Revision of a state-and-transition model to include descriptions of state functional attributes

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Abstract. Successful conservation of ecosystems and ecosystem services requires understanding the structural–functional relationships underlying resilience to disturbance pressures. State-and-transition models (STMs) are box-and-arrow diagrams conceptualizing system resilience, but many STMs lack functional descriptions. For a cattle-grazed sagebrush steppe ecosystem in northwestern Colorado, we aimed to update an existing STM by incorporating functional descriptions of the states to inform future hypotheses. In this STM, a diverse set of native perennial understory plants define a Diverse state, but long-term exclusion of disturbances to sagebrush results in a shift to a Depauperate state with increased bare ground interspaces and sagebrush dominance. We hypothesized that herbaceous species were inferior competitors to sagebrush over the long term for soil nitrogen. To examine evidence for this hypothesis, develop functional descriptions of the Diverse and Depauperate states, and identify more specific hypotheses for future studies, we measured the following: the mass, C:N, and distribution of the litter layer; nitrogen mineralization rates; nitrate pools; and soil attributes on plots classified as Diverse (n = 5) or Depauperate (n = 5). Plots in the Depauperate state had ~20% higher soil bulk density, half the clay and soil moisture concentrations, and 30% lower percent soil nitrogen compared to Diverse state plots; litter layer patchiness was nearly three times greater on the Depauperate plots than on the Diverse plots, but there was no significant difference between states in mean litter layer mass or C:N. We detected no significant differences between states in nitrogen mineralization rates or nitrate pools. This may be due to our sampling design, which examined nitrogen transformation at the plot level rather than at microsites within the plots, or it may be that another resource such as soil moisture is more limiting than nitrogen. Differences in soil texture between plots in the Diverse and Depauperate states may indirectly influence the competitive interactions between sagebrush and native herbaceous understory by controlling available soil resources. These results suggest that the vulnerability of sagebrush steppe ecosystems to state changes may be dependent on soil texture, which is highly variable across this broadly distributed ecosystem. Based on these insights, we present a revised STM and propose future work.

Key words: Artemisia tridentata; ssp. vaseyana ecological function; feedback; inverse-texture hypothesis; livestock grazing; nitrogen mineralization; northwest Colorado; rangeland; state-and-transition model.

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INTRODUCTION

Many ecosystems are experiencing major environmental changes, including climate change, altered nutrient cycling patterns, and intensified resource exploitation, that fundamentally alter ecosystem structure and function and result in the loss of critical ecosystem services (Scheffer
et al. 2001, Havstad et al. 2007, Quetier et al. 2007). Alterations to the structure (e.g., plant community composition, spatial arrangement) and function (e.g., nutrient cycling, hydrology) of ecosystems can exacerbate or diminish the effects of a disturbance (Briske et al. 2006) through changes to the internal feedback loops of the ecosystem. For example, plants may respond to herbivory by producing nitrogen-rich compensatory growth that increases nitrogen cycling and sustains abundances of palatable species; alternatively, when resource scarcity limits compensatory growth, grazed plants may be replaced by unpalatable, high C:N species which decompose and cycle N more slowly and compete better for limited resources, exacerbating the effects of herbivory (Hobbie 1992). Resilience is a measure of a system's ability to experience temporary alterations to structural or functional attributes yet maintain internal feedbacks that buffer these effects; the larger the changes a system can withstand, the more resilient that system is (Holling 1973). Successful conservation and restoration of ecosystems and the services they provide requires understanding of the structure–function relationships underlying their resilience to acute and chronic disturbance pressures (Holling 1973, Stringham et al. 2003, Briske et al. 2006).

Resilience dynamics across a landscape are moderated by local abiotic conditions such as soil texture, elevation, hydrology, and climate (Bestelmeyer et al. 2009, Lopez et al. 2013, Tietenjen 2016). In the United States, the ecological site land classification system defines land units at a scale relevant to management according to the specific abiotic characteristics (e.g., elevation, hydrology, topography, soils) that bound the potential vegetation and disturbance responses of that site (USDA-NRCS 2003, Bestelmeyer et al. 2009, Caudle et al. 2013). Specific resilience dynamics within an ecological site can be conceptualized by box-and-arrow diagrams called state-and-transition models (STMs; Fig. 1; Westoby et al. 1989). State-and-transition models make explicit the known and unknown attributes of an ecosystem, making them useful for both describing resilience dynamics and devising testable hypotheses to further refine that knowledge. Ideally, STMs are iteratively tested and revised based on what is learned about a system (Holling 1978, Jackson and Bartolome 2002, Kachergis et al. 2013b). Many STMs describe state resilience in terms of plant community structure observed over time or in association with particular disturbances such as fire, landslides, or grazing (Bagchi et al. 2013, Bestelmeyer et al. 2013, Kachergis et al. 2013a, 2014, Stein et al. 2016). While STMs that are defined purely by structural attributes can provide valuable information about vegetational change for a site, they do not describe the underlying structural–functional feedbacks that contribute to resilience. State-and-transition models that include such descriptions of ecological function can provide better guidance than structural descriptions alone for managers designing conservation and restoration prescriptions that enhance ecosystem resilience (Stringham et al. 2003, Bestelmeyer et al. 2006, Briske et al. 2008, Kachergis et al. 2011, Lopez et al. 2013).

Improving the functional descriptions for STMs of big sagebrush ecosystems is a priority for managing this ecosystem, which covers ~45 million hectares and provides forage and habitat for wildlife and domestic livestock, and economically important recreation (West 1983). Loss of native perennial understory and increased sagebrush dominance, as occurs in the transition from a Diverse sagebrush steppe state to Depauperate sagebrush shrubland state (Fig. 1), alters forage availability and habitat for both livestock and wildlife, modifies hydrologic function, increases soil erodibility, and facilitates invasion by exotic plants such as cheatgrass (Bromus tectorum), which in turn may increase wildfire frequency and extent (West 2000, Knick et al. 2003, Davies et al. 2011, Reisner et al. 2013, Chambers et al. 2014). These changes are widely viewed as undesirable by both ranchers and conservation managers, but it is not always clear how the transition is triggered nor how to reverse it.

Nitrogen has been shown to limit plant growth in semi-arid systems like sagebrush steppe (Charley and Cowling 1968, Bolton et al. 1990, West 1991), especially in soils with lower clay content (Van Veen et al. 1985, Barber 1995). According to resource competition theory, in nutrient-limited systems, species that are superior competitors might not only tolerate lower concentrations of soil nutrients, but also depress nutrient availability (Titman 1976, Tilman 1982,
For example, slow-growing, long-lived species may accumulate a limited nutrient in their aboveground tissues, thereby reducing nutrient concentrations in soil, and species with higher nutrient use efficiency may deposit litter with lower concentrations of the limiting nutrient, which could reduce rates of nutrient cycling (Hobbie 1992, 2015, Aerts and Chapin 2000, Knops et al. 2002, Chapman et al. 2006). Big sagebrush has been observed to better tolerate lower soil nitrogen availability and slower nitrogen cycling than relatively nitrogen-rich, short-lived herbaceous species (Chen and Stark 2000). Further, sagebrush also produces long-lived leaves containing substantial quantities of carbon-rich phytochemicals and lower leaf nitrogen concentrations (Kelsey et al. 1982, Turi et al. 2014), which may in turn reduce nitrogen

Fig. 1. State-and-transition model for the Mountain Loam ecological site in northwestern Colorado according to Kachergis et al. (2012). Boxes are potential alternate states with different species composition; arrows mark potential transitions associated with site history and environmental variation. Modified from Kachergis et al. (2012: Fig. 5, Table 5).
cycling and availability in the soil (Hobbie 1992, 2015).

Thus, we reasoned that on the nitrogen-poor soils of the Mountain Loam sagebrush steppe, and especially in areas with lower clay content within this ecological site (like those on which Depauperate state often occurred in Kachergis et al. 2012), big sagebrush may be a superior competitor for nitrogen compared to native bunchgrass species. However, because big sagebrush is slow-growing, this advantage may not become apparent as widespread understory loss until sagebrush has grown undisturbed for extended periods, as Kachergis et al. (2012) observed. If the structural differences between the Depauperate and Diverse states are related to functional differences in nitrogen cycling and availability, we would expect that (1) there would be lower soil N, lower soil moisture, and slower N mineralization rates on plots in the Depauperate state and that (2) the relative abundance of nitrate would be lower because the slower N mineralization would limit the availability of ammonium as a substrate for nitrifying soil bacteria. We expected the loss of herbaceous cover and expansion of sagebrush on the Depauperate state would (3) increase the patchiness of litter mass distribution, but that (4) the spatial heterogeneity of litter quality would be more homogenous due to a small contribution of herbaceous species and, finally (5) that the litter quality would be poorer on plots in the Depauperate state as indicated by greater C:N ratio. To examine evidence for these predictions and further develop the functional descriptions of the Diverse and Depauperate states for the Kachergis et al. (2012) STM, we measured leaf litter mass, C:N, and distribution; nitrogen mineralization rate; nitrate pools; and other soil attributes (e.g., texture) on plots classified in Diverse and Depauperate states in a mountain big sagebrush ecosystem in northwestern Colorado.

METHODS

Site selection and sampling design

The study area encompassed three private ranches on the Mountain Loam ecological site (USDA-NRCS 1994) in the Elkhead watershed in northwestern Colorado (40°38.5’ N, 107°12.5’ W). Mountain Loam soils in this area have deep clay loam or clay subsoils beneath a thin clay loam or clay surface soil and support mountain big sagebrush (Artemisia tridentata ssp. vaseyana) as the dominant species (Kachergis et al. 2012). Previous work by Kachergis (2011) and Kachergis et al. (2012) in this region produced a data-driven STM for the Mountain Loam ecological site, using agglomerative hierarchical cluster analysis of foliar cover to determine potential states and nonmetric multidimensional scaling to investigate the site characteristics and past management activities statistically correlated with those states. This STM included the transition from a Diverse to a Depauperate state (called “Dense” by the authors), described above, and associated with a long-term lack of shrub disturbance (e.g., by fire or herbicide; Fig. 1). To improve understanding of the ecological functional attributes associated with these states, we examined structural and functional ecosystem attributes on these Diverse and Depauperate states over the 2014 growing season.

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; these 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. The number of replicate plots was limited to five per state due to limited access to additional land.

Plots were 50 × 50 m and contained two transects placed 15 m apart, parallel to the hillslope and centered on the plot center. One set of two semi-permanent 50-m transects spaced 15 m apart were used for soil and litter sampling (see Soil sampling for N mineralization and Litter collection and chemical analysis methods below). Another set of five 50-m transects spaced 12.5 m apart were established for vegetation and site data sampling. 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 and site data sampling

Foliar cover by species was measured using the line-point intercept method (Bonham 1989) at
1-m intervals (points) along each transect (250 points per plot). The length of bare ground interspaces between perennial plant bases (i.e., basal gap) was measured using the continuous gap intercept method (Herrick et al. 2005, minimum gap size 25 cm). Vegetation state on each plot was verified as Diverse or Depauperate by visual inspection before sampling the plot, and further validated after sampling by comparing measured foliar cover and basal gap size to the descriptions for each state presented in Kachergis (2011) and Kachergis et al. (2012). We also tested for statistical differences between our determined states with respect to vegetation attributes considered most illustrative of those states (i.e., basal gap size and sagebrush/grass/herbaceous/native herbaceous percent cover). These data are summarized in Appendix S1: Tables S1, S2).

A soil pit was dug to at least 50 cm at the plot center and soil characteristics described following NRCS protocols (Schoeneberger 2002). Plot slope was measured by inclinometer, aspect by compass, and elevation by GPS. Aspect was transformed into a continuous variable ranging from 0 to 2 whose largest values are associated with more productive northeast facing slopes and lowest values with less productive southwest-facing slopes (Beers et al. 1966). Study area elevation and slope ranged from 2086 to 2249 m and 0% to 36%, respectively.

Precipitation was measured by a rain gauge located near the center of the study area and recorded for each precipitation event by a local landowner (Table 1). In addition, mean monthly temperature and precipitation for 2014 and the 30-yr average were downloaded for the closest Colorado Climate Center weather station located in Hayden, Colorado, USA, approximately 30 km south of and 177 m below the center of the study area. Mean monthly precipitation is derived from measurements of each individual precipitation event taken from a rain gauge in the study area.

Soil sampling for N mineralization

Soil sampling for nitrogen mineralization estimates occurred during the 2014 growing season over three incubation periods. Incubation periods were consecutive and lasted at least 30 d, with specific sampling dates determined by site accessibility and availability of labor force:

1. Early season: June 5 through July 7th and 8th (32/33 d)
2. Mid-season: July 7th and 8th through August 13th and 14th (36/37 d)
3. Late season: August 13th and 14th through September 28th and 29th and October 3rd (45/46/47/51 d). The end-date of this period varied due to weather which made three of the sites inaccessible until October 3rd.

At the beginning of each incubation period, two sets of soil samples were created: one set of extracted soil cores and one set of PVC tubes installed in situ in the field. Each set was comprised of six samples, taken from three random points along each transect. Each sampler (soil corer or PVC tube) extracted soil in a 5 cm diameter tube to 20 cm depth. We chose the depth of 20 cm because this is the depth to which Kachergis et al. (2012) found the greatest root density on Mountain Loam sites. PVC tubes were capped to prevent leaching (Binkley and Hart 1989). The 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. After 30–50 d, the in situ PVC tubes were removed, a new batch of six PVC tubes installed and a new set of soil cores taken at new random points along the transects. Each set of initial and PVC tubes 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.

Soil physical and chemical analysis

For each incubation period, each set of soil cores and each set of PVC samples were composited by plot, sieved to 2 mm and roots were removed by hand. Subsamples were taken from the first set of composite samples (early season) 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 laboratory following McLean (1982). Total N and C were determined from a 10-g subsample using a LECO Tru-SPEC elemental analyzer (Leco, St. Joseph, Michigan, USA). Inorganic C was determined by pressure transducer following acid addition. An independent set of six cores per plot, taken from three different random points per transect, were used to measure soil bulk density in late September or early October. Bulk density of the soil fraction <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, and inorganic nitrogen concentrations per gram of dry soil to

Fig. 2. Monthly temperature and precipitation for 2014 compared to the 30-yr average as measured at the Colorado Climate Center weather station in Hayden, Colorado, USA, approximately 30 km south of and 177 m below the study area.
grams per unit soil 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 subsample and inorganic nitrogen was extracted from a 15-g subsample using 75 mL of 2 mol/L KCl within one week of collection (Keeney and Nelson 1987). 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, Texas, USA). Net nitrogen mineralization for each incubation period at each plot was computed as the difference in total inorganic nitrogen (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 mass of nitrogen per volume of soil was also computed, since total nitrogen available will influence nitrogen mineralization rates. Finally, the ratio of nitrate to total inorganic nitrogen (NO₃:N) 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 collection and chemical analysis

Aboveground leaf litter and duff (hereafter referred to simply as “litter” or the “litter layer”) were 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. Hence, there were six subsamples per plot. Litter samples were air-dried for several weeks in the laboratory and the herbaceous fraction isolated. Each sample was ground, weighed and C and N concentrations determined with an elemental analyzer (Bremner 1996, Nelson and Sommers 1996). Large mineral soil aggregate contaminants were removed by hand and surface contamination on the litter particles themselves remained. A dry ashing method similar to Nes (1975) was employed to correct for this mineral soil contamination. A subsample of each herbaceous litter sample collected was ignited at 600°C for 5 h in a muffle furnace (Nes 1975), and the mass of the resulting ash, assumed to be derived primarily from mineral soil, was determined as a proportion of the original sample mass. Thus, percent ash content was used to gravimetrically determine the extent of mineral soil contamination and thereby to adjust measured C, N, and litter mass values.

Data analysis

Exploratory data analysis was performed generating summary statistics and graphics. To model litter mass and litter C:N, for which we had subsamples within each plot, we fit a two-level linear mixed model with state fixed effects for Diverse and Depauperate and random effects for plots nested in communities and subsamples nested in plots. Comparing between state types, F tests were used to test for differences in means, while likelihood ratio tests were used to test for differences in within-plot variances. Standard residual diagnostic plots were used to check the assumptions of the model.

Differences in percent and grams soil carbon and nitrogen, soil C:N ratio and pH, for which data were summarized at the plot level at a single time point, were modeled using the t test. Due to skewed sampling distributions, differences in percent absolute foliar cover were modeled using the Wilcoxon rank sum test. P-values were corrected for multiple comparisons according to Hommel (1988). Patterns in soil moisture, nitrogen mineralization rate, and the proportion of inorganic nitrogen as nitrate (NO₃:N), for which data were summarized by plot and measured at multiple incubation periods, were modeled using a two-factor, repeated measures ANOVA. Litter modeling was done using SAS for Windows software, version 9.4 (SAS Institute, Inc., Cary, North Carolina, USA). Vegetation and soil modeling was done in R, version 0.99.491 (R Foundation for Statistical Computing, Vienna, Austria). For all tests, results were considered statistically significant at P-values <0.05.

RESULTS

Similar to Kachergis et al. (2012), we found that Depauperate state soils had about half the
clay content of the *Diverse* state soils (Fig. 3); soil bulk density of the *Depauperate* state was 20% greater than the *Diverse* state soils (Table 2). As anticipated, percent soil nitrogen was 30% lower in the *Depauperate* state soils compared to the *Diverse* soils, but when normalized by soil bulk density the two states showed no difference in total soil nitrogen content (Table 2). Consistent with our predictions, soil moisture on the *Depauperate* state soils was about half that of the *Diverse* state soils (Table 3, Fig. 4).

States also differed in litter attributes somewhat as predicted: The patchiness of litter mass on the surface of soil in *Depauperate* plots was about three times greater than *Diverse* plots (Table 2). Although we detected no statistically significant ($\alpha = 0.05$) difference between states in mean litter C:N mean or in the variance of litter C:N within plots (Table 2), the mean C:N of litter in *Depauperate* plots was slightly higher (15%) than that in *Diverse* plots ($P = 0.08$), as predicted.

We found no statistically significant differences between states for any of the nitrogen cycling metrics (Table 3, Fig. 5). We did, however, detect significant effects of incubation period. From the early to mid-season incubation periods, soil moisture on both states declined by ~20% (Table 3, Fig. 4), while the proportion of inorganic nitrogen as nitrate (NO\textsubscript{3}:iN) more than doubled from the mid- to the late-season incubation periods. We also observed decreases in the non-normalized mineralization rate to nearly zero on both states during the mid-season incubation period, although this trend was not statistically significant for $\alpha = 0.05$ ($P = 0.06$) and disappeared once mineralization rate was normalized by total soil nitrogen (Table 3, Fig. 5). There were no interactions between states and incubation periods for any of the metrics considered (Table 3).

**Discussion**

We aimed to revise an existing, data-driven STM focused on structural descriptions of states to include descriptions of ecological function which we reasoned could contribute to state transition. We hypothesized that the lower clay content of *Depauperate* soils would allow plots on this state to retain less soil nitrogen and moisture, and thus exhibit slower nitrogen mineralization and less inorganic nitrogen as nitrate. While we did find that plots in the *Depauperate* state had substantially lower clay content, soil moisture, and percent soil nitrogen, these differences did not translate into plot-level differences in nitrogen transformation between states. Moreover, we found no difference in total soil nitrogen between states, suggesting that the higher percent nitrogen detected in soils on plots in the *Diverse* state was indicative of that state’s lower soil bulk density, rather than a greater abundance of nitrogen. In addition, our observation of period effects, but no state effects, on nitrogen transformation rates may indicate that variations in soil conditions (e.g., soil moisture, temperature) over the course of the growing season are a greater moderator of nitrogen transformation in this system than differences in soil conditions between states. For example, increases in soil moisture from the mid- to late-season incubation periods may have increased the activity of nitrifying bacteria, resulting in the higher NO\textsubscript{3}:iN observed in the late-season period.

We also predicted that the structural differences between states (greater bare ground inter-spaces and greater sagebrush dominance on plots in the *Depauperate* state) would contribute to differences in the distribution and quality (C:N ratio) of the litter layer. As predicted, we observed the mass of the litter layer to be more patchily distributed on plots in the *Depauperate* state and to have a higher C:N ratio (albeit the
significance of the latter difference was slightly beyond the alpha value of 0.05), but the spatial variability of the C:N ratio did not meet our expectations (it was not lower in the Depauperate state). Thus, while the leaf litter layer on the sagebrush-dominated Depauperate state may be somewhat less nitrogen rich overall, native herbaceous cover on the Diverse state may have been replaced by bare ground interspaces on the Depauperate state with no net effect on the spatial variability of litter C:N.

It is unclear whether the differences we observed between states in soil moisture, percent nitrogen, and litter characteristics contributed to understory loss, resulted from understory loss, or are simply a function of pre-existing differences in soil properties (e.g., texture). We have revised the Kachergis et al. (2012) STM Transition 2 to document the differing functional attributes we found on the two states, and to highlight remaining uncertainty regarding the functional differences between states and the mechanistic links among the structure and function of each state, especially as related to plant-soil interactions (Fig. 6).

The resolution and structure of our sampling design may have contributed to our inability to detect differences between states and to sufficiently test our hypotheses. Long-grazed sagebrush systems like our study area have often been characterized as exhibiting “islands of fertility,” where belowground resources, especially nitrogen, are concentrated beneath shrubs and scarce in interspaces, especially as herbaceous cover declines (Schlesinger et al. 1990, 1996, Allington and Valone 2014). Indeed, the patchier spatial distribution of leaf litter we detected on the Depauperate state may be linked to more heterogeneous patterns of belowground resource pools and nitrogen cycling as this litter decomposes, but our coarse sampling resolution (aggregated to the plot level) would not have detected this. Others who have linked differences in leaf nitrogen concentration to differences in available soil nitrogen have stratified soil sampling locations by species or functional type (Wedin and Tilman 1990, Berendse 1994, Reich et al. 2001). Such finer-scale investigation of nitrogen cycling differences between states at microsites within plots might have revealed stronger structure-function relationships. In addition, soil texture is known to broadly influence vegetation associations by control of resource retention, both

Table 2. Results of tests for differences in soil attribute means, leaf litter attribute means, and leaf litter attribute variances on Depauperate and Diverse states sampled in 2014 on the Mountain Loam ecological site, Elkhead Watershed, Routt County, Colorado.

| Attribute                      | State                  | Test statistic (T or F) | P       |
|-------------------------------|------------------------|-------------------------|---------|
| Soil                          |                        |                         |         |
| Bulk density (g/m² to 20 cm depth) | 661 ± 16               | 544 ± 18                | 4.8     | 0.01   |
| Percent carbon                | 1.7 ± 0.09             | 2.5 ± 0.3               | –2.8    | 0.15   |
| Percent nitrogen              | 0.17 ± 0.007           | 0.24 ± 0.02             | –3.7    | 0.03   |
| Total carbon (g/m² to 20 cm depth) | 11.3 ± 0.6             | 13.4 ± 1.1              | –1.7    | 0.41   |
| Total nitrogen (g/m² to 20 cm depth) | 1.1 ± 0.04             | 1.3 ± 0.07              | –2.3    | 0.21   |
| C:N                           | 10.4 ± 0.2             | 10.3 ± 0.3              | 0.16    | 0.88   |
| pH                            | 5.7 ± 0.04             | 5.6 ± 0.02              | 0.5     | 0.88   |
| Leaf litter (means)           |                        |                         |         |
| Leaf litter mass (g/m²)       | 110 ± 27               | 75 ± 21                 | 1.06    | 0.33   |
| Leaf litter C:N               | 37 ± 1.9               | 32 ± 1.9                | 3.96    | 0.08   |
| Leaf litter (variances)       |                        |                         |         |
| Mass (variance)               | 135.2 (79.9, 249.9)    | 43.0 (26.1, 78.1)       | 7.85    | 0.005  |
| C:N (variance)                | 39.5 (23.9, 71.8)      | 41.4 (24.9, 75.9)       | 0.01    | 0.91   |

Notes: CI, confidence interval; SE, standard error. Mean soil attribute differences were tested using the t test ($n = 5$) and values reported by state are mean ± SE. Mean litter attribute differences were tested using $F$ tests and values reported by state are mean ± SE. Differences in within-plot variances of litter attributes were tested using the likelihood ratio test based on a chi-square distribution with 1 degree of freedom; values reported for tests of variances are the estimate and 95% confidence interval. P-values considered significant at $a = 0.05$ are reported in bold.
generally and by depth (Noy-Meir 1973, Sala et al. 1988, Bagchi and Ritchie 2011, Gaur and Mohanty 2013). Thus, competitive interactions between sagebrush and native herbaceous plants, and the impact of these different plant types on soil resources, may be more apparent at shallower or deeper depths than we sampled (0–20 cm).

It may be that soil moisture, a function of soil texture, is a key limiting resource in the Mountain Loam ecological site, rather than nitrogen and nitrogen cycling rates. Coarser-textured soils tend to lose moisture at lower water potentials than finer-textured soils. Thus, on coarser-textured soils native herbaceous species, which tend to be relatively shallow-rooted, might be particularly poor competitors for limited soil moisture compared to deep-rooted big sagebrush. This could mean that the native herbaceous understory on coarser-textured soils is more vulnerable to resource stress (e.g., summer drought) and disturbances (e.g., grazing) than the native understory on finer-textured soils (Sturges 1977, Darrouzet-Nardi et al. 2006, Chesus and Ocheltree unpublished data). This texture-vulnerability hypothesis could explain both the high sagebrush cover and the absence of diverse native herbaceous understory and the on the Depauperate state, as well as the tendency for the Depauperate state to occur on soils with lower clay content. Of course, this assumes that the vegetation on plots now observed as Depauperate once resembled the Diverse state, and is not merely a function of pre-existing differences in soil texture and other properties. Extensive landowner interviews by Kachergis (2011) and Kachergis et al. (2012) to collect site histories of Diverse and Depauperate plots, as well as visual inspection of areas long fenced off from grazing and adjacent to Depauperate plots, both suggest that those plots once resembled the Diverse state in terms of plant community composition and cover. Critical to validation of this hypothesis would be location and examination of Diverse plots on coarser-textured soils. If Diverse states cannot be found on lower clay sites, then perhaps the Diverse and Depauperate states represent the natural variation in vegetation concomitant with soil texture, rather than alternate states linked by a transition. Such a finding would indicate that the Mountain Loam ecological site as defined by Kachergis et al. (2012), warrants substantial refinement.

Future work should include examination of soil resources at microsites within plots and

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**Table 3. ANOVA results testing for differences in soil moisture, absolute and normalized soil nitrogen mineralization rates, and proportion of inorganic soil nitrogen as nitrate (NO$_3$-N) between Depauperate and Diverse states over three incubation periods sampled in 2014 on the Mountain Loam ecological site, Elkhead Watershed, Routt County, Colorado.**

| Contrast                        | df | SS   | F     | p    |
|---------------------------------|----|------|-------|------|
| Soil moisture                   |    |      |       |      |
| State                           | 1  | 247  | 60.3  | <0.001|
| Period                          | 2  | 42.3 | 17.7  | <0.001|
| State × Period                  | 2  | 0.96 | 0.4   | 0.68  |
| Mineralization rate (absolute)  |    |      |       |      |
| State                           | 1  | 0.001| 0.39  | 0.55  |
| Period                          | 2  | 0.03 | 3.48  | 0.06  |
| State × Period                  | 2  | 0.007| 0.79  | 0.47  |
| Mineralization rate (normalized)|    |      |       |      |
| State                           | 1  | 0.00005| 0.18 | 0.90  |
| Period                          | 2  | 0.004| 0.49  | 0.62  |
| State × Period                  | 2  | 0.006| 0.72  | 0.50  |
| NO$_3$:N                        |    |      |       |      |
| State                           | 1  | 0.00001| 0  | 0.99  |
| Period                          | 2  | 0.39 | 7.1   | 0.006 |
| State × Period                  | 2  | 0.07 | 1.3   | 0.31  |

**Note:** P-values considered significant at α = 0.05 are reported in bold.

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**Fig. 4. Trends in percent soil moisture at the beginning of each incubation period on Depauperate and Diverse states sampled in the Elkhead Watershed, Routt County, Colorado, USA.**
along the vertical soil profile on sites classified as Diverse and Depauperate states occurring across a similar range of soil textures within the Mountain Loam ecological site, to determine the relative contributions of soil texture and other functional attributes (e.g., plant traits) on the interactions among sagebrush, herbaceous species, and soil resources. Experimental manipulations of factors
such as shrub disturbance and grazing intensity on *Diverse* states across a soil textural gradient within the Mountain Loam ecological site could also reveal whether sites with lower clay content in this ecological site are more vulnerable to understory loss given certain external pressures (e.g., grazing). Further investigation of the texture-vulnerability hypothesis could be of particular interest for rangeland management. For example, if the *Diverse* state is more vulnerable to a transition to the *Depauperate* state where soils are coarse or nutrients are more limiting (which would make nutrient losses to disturbances such as grazing more costly for the relatively nutrient rich, herbaceous plants), then stocking rates on coarser-textured soils within the *Diverse* state may need to be more conservative than site productivity alone might suggest. Indeed, in semiarid regions such as the sagebrush steppe, plant communities on coarser-textured soils tend to have higher aboveground net primary productivity, due to deeper moisture penetration and less evaporative moisture loss, than communities on finer-textured soils (Noy-Meir 1973, Sala et al. 1988). However, if coarser-textured soils, while more productive, are also more vulnerable to

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**Fig. 6. Transition 2 from the Kachergis et al. (2012) Mountain Loam state-and-transition model, revised to document functional attribute differences and to highlight remaining uncertainties regarding state functional differences and plant–soil interactions.**

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**Mountain loam transition 2**

Associated with sites experiencing lack of shrub disturbance (spraying or fire) for several decades. Compared to the *Diverse* state, *Depauperate* states tend to exhibit:

- **coarser soil texture**
- **greater soil bulk density**
- **greater soil percent nitrogen**
- **greater soil moisture**
- **Patchier distribution of leaf litter**

Remaining questions:

- How does soil texture influence soil nitrogen/moisture limitation on these states?
- How do shrub disturbance and grazing interact with soil texture to influence resource limitation on these states?
- How do differences in soil nitrogen and moisture content influence competition between sagebrush and understory species on these states?
- How do soil moisture, nitrogen, and nitrogen cycling compare at microsites within plots and along the soil vertical profile?
understory loss due to resource stress, stocking rates may need to be revised to account for both soil texture and site productivity.

Despite remaining uncertainties, our work is an important contribution to the field of STM development and improvement. Given that STMs are increasingly used for management prescriptions and decision making (Bestelmeyer et al. 2004, Forbis et al. 2006, Caudle et al. 2013, Frid et al. 2013), it is critical that they may be data-driven and include functional and structural descriptions of states, as well as explicitly identify remaining areas of uncertainty. We have provided an updated version of the Diverse to Depauperate transition, as well as explicit mention of key uncertainties (Fig. 6). We have demonstrated a rigorous methodology for evaluating functional attributes of states within a data-driven STM framework to address questions about the ecological drivers of potential state transitions. Such an approach should be part of an iterative process which, along with active adaptive management and ongoing monitoring of state attributes, works to explicitly address remaining model uncertainties with both experimental and observational approaches (Kachergis et al. 2013b). Ultimately, including descriptions of ecological processes and factors such as soil texture, resource cycling dynamics, and moisture regimes in STM state descriptions will improve our understanding of what may make states vulnerable to transitions and improve the utility of STMs to managers interested in preventing, and even reversing, undesirable state transitions.

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