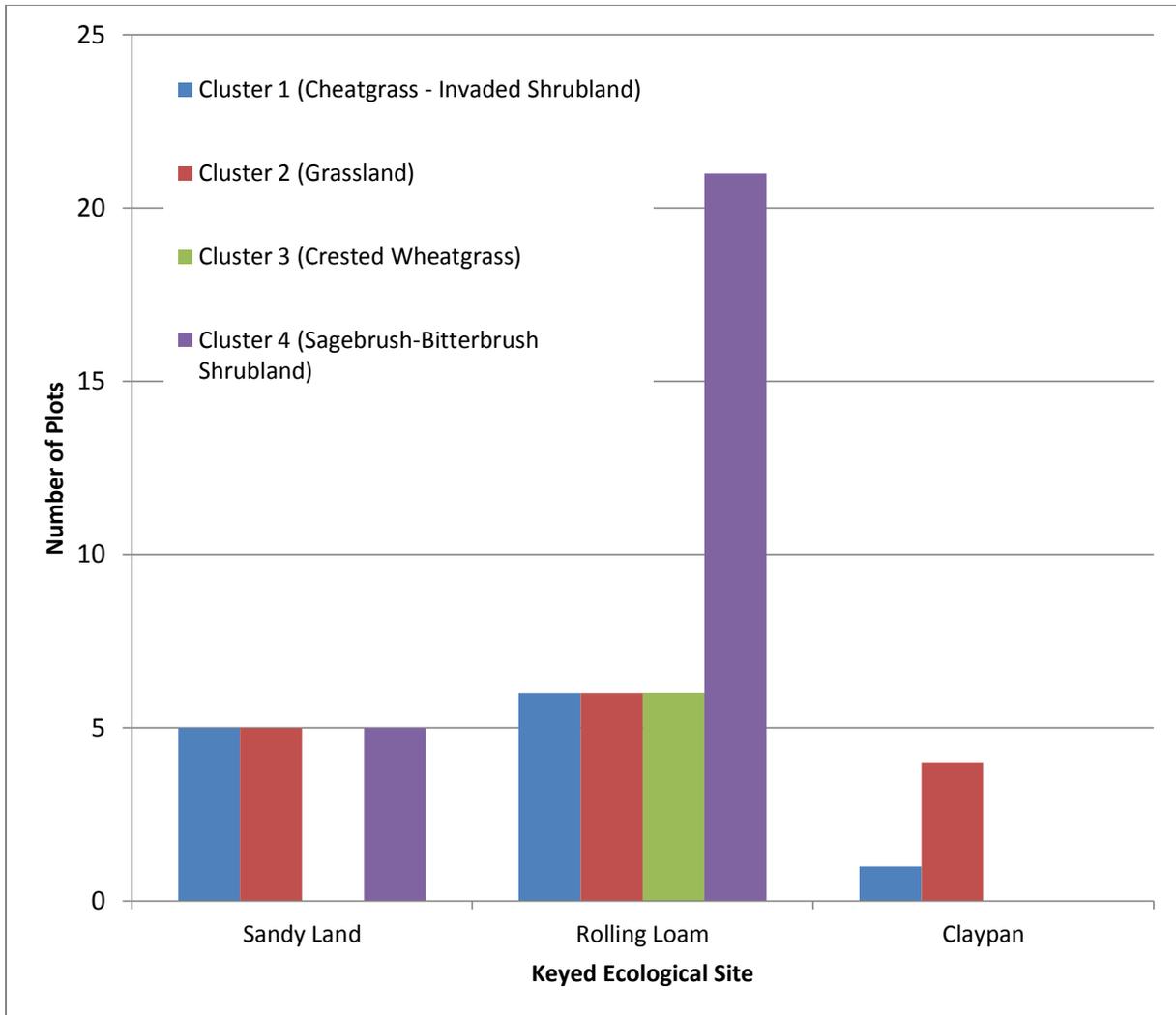
**Figure 2.6** Comparison of understory features between control and mechanically treated plots, and between drag and mow mechanical treatments in the eastern Moffat County study area in 2013 and 2014. Error bars represent one standard error. An asterisk (\*) indicates treatment comparisons that are significantly different at alpha = 0.05.



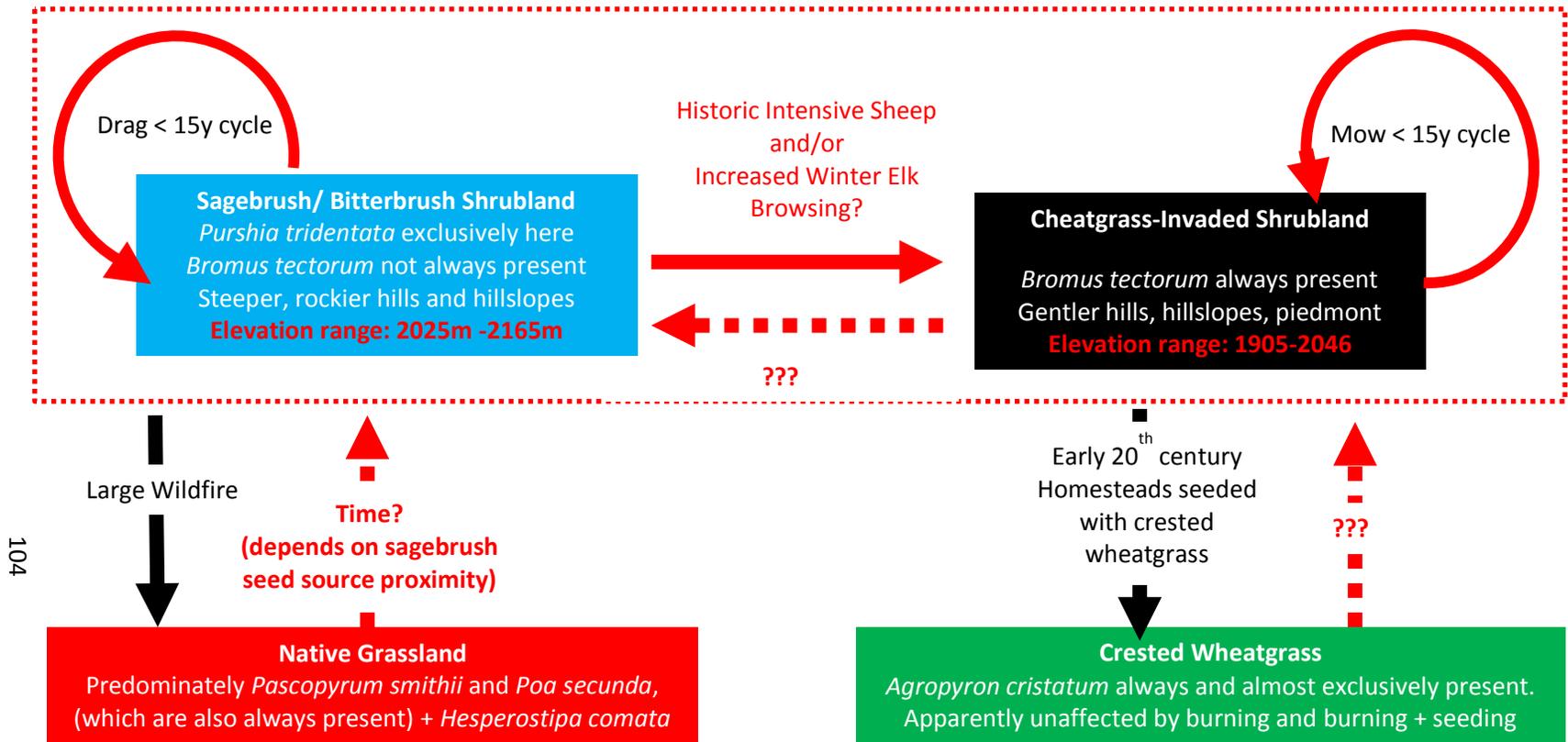
**Figure 2.7** Comparison of structural features between the Cheatgrass-Invaded Shrubland (Cluster 1) and the Sagebrush/Bitterbrush Shrubland (Cluster 4) in the study area in eastern Moffat County, Colorado in 2013 and 2014. Error bars represent one standard error. An asterisk (\*) indicates statistically significant comparisons at alpha = 0.05.



**Figure 2.8** Comparison of *Bromus tectorum* (cheatgrass) cover between burned and unburned plots, and between seeded and not seeded burned plots, in the eastern Moffat County study area in 2013 and 2014. Error bars represent one standard error. Unburned treatments had significantly higher cheatgrass cover compared to unburned plots. No significant difference in cheatgrass cover was identified between seeded and not-seeded burned treatments.



**Figure 2.9** Number of plots sampled in 2013 and 2014 in the eastern Moffat County, Colorado study area, by keyed ecological site.



**Figure 2.20** Data-driven STM for Wyoming sagebrush steppe in eastern Moffat County based on 2013 and 2014 field sampling. Red arrows and text indicate areas of remaining uncertainty. According to the project protocol, remaining uncertainties should be addressed with adaptive management experiments and additional field sampling, both designed in collaboration with project stakeholders and knowledge contributors.

### **Chapter 3.**

#### **Nitrogen-Cycling in a Mountain Big Sagebrush Ecosystem: An Ecological Process-Based Approach to State-Transition-Model Development**

##### **INTRODUCTION**

Successful management and conservation of ecosystems depends on having and communicating a solid understanding of the relationships and feedbacks between system structure and ecological processes. The extent to which systems can maintain these structure-function relationships despite disturbances to structural or functional attributes has been termed its range of “resilience” (Holling 1973). Negative feedbacks between ecosystem processes and structure tend to absorb disturbance and maintain resilience; positive feedbacks amplify changes to structure and function, causing a system to lose resilience (Briske et al. 2006).

Conceptual state-and-transition models (STMs) are used to summarize what is known and unknown about these dynamics in specific systems, in order to inform and guide future management and scientific investigation (Westoby et al. 1989). Plant associations that are both structurally and functionally distinct are termed “states” in this framework; state transitions arise when triggering events (i.e., anthropogenic or environmental disturbances) sufficiently alter state structure and/or function to such an extent that it can no longer be maintained by the same negative feedbacks; instead, positive feedbacks amplify structural-functional change until a new state is created, maintained by a new set of structural-ecological process feedbacks (Briske et al. 2006). The switch from negative to positive ecological process feedbacks is often described as a “threshold” of change in ecological function; beyond this threshold, the system is no longer resilient, structural-functional change is accelerated rather than resisted, and

significant energy investment (e.g., management intervention) is necessary to restore the original state (Friedel 1991, Laycock 1991, Lockwood and Lockwood 1993, Briske et al. 2006, Scheffer 2012).

Plant associations which differ in structure but are otherwise functionally similar are termed “communities” and considered to exhibit the range of structural variability within a state; alterations to communities within a state tend to be readily reversible with removal of the driving disturbance (e.g., short-term weather changes or herbivory patterns) (Briske et al. 2006). STMs attempt to communicate the range of resilience of the different states and communities within an ecosystem, and the potential functional pathways by which resilience is lost as a state transitions to a new resilience regime.

STMs have been criticized for focusing on practices rather than processes; that is, many STMs emphasize management actions or natural disturbances observed to be associated with the creation or maintenance of certain plant associations, but fail to address the specific ecological processes involved (Stringham et al. 2003, Tidwell et al. 2013). This failure of STMs to specifically address state transitions and thresholds in terms of ecological function severely limits practical utility of STMs to consistently guide successful management and restoration projects (Bestelmeyer 2006, Herrick et al. 2006, Tidwell et al. 2013). Identification of the specific ecological processes involved in maintaining states and perpetuating state-transitions would improve the specificity of STMs in describing functional thresholds and provide key information for preventing undesirable state-changes and developing potential restoration pathways.

There is a widely documented state-transition pattern in rangelands dominated by big sagebrush (*Artemisia tridentata*) of persistent loss of herbaceous understory cover and diversity and increasing *Artemisia* cover and height that appears to occur when moderate to heavy summer livestock grazing is present concomitant with long-term lack of fire or other brush disturbance (Van Poolen and Lacey 1979, Brotherson and Brotherson 1981, West et al. 1999, Miller et al. 2011). These “Diverse” (i.e., with a widespread, diverse understory) and “Depauperate” (i.e., with a sparse, less diverse understory) sagebrush communities have been presented as alternate states separated by some functional threshold, but the specific structural-functional relationships that maintain each state and the mechanism by which ecological process feedbacks are altered to drive the transition between states has largely remained unaddressed (West et al. 1999, Kachergis et al. 2012, Evers et al. 2013).

I hypothesize that nitrogen cycling is a critical ecological process involved in the Diverse-to-Depauperate state-transition. Below, I provide an overview of the big sagebrush-steppe ecosystem, particularly that of the subspecies *Artemisia tridentata* spp. *vaseyana*, and the influences of plant community structure, fire and grazing on nitrogen-cycling in that system. I then propose a mechanism of understory loss that explains the Diverse-to-Depauperate state-transition in terms of changes to litter pool quality and thereby nitrogen cycling rates. Next, I present results derived from a pilot observational field study of soil physical characteristics and nitrogen-cycling dynamics and evaluate the hypothesized mechanism in light of this evidence. Finally, I present a revised mechanism and discuss implications for management and future research.

## THE MOUNTAIN BIG SAGEBRUSH ECOSYSTEM AND NITROGEN CYCLING

### *Plant Community Structure*

Mountain big sagebrush (MBS; *Artemisia tridentata* ssp. *vaseyana*) is found in relatively cool, moist, deep clay loam soils on high elevation plateaus, mountain slopes, and bottomlands (West and Young 2000). Despite relatively mesic soil conditions locally, broader climatic conditions across the range of MBS are semi-arid with long dry spells in summer and most moisture coming as winter snow (Smith et al. 1997, West and Young 2000). A wide variety of perennial herbaceous species are found in close association with MBS, including bluebunch wheatgrass (*Pseudoroegneria spicata*), Letterman's needlegrass (*Achnatherum letermanii*), sandberg's bluegrass (*Poa secunda*), western wheatgrass (*Pascopyrum smithii*) and various forbs, few of which are nitrogen fixers (West and Young 2000, Kachergis et al. 2012).

Soils of MBS steppe tend to be nitrogen-limited, in part due to slower decomposition rates resulting from the semi-arid climate (Smith et al. 1997). Mountain big sagebrush produces long-lived leaves rich in phenolic anti-herbivory compounds, resorbs nitrogen efficiently before senescence, and is associated with arbuscular mycorrhizal fungi that can aid in "mining" of inorganic nitrogen from the soil (Allen et al. 1995, Coyne et al. 1995, Smith et al. 1997). As a result, sagebrush is well-adapted to sites with slow nitrogen turnover and its slow-to-decompose, nitrogen-poor litter may reinforce slow rates of nitrogen cycling (Aerts and Chapin 2000). Compared to sagebrush, the deciduous herbaceous species in the MBS steppe understory tend to produce foliage that is relatively nitrogen-rich and short-lived (Coyne et al. 1995, Smith et al. 1997). These traits could lead to relatively rapid rates of herbaceous litter

decomposition and of recycling of the nitrogen derived from herbaceous litter, which in turn could help sustain the population of relatively fast growing, nitrogen-rich, understory herbs (Hobbie 1992). Thus, microsites beneath sagebrush tend to exhibit higher soil nitrogen concentrations and slower nitrogen cycling rates compared to microsites beneath herbaceous species (Doescher et al 1984, Schlesinger et al. 1990, Chen and Stark 2000). This patchy resource distribution likely both facilitates the coexistence of different functional group types and results from their differing nitrogen use strategies. (Wedin and Tilman 1990, Van Cleve et al. 1991, Hobbie 1992, Berendse 1994, Aerts and Chapin 2000).

### *Large Ungulate Herbivory*

Grazing has been observed to intensify resource heterogeneity in arid and semi-arid landscapes where nitrogen is limiting (Schlesinger et al. 1990, Allington et al. 2014). In such regions, grazed plants may be unable to access sufficient nitrogen for adequate compensatory regrowth, reducing their vigor as well as the region over which they access and influence belowground resources, sometimes referred to as their “ecological field” (Walker et al. 1989), potentially resulting in competitive release of soil nitrogen pools which may then be usurped by neighboring plants (Davies et al. 2007, Eilts et al. 2011). If nitrogen-use efficient species, such as sagebrush, were to acquire a greater share of soil nitrogen due to grazing on neighboring herbaceous species, this might increase the spatial extent of resource-poor patches in the landscape via the litter feedbacks described above.

Not all nitrogen-poor environments experience herbaceous species loss in the face of grazing. The extent to which compensatory growth is limited in nitrogen poor environments

depends on the timing, intensity, and duration of grazing. Resources may be adequate for regrowth of grazed plants even in nitrogen-limited environments if grazing intensity is low, short-term, or occurs during a time of year when plant resource demands are small (Archer and Smeins 1991). The extent to which plant associations evolved with large herbivores can also affect compensatory growth responses to herbivory.

The MSB steppe probably co-evolved to some extent with large prehistoric browsing mammals, but major climatic changes during the late Pleistocene (12,000 years ago) interrupted this coevolution and drove the extinction of many large ungulates (Grayson 1991). After the Late Pleistocene, populations of large grazing ungulates in the intermountain valleys of the Rocky Mountains were relatively small compared to the large numbers of bison grazing rhizomatous and sod-forming grasses to the east (Mack and Thompson 1982)<sup>3</sup>. Thus, coevolution of MBS steppe plant associations with intense grazing by large native ungulates was likely very limited. European settlement in the 19<sup>th</sup> and 20<sup>th</sup> centuries introduced domestic livestock grazers at high intensities. East of the Rockies where bison had once been abundant, “one bovid essentially replaced another” and native grasses tended to persist despite high stocking rates. By contrast, in the Intermountain West, unprecedented high grazing pressure from domestic ungulates has had a substantial impact, in many areas drastically altering composition and structure of native bunchgrass communities (Mack and Thomspson 1982).

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<sup>3</sup> Historical and paleontological records provide evidence that large ungulates, especially bison, were rare west of the Rocky Mountains. Examination of common close associates, such as the dung beetle genus *Onthophagus*, also provides evidence to this effect. There are 34 species of *Onthophagus* on the sod-forming grasslands east of the Rocky Mountains, but none in the bunchgrass-dominated regions of the Rockies and western slope. Bison, elk, and deer co-occurrence in the Intermountain West may have been restricted by a dis-synchrony between grass phenology and the timing of calving and peak milk-production. While C3 bunchgrasses which predominate to the west of the Rockies mature relatively early, the mixture of C3 and C4 species to the east would offer forage throughout the spring and summer to support calves and milk production (Mack and Thompson 1982).

## *Fire Regime*

MBS does not persist after fire due to high individual mortality rates, an inability to re-sprout, and poor survival of seeds (Sapsis and Kauffman, 1991). Therefore, post-fire MBS recruitment entirely depends upon seed dispersal from the surviving seedbank and nearby intact sagebrush stands (Bates et al. 2009, Davies et al. 2014). The pre-settlement fire return interval in MBS steppe is thought to have been relatively frequent over relatively small patch sizes compared to more arid big sagebrush complexes, although estimates of historic fire return interval in MBS vary from 15-150 years (Miller and Heyerdahl 2008, Baker 2006). The landscape was also frequently burned by aboriginal Native American groups, presumably to increase the cover of desirable herbaceous plants and to drive game (Barrett and Arno 1982, McAdoo et al. 2013). As a result, the MBS steppe landscape generally exists as a mosaic of herbaceous and shrub-dominated patches, whose composition and structure represent various stages of post-fire regeneration, influenced by pre-fire composition, fire conditions, and other concomitant disturbances such as drought or grazing (Baker 2006, Seefeldt et al. 2007, Evers et al. 2013).

Fire transforms organic and mineral matter through oxidation and heat stress. These transformations alter the structure, volatility, and mobility of nitrogen compounds (Boerner 1982). The immediate effect of fire on semi-arid shrub land systems appears to be an increase in ammonium concentrations in the upper soil horizons. However, nitrogen fixation rates tend to decline immediately after fire, indicating that the increase in ammonium comes largely from ash deposits of partially-combusted organic matter, rather than microbial mineralization of organic nitrogen. Over the next few years, ammonium concentrations gradually decline while

nitrate concentrations increase. Enhanced nitrification is likely facilitated not only by increased ammonium deposits available to nitrifiers, but also by deactivation of secondary metabolites (which tend to slow decomposition) via sorption with charcoal deposits (DeLuca et al. 2002, 2006). Elevated levels of nitrate have been observed to remain four years after fire in sagebrush (Rau et al. 2007). Indeed, the first few years after fire, shrub lands typically exhibit a widespread flush of herbaceous cover (Bates et al. 2009, Davies et al. 2009a, 2012) and enhanced foliar N concentrations (Rundel and Parsons 1980), indicating plants are accessing newly available, more homogeneously distributed nitrogen pools.

#### AN ECOLOGICAL PROCESS MECHANISM FOR UNDERSTORY LOSS IN MSB

Clearly, fire and grazing can have significant impacts on the concentration, availability, and cycling of nitrogen in soil. Because nitrogen is a limiting nutrient in many ecosystems and plant species differ widely with respect to traits related to nitrogen use and acquisition, alterations to nitrogen dynamics can be expected to alter plant community composition (Chapin 1993, Aerts and Chapin 2000). As elaborated below, I propose that the Diverse state in MSB shrublands is maintained by a negative feedback between structure and function. When grazing intensity is low and herbaceous plants are relatively abundant, high-quality herbaceous litter supports the fast nutrient cycling necessary to maintain the diverse herbaceous understory. However, faced with intensive summer grazing, herbaceous species may be unable to sustain adequate compensatory growth to maintain access to belowground nutrient pools, reducing their competitive potential (Schlesinger et al. 1990). Sagebrush gains access to resource stores once immobilized by herbaceous species, growing larger and more expansive

and providing more litter to the litter pool. This drives a switch to a positive feedback between structure and function whereby the increasing proportion of nitrogen-poor sagebrush litter in the litter pool lowers litter pool quality, slowing nitrogen cycling rates, further favoring MSB expansion and diminishing herbaceous cover and diversity (Figure 3.1).

Exclusion of fire from the system allows sagebrush dominance to increase over longer time periods, and the more understory fine fuels are lost, the lower the risk of fire. Thus, an additional positive feedback between lack of fire, increased sagebrush dominance, and understory loss can also perpetuate the transition to a Depauperate state.

If this mechanism is responsible for the Diverse to Dense state-transition, we would expect the Depauperate state to exhibit:

- 1) slower rates of nitrogen-mineralization and a smaller proportion of the total nitrogen pool as inorganic nitrogen (IN:TN), compared to the Diverse state;
- 2) a poorer quality litter pool (higher C:N ratio) compared to the Diverse state.

We conducted a pilot observational field study to examine evidence for these predictions by comparing soil properties, litter pool quantity, quality, and distribution, and nitrogen transformation rates of the Diverse and Dense states.

## METHODS

### *Site Selection and Sampling Design*

Nitrogen mineralization rates were determined via three *in situ* soil incubations over the 2014 growing season on three private ranches on the Mountain Loam ecological site in the

Elkhead watershed in Routt County, Colorado. Kachergis et al. (2012) created a data-driven STM for the Mountain Loam ecological site based on patterns of species composition and past management activities within this study area. This STM included a transition from a Diverse to a Depauperate state (called “Dense” by the authors) associated with long-term lack of shrub disturbance (i.e., lack of fire, herbicide, or mechanical disturbance); both states experienced moderate to high grazing intensity.

Where landowners involved in the previous study were willing to grant access for additional soil sampling, the same plot centers established by Kachergis et al. (2012) were used; this included two Diverse and two Depauperate plots. An additional six plots (three per state) were randomly chosen within the study area on the Mountain Loam ecological site as delineated in Web Soil Survey (USDA-NRCS 2009) using ArcGIS 10. Plots were 50 x 50 m and contained two sets of transects, each centered in the plot and parallel to hillslope. One set of two semi-permanent 50 m transects spaced 15 m apart were used for soil and litter sampling (described below). Another set of five 50 m transects spaced 12.5 m apart were established for vegetation sampling. Foliar and basal cover by species was determined using the line-point-intercept method (Bonham 1989) at 1-m intervals (points) along each transect (250 points per plot). Species richness was determined via a 15-minute timed search through the entire plot. A soil pit was dug to at least 50 cm at the plot center and described following NRCS protocols (Schoeneberger et al. 1998). Plot slope, aspect and elevation were recorded Aspect was transformed following Beers et al. (1966) into a continuous variable whose largest values are associated with more productive northeast facing slopes and lowest values with less productive

southwest facing slopes.. The vegetation and site characteristics of each state are summarized in Table 3.1.

To verify that the new plots occurred on the appropriate ecological site, soil pit attributes were compared to the NRCS Mountain Loam range site description and descriptions reported by Kachergis et al. (2012). Vegetation state on each plot was verified as Diverse or Depauperate according to the functional group and species composition descriptions presented in Kachergis (2011) and Kachergis et al. (2012).

### *Soil and Litter Sampling*

Soil sampling occurred during the 2014 growing season over three incubation periods:

- Incubation A (Early Season): June 5 – July 7<sup>th</sup> and 8<sup>th</sup> (32/33 days)
- Incubation B (Mid-Season): July 7<sup>th</sup> and 8<sup>th</sup> – August 13<sup>th</sup> and 14<sup>th</sup> (36/37 days)
- Incubation C (Late-Season): August 13<sup>th</sup> and 14<sup>th</sup> – September 28<sup>th</sup> and 29<sup>th</sup> and October 3<sup>rd</sup> (45/46/47/51 days). The end-date of this period varied due to weather which made three of the sites inaccessible until October 3<sup>rd</sup>.

Soil samples were taken to a depth of 20 cm as this was the depth to which Kachergis et al. (2012) found the greatest root density on Mountain Loam sites. At the beginning of each incubation period, a set of soil cores 5 cm in diameter and 20 cm deep were taken at three random points along each transect, for a total of six cores per plot per incubation period. Likewise, three sections of 5 cm diameter PVC were installed to 20 cm depth at three different random points along each transect and capped to prevent leaching (Binkley and Hart 1989,

Mueller et al. 2013). These PVC chambers served as soil incubators, allowing soil microbial activity to continue under field temperature and moisture conditions, while cutting off plant access to soil N within the chamber by isolating the soil from surrounding plant roots. At the start of the next incubation period, the PVC cores installed at the beginning of the prior period were collected and a new batch installed. Each set of fresh and PVC cores collected was placed in an ice-filled cooler and chilled as soon as possible to 4°C to inhibit further microbial activity until nitrogen extraction.

Litter was collected from the ground surface at the end of the sampling period (September and October dates above) in a 36 cm diameter ring beneath three random points per transect not impacted by soil sampling.

#### *Soil Physical and Chemical Analysis*

For each incubation period (A-C), each set of soil cores and each set of PVC samples was composited by plot, sieved to 2 mm and roots were removed by hand. Subsamples were taken from the first set of composite samples (A) for each plot to determine soil texture, pH, Total C and N, and Inorganic C. Soil texture was determined hydrometrically from a 40 g subsample (Gee and Bauder 1986). Soil pH was determined in the lab following McLean (1982). Total N and C were determined from a 10 g subsample using a LECO Tru-SPEC elemental analyzer (Leco Corp., St. Joseph, MI). Inorganic C was determined by pressure transducer following acid addition. An independent set (D) of six cores per plot (taken from three different random points per transect) were taken to measure soil bulk density in late September or early October. Bulk density of the soil fraction less than 2 mm was determined gravimetrically for each of the 60

cores after sieving each to 2 mm and removing root fragments. Bulk density was used to normalize soil carbon, nitrogen, moisture, clay, and inorganic nitrogen concentrations per gram of dry soil to grams per volume, expressed as mass per square meter of surface soil to 20 cm depth.

For each composite soil sample, percent moisture was determined gravimetrically from a 10 g sub-sample and inorganic nitrogen was extracted from a 15 g subsample using 75 ml of 2M KCL within one week of collection. Nitrate and ammonium concentrations were determined from extracts to minimum standard of 0.01 ppm using an Alpkem Flow Solution IV Automated wet chemistry system (O.I. Analytical, College Station, TX). These concentrations were corrected for grams dry soil using soil moisture, then normalized by bulk density as described above. Net nitrogen mineralization for each incubation period at each plot was computed as the difference in total inorganic N (ammonium and nitrate) between the PVC and soil cores for that period, divided by the number of incubation days. A mineralization rate normalized by the total nitrogen per volume was also computed, since total nitrogen available will influence nitrogen mineralization rates. Finally, the ratio of nitrate to total inorganic nitrogen ( $\text{NO}_3\text{:IN}$ ) at the start of each incubation period was computed as an indicator to compare relative nitrogen cycling rates and soil nitrogen conservation between states. Soil nitrate turnover is very high and nitrate is readily lost from the system (e.g., via denitrification and leaching) meaning a higher proportion of inorganic nitrogen as nitrate can indicate faster nitrogen cycling and a generally “leakier” system (Schimel and Bennett 2004, Chapman et al. 2006).

### *Litter Analysis*

Litter samples were air-dried in the lab, the herbaceous fraction isolated, and large soil aggregate contaminants removed. Each sample was weighed and C and N concentrations determined by CN Furnace (Bremner 1996, Nelson and Sommers 1996). Sub-samples of each herbaceous sample were ashed to determine percent soil contamination of litter samples. Ash content is taken gravimetrically after ignition for 5 hours at 600 degrees C in a muffle furnace (Nes 1975). Percent ash content was used to correct litter pool mass and C and N values for mineral soil contamination.

### *Data Analysis*

T-tests were used to test for differences between states in mean soil attributes (pH, moisture, C and N concentrations, and C:N ratio), mean litter attributes (mass, C and N concentrations, and C:N ratio) and  $\text{NO}_3:\text{IN}$  ratio. Wilcoxon rank sum test was used to test for differences between states for mineralization rates, which had highly skewed and non-normal sampling distributions. Due to the small number of replicates in this pilot study, statistical significance was assessed at an alpha of 0.1.

## RESULTS

Clay, nitrogen, and soil moisture content were all significantly greater in the Diverse compared to the Depauperate states; differences in soil carbon were not significant ( $p = 0.14$ ); no significant differences in soil C:N ratio or pH were detected (Figure 3.2). The Depauperate litter pool was of significantly lower quality (higher C:N) than the Diverse litter pool ( $p = 0.08$ );

states did not differ significantly in litter pool mass, carbon or nitrogen concentration (Figure 3.3).

Non-normalized net nitrogen mineralization rates tended to be lower in the Depauperate plots compared to Diverse, although the difference was only statistically significant over the July – August incubation period ( $W = 4$ ,  $p = 0.095$ , Figure 3.4A). However, when mineralization rates were normalized by total nitrogen available, these differences largely disappeared (Figure 3.4B).  $\text{NO}_3:\text{IN}$  ratio was significantly higher in Depauperate plots over the June – July period ( $p = 0.08$ ) and significantly higher in Diverse plots over the July – August ( $p = 0.06$ ) incubation periods; no significant difference in ratios was detected over the August – October period nor in mean  $\text{NO}_3:\text{IN}$  ratio across all periods (Figure 3.5).

## DISCUSSION

Litter pool C:N was significantly higher and nitrogen mineralization tended to be lower in the Depauperate plots. This is consistent with the idea that differences in species composition of sites can affect litter quality, and that differences in litter quality among sites can affect nitrogen availability, as has been observed by others (Wedin and Tilman 1990, Van Cleve et al. 1991, Berendse 1994). However, it is likely that other site characteristics interact with litter quality to influence nitrogen transformation. Diverse soils are significantly finer-textured than Depauperate soils, allowing them to hold more soil organic matter and moisture (Figure 3.2); thus Diverse soils simply have a greater potential for nitrogen transformation, regardless of litter inputs. That normalizing mineralization rates by total available nitrogen largely erased the differences in mineralization rates between states suggests that rates of

nitrogen transformation may be driven in large part by soil texture, rather than litter quality alone.

Beyond directly influencing the amount of nitrogen available to microbes for transformation, soil texture differences between the two states may also influence the response of nitrogen cycling, and thereby vegetation structure, to disturbances such as grazing and drought. Because coarser soils retain less soil moisture they are likely vulnerable to slowing of nitrogen transformation during drought periods. This interaction may explain why the differences in nitrogen mineralization rates and  $\text{NO}_3:\text{IN}$  ratio between states was most significant during the July – August incubation, since this interval coincides with the hottest, driest period of the growing season. In addition, nutrient-poorer, coarser soils may be less able to support compensatory growth after intense grazing. When heavy grazing co-occurs with summer drought, coarser-textured soils may be especially vulnerable to herbaceous species loss, as nitrogen cycling slows and compensatory growth is limited by resource scarcity. Similar texture-driven vulnerabilities have been observed for Wyoming big sagebrush communities at risk of invasion by cheatgrass. Communities on coarser-textured soils exhibited greater water stress, lower productivity, and greater vulnerability to invasion than similar communities on finer-textured soils; this vulnerability was heightened by moderate to heavy grazing (Reisner et al. 2013).

While coarser soils may put herbaceous species at greater risk during droughty periods, they may actually convey a competitive advantage to sagebrush, by allowing water to drain to depths where it is inaccessible to herbaceous species but within reach of deep-rooted

sagebrush. As sagebrush plants access resource pools abandoned by lost herbaceous cover, they may grow in dominance and contribute more nitrogen-poor litter to the litter pool, further altering nitrogen-cycling rates. In this way, soil texture influences nitrogen-cycling, which in turn influences species composition, by directly affecting the soil moisture and organic matter pools available to microbes, as well as by indirectly influencing plant species competitive interactions and the litter pool that results.

In this way, the Depauperate state observed by Kachergis et al. (2012) may result from the interaction of heavy summer grazing with lower-fertility, less-resilient, coarser-textured soils within an ecological site. Others have also found that small-scale abiotic gradients can influence vegetation structure and function within a given regime of climate, topographic, and soil attributes (Charley and West 1975, Lane et al. 1998, Bestelmeyer et al. 2009, Kachergis et al. 2012, Tietjen 2015).

To test the hypothesis that coarser textured soils within the Mountain Loam ecological site are less resilient with respect to nitrogen cycling and compensatory growth in the face of heavy summer grazing, one could manipulate grazing intensities and timing on coarser- and finer-textured sites currently exhibiting species compositions similar to the Diverse state and monitor the species compositional and nitrogen cycling response over the long term. It would be informative to investigate these nitrogen transformation rates not only at the plot level, but also beneath shrubs as compared to beneath herbaceous cover and in interspaces within the plot. Others have found that nutrient concentrations and cycling rates can differ significantly among vegetation microsites, and may be influenced by vegetation functional traits and litter

quality (Charley and West 1975, Charley and West 1977, Blank et al. 1994, Chen and Stark 2000). While such a study could reveal the relationships between soil fertility, soil texture, and vegetation response to grazing, it might be challenging to find Mountain Loam study sites on which to manipulate grazing intensity that haven't already been influenced by long-term livestock grazing over the last century and a half.

### MANAGEMENT IMPLICATIONS

The possibility that coarser texture soils are more vulnerable to understory loss than finer textured soils has substantial implications for grazing management in the west. Stocking rate recommendations are often based on estimates of site productivity. The inverse texture hypothesis (ITH, Noy-Meir 1973) posits that productivity in (semi)-arid regions (where most water loss is due to evaporation) will be greater on coarser-textured soils (which allow water to drain) compared to finer-textured soils (which have a higher water holding capacity and are thus vulnerable to evaporative water loss); in humid regions the trend is reversed. Numerous studies of ANPP along precipitation and textural gradients have largely corroborated the ITH (Sala et al. 1988, Epstein et al. 1997, Sala et al. 2015, Tietjen 2015, Zhang et al. 2015). As a result of the ITH, in the (semi)-arid west, coarser-textured soils are often assumed able to sustain greater livestock densities than finer-textured soils.

However, if herbaceous species on coarser-textured soils are also especially vulnerable to resource stress, such as water stress during high summer or tissue and nutrient losses due to grazing, these sites may not actually be able to support the stocking intensities that production estimates suggest. Sites with finer-textured soils, while tending to be less productive overall,

may actually be more resilient to higher stocking rates of grazers (e.g., cattle) in peak summer than more productive coarse-textured soils. However coarse textured soils may well support high summer browser (e.g., sheep, elk) densities, since browsers target deeper-rooted species benefitting from well-drained coarse textured soils. Others have found that, given a specific precipitation regime, soil texture influences the functional group composition of ANPP, with forb and shrub species comprising a greater proportion of ANPP on coarse textured than on fine-textured soils (Lane et al. 1998).

Thus, to maintain rangeland resilience and avoid approaching tipping points, stocking recommendations may need to consider both soil texture and livestock/forage type in addition to production potential. The role of soil texture in rangeland resilience and implications for stocking rate and livestock type warrants additional investigation under a variety of rangeland ecosystems and climate conditions.

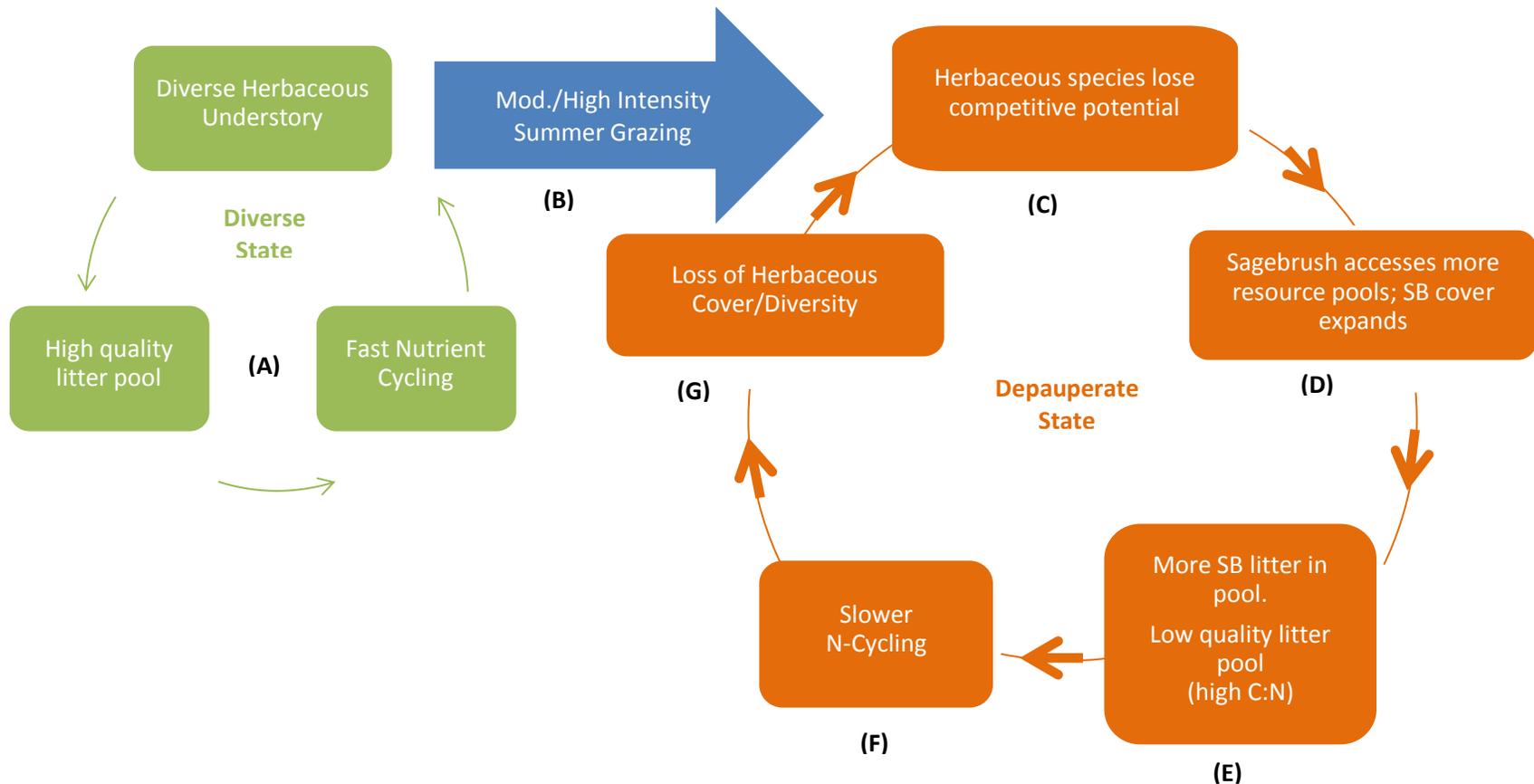
## CONCLUSION

Incorporation of specific ecological processes and their relationships to system resilience into STMs can significantly improve STM utility for preventing and reversing undesirable state-transitions. In the MSB system studied, slower nitrogen mineralization and cycling, coarser soil texture, and poorer quality litter appear to influence herbaceous understory loss (Figure 3.6). However, limitations in the study design, including small sample size, retrospective nature, and lack of stratification across all combinations of grazing regime, fire history, and texture limit the robustness of these findings. Additional work is required to better characterize the specific roles and interactions of soil texture, nitrogen cycling, and litter

traits of sagebrush vegetation in determining the vulnerability of MSB plant associations to state-transitions, and the characteristics of the resulting alternative states.

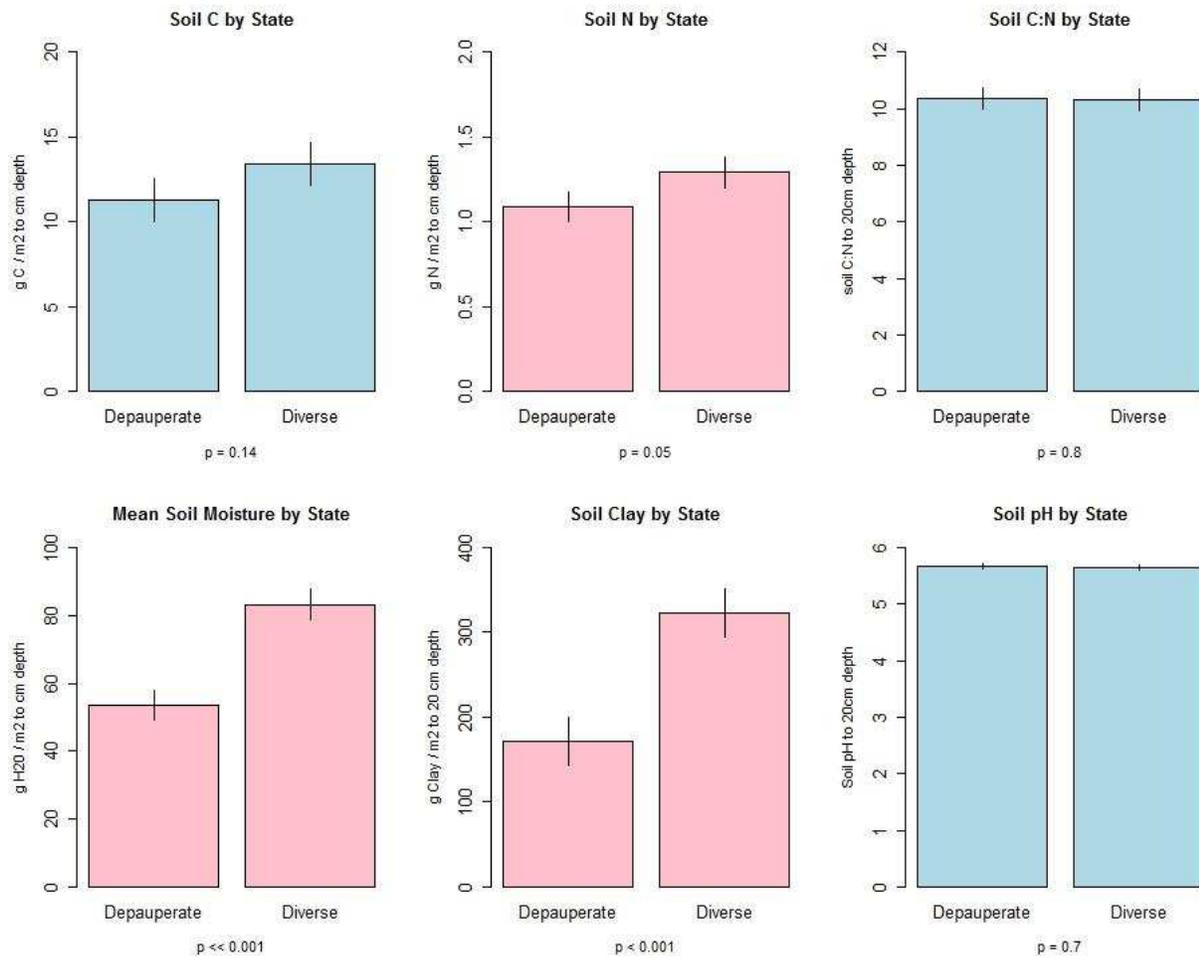
**Table 3.1** Summary of vegetation and soil attributes of the Depauperate and Diverse plots sampled in 2014 on the Mountain Loam ecological site, Elkhead Watershed, Routt County, Colorado. Absolute foliar and basal plant cover was measured using the line-point-intercept method (five 50 m transects, 250 points per plot). Species richness was derived from a whole-plot search of each 50 m x 50 m plot.

Attribute	Depauperate	Diverse
Site Attributes		
Elevation	2100 ± 2	2167 ± 27
Slope (%)	3 ± 1	16 ± 3
Transformed Aspect	1.75 ± 0.11	0.87 ± 0.32
Clay (%)	26 ± 2	59 ± 4
Perennial Foliar Cover (absolute %)		
Total	78 ± 3	74 ± 7
Shrub	55 ± 6	23 ± 4
Grass	17 ± 3	20 ± 3
Forb	10 ± 2	23 ± 6
Basal Cover (absolute %)		
Plant	21 ± 2	21 ± 3
Bare Ground	7 ± 1	5 ± 3
Litter	60 ± 3	57 ± 6
Species Richness	28 ± 3	29 ± 3

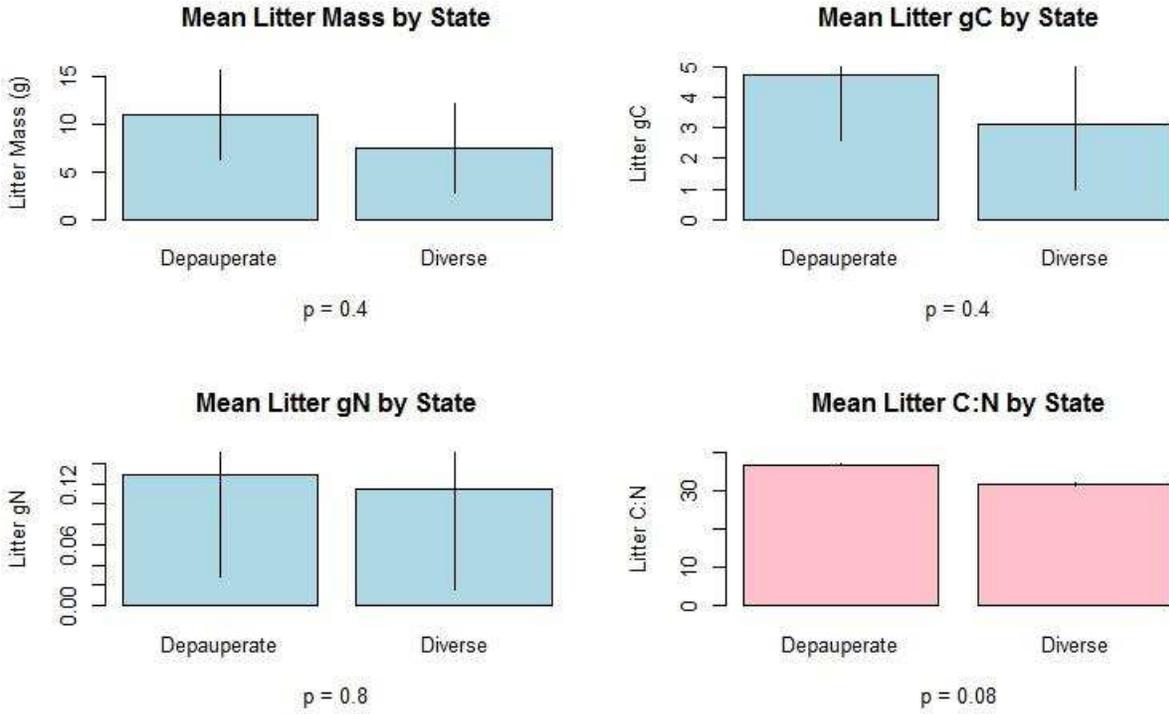


**Figure 3.1** Proposed ecological process-based mechanism for the Diverse to Dense Transition on the Mountain Loam ecological site in northwestern Colorado under a moderate/high summer grazing regime, as presented by Kachergis et al. (2012). Here the Dense state is called Depauperate since the defining characteristics of the state transition is loss of herbaceous understory cover and diversity and concomitant increases in sagebrush cover (not necessarily density).

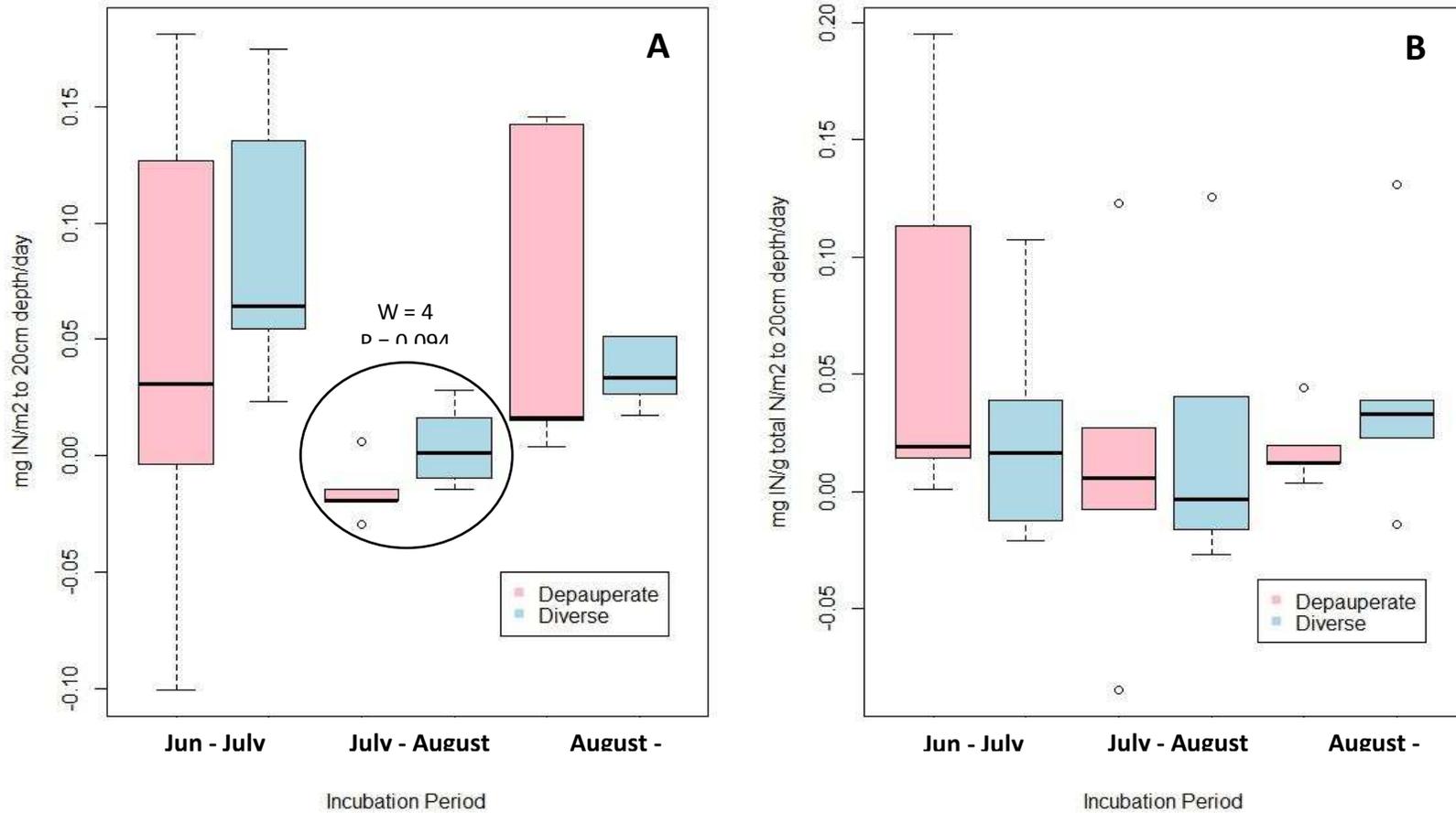
A) Fast nutrient cycling through a high quality litter pool maintains the Diverse state. B) Moderate- to high-intensity summer grazing of herbaceous species in semi-arid regions can (C) reduce the competitive potential of herbaceous species and thus their hold on resource pools. D) Sagebrush usurp access to resource pools and grow larger and more expansive. E) Sagebrush provide a greater proportion of the litter pool, reducing litter pool quality (C:N), resulting in F) Slower rates of nitrogen cycling. G) Insufficient mineralized N available to support herbaceous cover and diversity results in understory loss. As herbaceous cover declines, sagebrush can gain greater access to soil resources and continue to expand cover and dominance. In this way herbaceous understory is lost as sagebrush dominance increases to produce the Depauperate state.



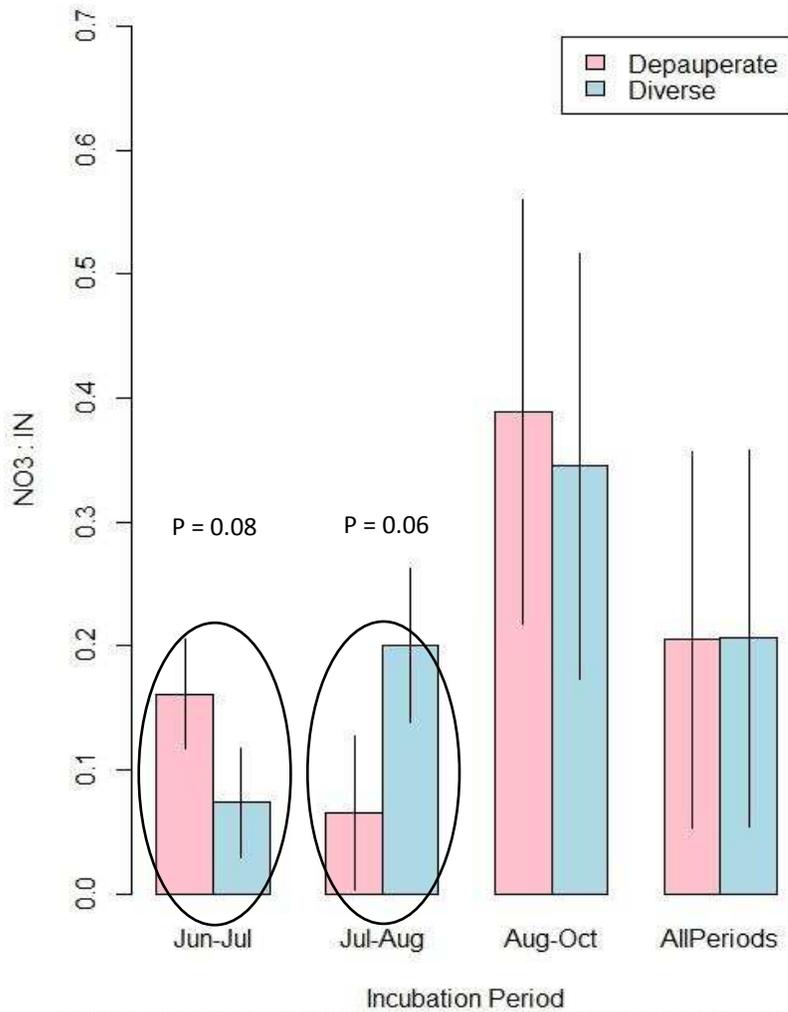
**Figure 3.2** Mean percent moisture, percent clay, pH, percent clay, percent nitrogen, and C:N ratio of soils taken from Depauperate and Diverse sagebrush states on the Mountain Loam Ecological Site in the Elkhead Watershed, Routt County, Colorado in 2014. Error bars represent the standard error of the difference between means. Charts shown in red express statistically significant differences in means between states at alpha = 0.1



**Figure 3.3** Mean litter mass, grams C, grams N and C:N ratio for the Depauperate and Diverse sagebrush states on the Mountain Loam Ecological Site in the Elkhead Watershed, Routt County, Colorado in 2014. Error bars represent the standard error of the difference between means. Chart shown in red expresses statistically significant difference in means between states at alpha = 0.1



**Figure 3.4.** Net N-Mineralization over three incubation periods in 2014 on the Diverse and Depauperate states of the Mountain Loam ecological site, Elkhead watershed, Routt County, Colorado, reported as A) rate per soil volume and B) rate per grams of total N per soil volume. The Wilcoxon Rank Sum test was used to test for differences in rates between states in each incubation period. The only significant difference was for the July-August incubation period when rates were not normalized by total N ( $W = 4$ ,  $p = 0.095$ ). There was no difference between states in any period for mineralization rate normalized by total N. Alpha = 0.1.



**Figure 3.5.** Proportion of inorganic soil nitrogen (IN) as nitrate (NO<sub>3</sub>) across three Incubation periods in 2014 on Diverse and Depauperate states of the Mountain Loam ecological site in the Elkhead watershed, Routt County, Colorado. The ratio was significantly higher in Depauperate in the June-July incubation ( $p = 0.08$ ) and significantly higher in Diverse in the July – August incubation ( $p = 0.06$ ). Alpha = 0.1. Error bars represent the standard error of the difference between means.



long-term summer  
grazing  
+  
Lack of fire for  
> 50 years  
+  
sandy soils more  
vulnerable



**Diverse Sagebrush Shrubland**

*Mountain Big Sagebrush*  
+ *Snowberry*  
+ native forbs & bunchgrasses

**N-Mineralization:** FASTER  
**Litter Pool Quality:** HIGHER  
**Soil Texture:** FINER

**Depauperate SB Shrubland**

*“Decadent” Mountain Big Sagebrush*  
large interspaces  
primarily rhizomatous grasses

**N-Mineralization:** SLOWER  
**Litter Pool Quality:** LOWER  
**Soil Texture:** COARSER

**Figure 3.6.** Diverse to Depauperate (Dense) state-transition for the Mountain Loam STM proposed by Kachergis et al. (2012), updated with descriptions of ecological process characterizing each state (orange text).

## Chapter 4.

### Conclusion

#### INTRODUCTION

In undertaking this thesis work, I set out to improve both our understanding of sagebrush-steppe ecosystem dynamics and approaches for developing accurate and relevant STMs. The ensuing work generated many interesting results, and at least as many new questions, but also brought to light a number of challenges both to our understanding of sagebrush ecology and the STM development process. In conclusion, I summarize these results, questions, and challenges below, and present some thoughts to consider for improving future work of this kind.

#### STRUCTURAL – FUNCTIONAL PATTERNS IN SAGEBRUSH STEPPE VEGETATION DYNAMICS

#### and REMAINING QUESTIONS

#### *Wyoming Big Sagebrush Study Area*

The three states and associated disturbances identified in the Wyoming big sagebrush study area are consistent with those reported in the literature: a sagebrush shrubland state associated with little disturbance, a native grassland state associated with past wildfire, and a state dominated by crested wheatgrass understory associated with reclaimed homesteads. The shrubland state consisted of two communities: one characterized by both sagebrush and antelope bitterbrush shrub cover and a diverse herbaceous understory; the other with primarily sagebrush shrub cover and an understory dominated by needle-and-thread grass. Quantitative analyses revealed elevation as the primary variable explaining differences between these shrubland communities, but this attribute may be correlated with other differences revealed

from stakeholder knowledge of the region, particularly historic grazing regime, livestock type, and/or wildlife use patterns. Further investigation of these data, gleaned from interviews with stakeholders, will be used to refine this STM.

Contrary to the predominate patterns reported in the literature, the grassland states exhibited the lowest mean cheatgrass cover and the shrublands the highest. This may indicate that native shrubland understory is resilient to post-fire cheatgrass invasion after fire within some range of conditions (e.g., pre-fire vigor of herbaceous species, pre- and post-fire precipitation patterns, invasion vectors, fire conditions), the specifics of which warrant additional focused study. The effect of post-fire seeding of native species on herbaceous community recovery remains unclear. Shrublands appear to recover from mechanical shrub treatments in 15 years or less; the drag treatment may improve recovery times and forb component, although low sample sizes limit the conclusiveness of trends observed.

#### *Mountain Big Sagebrush Study Area*

Nitrogen transformation rates do differ between Diverse and Depauperate shrubland states in the Mountain big sagebrush system studied. However, these differences appear to be influenced not only by litter quality, but also substantial soil texture differences between two associations. It may be that texture is the primary factor governing herbaceous understory vulnerability to long-term summer grazing, by controlling soil moisture, fertility, and nitrogen cycling rates, and thereby compensatory growth response. However, without complete stratification of states sampled across all combinations of soil texture and grazing history, it is

difficult to know the scope of interaction between these factors and their effect on system resilience.

## METHODS TO IMPROVE STMs

### *Investigate the Influences of Multiple Environmental Gradients and Disturbances on Vegetation*

The NRCS ecological site concept aims to classify land according to the abiotic characteristics (e.g., topography, soils, and climate) that govern plant association structure and function. Thus, STMs are often developed at the ecological site scale, since this resolution is considered to encompass the limits of a system's resilience (Bestelmeyer et al. 2009). However, abiotic gradients can exist at multiple spatial scales, including within an ecological site (Charley and West 1975, Lane et al. 1998, Bestelmeyer et al. 2009, Kachergis et al. 2012, Tietjen 2015). Thus, it is important to investigate the extent of these gradients within and among ecological sites of interest and their potential influences on the attributes to be described in an STM. Unconstrained ordination techniques such as Nonmetric Multidimensional Scaling (NMS) can reveal abiotic gradients as correlations between abiotic attributes and patterns in the distribution of sample unit attributes (e.g., species cover or site characteristics). NMS can also reveal patterns in sample unit attribute distribution that are unaccounted for by the explanatory variables measured; this may indicate the influence of a gradient in some variable not included in the original sampling design.

When sample units in ordination space appear to be strongly influenced by one or more distinct, wide-ranging abiotic gradients, a single STM may be insufficient to describe the resilience dynamics of the entire study area. However if the range of the gradient is relatively

narrow, and/or the distribution of sample unit groups of interest (e.g., States or Ecological sites) appears to have little correlation to study area gradients, a single STM that describes local abiotic influences on vegetation dynamics may be sufficient to describe vegetation-site-disturbance dynamics of the study area. Thus the range of abiotic variability described by an STM may not necessarily correlate with the abiotic boundaries described by an ecological site.

The relative contributions of abiotic characteristics and disturbance factors to the plant associations in a system can be revealed using multinomial logistic regression; a least absolute shrinkage and selection operator (LASSO) may assist in selecting the most influential explanatory variables from a suite of highly-correlated covariates. These variables may then guide the development of specific testable hypotheses regarding mechanisms by which disturbances, site characteristics, and functional attributes of a system may interact to influence vegetation association patterns.

#### *Define States According to Both Structure and Function*

STMs have been criticized for failing to portray non-equilibrium dynamics and the roles of ecosystem processes in vegetation association patterns. Defining states as both structurally *and* functionally distinct plant associations makes functional change implicit in the state-transitions included in the resulting STM. These functional differences can then be considered in conjunction with structural characteristics, prominent environmental gradients and influential disturbance factors to hypothesize testable ecological process mechanisms to explain observed vegetation association patterns and disturbance responses. However, careful consideration should be made prior to sampling as to the functional attributes to measure, to insure that the

most plausible explanatory variables are considered. STMs that describe the specific structural-functional dynamics of states provide more information about what makes states vulnerable to transition or resistant to restoration, and may better guide management actions to prevent undesirable transitions and devise better restoration strategies.

#### *Evidence Should Include Observational and Experimentally-Derived Data*

This work demonstrates that the collaborative STM development process proposed by Kachergis et al. (2013c) can successfully generate a conceptual, knowledge-integrative STM for a management region that is relevant to stakeholder interests and backed by empirical evidence. However, the resulting STM presented here contains many assumptions and leaves many uncertainties unresolved (Figure 2.8). To fully implement the Kachergis et al. process, hypotheses associated with these uncertainties must be experimentally tested to reveal which observed patterns represent actual cause-effect relationships, and which are merely correlated. This may be done using rigorously designed adaptive management experiments to make inferences to the specific study area (Step 3 in the Kachergis et al. process, see Figure 1.1), or more broadly across a number of similar systems; rigorous meta-analysis of existing experimental data from similar systems may also be helpful where implementation of new treatments and additional field sampling is infeasible. Because environmental gradients can govern the resilience of systems to disturbance, experiments should not only manipulate treatment types, but also include a large number of replicates across the range of predominate environmental gradients in the study area.

## ADDITIONAL CHALLENGES

While the studies described above made strides to address common criticisms of STMs, additional challenges remain. One of the most obvious omissions from the work presented here is the lack of consideration of the influence of climate variability on ecosystem resilience. Climate can influence both the frequency and severity of disturbance (e.g., drought may make fires more likely and more severe) and the direct vegetation response to disturbance (e.g., favorable precipitation may improve understory regrowth after fire). Climate also interacts with other abiotic conditions to influence resilience of structural-functional relationships in a system. For example the timing of precipitation events may interact with soil texture to influence soil moisture profiles and thereby plant functional group composition (Sala et al. 2015). However, it is nearly impossible to infer the influence of climate variability on these factors in retrospective, point-in-time observational studies. Future experiments building off the work presented here would do well to include long-term monitoring of climate data, or even precipitation-temperature manipulation treatments, in the study design.

In addition, while uncertainties regarding the relationships between system components are relatively explicit in the models presented here, the actual probabilities of disturbance and associated uncertainties remain unaddressed. Long-term datasets or large-scale experimental manipulations might reveal these patterns, or they might be derived from meta-analysis of the literature. However, an additional approach might be to use the odds ratios derived from a Multinomial Logistic Regression to determine the *relative* risk of transition to a state from some initial reference condition. This approach makes some assumptions about the structure of the

STM – most notably that all states can transition from an initial state – and it requires substantial sample size and confidence in the ecological plausibility of the explanatory variables included in the model. However this approach may be fruitful for generating plausible, initial STM probabilities that can then be tested experimentally or in a simulation.

Finally, the integrative approach used here, while an excellent avenue for generating many research questions of interest to stakeholders, can also create challenges in achieving adequate sample sizes. This can come about if researchers become “spread too thin” trying to address all the questions of interest with limited resources. In addition, limitations in access to a variety of sampling locations to may result in pseudo-replication of plots within a few treatments. Thus, it is imperative that researchers following the Kachergis et al. approach follow a very intentional balancing act between gathering stakeholder input and limiting research scope to that which can be achieved with the resources available. After all, while an iterative process that generates both questions and answers can improve long-term research outcomes, it can also substantially hinder the process when statistical power is insufficient to adequately answer the questions of interest.

#### FINAL THOUGHTS

State-and-Transition models have great potential both as an outreach and education tool and for improving knowledge of ecosystem dynamics. A knowledge-integrative, collaborative approach to model development can certainly facilitate both objectives. However, at the same time, there is substantial potential for project participants to become caught in the trap of “serving two masters”, where success is defined both by successful implementation of

the *process* as well as by achieving scientifically rigorous and meaningful *results*. While these two goals may at times be synergistic, they may also conflict. For example, collaborative efforts may leverage additional resources for expanded field sampling or new datasets, while the need to achieve necessary statistical power may necessitate the abandonment of a research question of great interest to some stakeholders. Thus, it is important for collaborative projects to set clear expectations for all participants, make clear the potential for difficult trade-offs, and clarify project objectives at the beginning and throughout the research process. It is also important for leadership of collaborative projects to include both individuals with people-management skills and those with research project management and study design expertise, and that these individuals recognize and support the varied goals of the project.

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