


Plant community change in three Mongolian steppe ecosystems 1994–2013: applications to state-and-transition models

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Abstract. Interacting effects of climate change and livestock grazing on semi-arid grassland ecosystems have not been well studied, especially on a long-term basis. This paper analyzes changes in plant community composition in relation to grazing intensity and climate change based on repeated monitoring along long-term grazing intensity gradients in three Mongolian ecological zones over 20 yr. We synthesized our findings into state-and-transition models of vegetation change, contributing to our understanding of ecological dynamics in relation to management and environmental change, and to the development of tools for resilience-based rangeland management. In the mountain steppe (MS), community composition was driven largely by climate, and transitions from one community to another were associated with climate change or combined climate and grazing effects. The MS experienced the largest number of long-term transitions (14 of 15 plots) over 20 yr. In the steppe (ST), grazing intensity was the strongest influence on community composition, but transitions between communities from the early 1990s to 2013 were most strongly correlated with climate change. Ten of the 15 ST plots transitioned to other communities over 20 yr. Community composition in the desert steppe (DS) was unrelated to either grazing intensity or climate change and only six of 15 plots transitioned permanently over 20 yr. The MS appears most vulnerable to climate-induced community change, as others have suggested. Some degraded ST communities are resilient to climate change, while ST communities on drier sites are vulnerable to grazing-induced community changes. Our findings illustrate the utility of state-and-transition models as a means to synthesize and depict plant community dynamics in relation to climate and management factors. These models identify communities that may be growing rarer or more common under the combined effects of climate change and grazing, and highlight species and communities that may be useful conservation targets or indicators of climate- or grazing-induced change.

Key words: classification; classification and regression tree; climate change; livestock grazing; Mongolia; ordination; rangeland; resilience-based management; semi-arid grassland.

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INTRODUCTION

Rangelands cover about 40% of Earth's terrestrial surface area (Gibson 2009, Wang and

Wesche 2016) and temperate rangelands are considered one of the most threatened ecosystems globally (Sala et al. 2000). The majority of Mongolia's land area is semi-arid and about 80% of its

total territory are rangelands (Hilbig 1995, Serge-lenkhuu et al. 2012), which have been grazed by domestic livestock in an extensive, mobile pastoral system, for thousands of years (Hanks 2010, Honeychurch 2014). Ecological responses of semi-arid grassland ecosystems to combined human disturbances (e.g., livestock grazing) and environmental stress (e.g., climate change) have not been thoroughly studied (Dangal et al. 2016), especially on a long-term basis. This paper reports on a 20-yr observational study of plant community change in relation to grazing intensity and climate change across three ecological zones in Mongolia. As such, it contributes much-needed information on the combined effects of grazing and climate change in one of the world's most important grasslands, with implications for adaptation planning and resilience management in other similar temperate grasslands around the globe.

For more than 4000 yr, mobile pastoralism has been the dominant land use in Mongolia (Fernandez-Gimenez 1999, Hanks 2010, Honeychurch 2014). In the 20th century, Mongolia's rangelands were grazed under several different governance regimes until the early 1990s, when Mongolia transitioned to a market economy and democracy (Fernandez-Gimenez 1999, Johnson et al. 2006, Ojima et al. 2013). Following the transition to a market economy and privatization of state-owned livestock in 1992, livestock populations grew rapidly. The national herd reached a historical record high of 102 million sheep units in 2016 (Mongolian Statistical Information Service, <http://www.1212.mn>), more than double the average stocking level prior to 1990. In addition, rapid climate change is affecting Mongolian grasslands, with an increase of 2.14°C documented over the last 65 yr (Dagvadorj et al. 2009). Extreme weather events such as drought and severe winter weather (*dzud*) may be growing more intense and frequent (Karnieli et al. 2005, Sternberg et al. 2009). Tree-ring analyses indicate that the drought of the early 21st century was the most severe of the past millennium (Pederson et al. 2014).

The combined pressures of increased stocking densities and warming climate have raised concerns about the condition of Mongolia's rangelands. A recent nation-wide assessment of the Mongolia's rangeland health (NAMEM, and

MEGDT 2015) found that 65% of 1450 long-term monitoring sites were altered from reference conditions, and 48% would require more than three years to recover. Seven percent of sites were determined to have persistent degradation that would take longer than 10 yr to recover. The Desertification Atlas of Mongolia reports similar results (Bulgan et al. 2013). According to the atlas, some level of desertification affects 87.9% of Mongolian territory. However, only 9.9% of these changes are classified as very severe and 6.7% as severe (Bulgan et al. 2013).

Repeated monitoring studies have documented declining production and species diversity (Sheehy et al. 2012), and shifts in plant functional types, species cover and richness (Khishigbayar et al. 2015) in some regions, although Khishigbayar et al. (2015) found no changes in total standing biomass or cover at any of their sites. Remote-sensing studies have reported both increases (Liu et al. 2013, Eckert et al. 2015, John et al. 2016) and decreases (Hilker et al. 2014, Eckert et al. 2015, John et al. 2016) in greenness or productivity over the past two decades. Both positive and negative changes are explained in large part by precipitation trends (Liu et al. 2013, Eckert et al. 2015, John et al. 2016), with other contributing factors including deforestation, mining, urban expansion, forest fires, grassland regeneration, increasing livestock densities, and/or changes in herd composition.

Studying how Mongolian grasslands are responding to abrupt changes in both grazing regimes and climate is important to understanding and managing the dynamics of grasslands that are vital to the pastoralist communities who depend upon on the sustainability of this land. Because Mongolian grasslands are similar to many other economically and ecologically important systems, such as the North American Great Plains, where the changes in climate are not yet as severe, learning how to manage Mongolian grasslands under changing climate and human disturbances has implications beyond Mongolia. Ecological changes in Mongolia could be a harbinger of things to come in other areas.

In this paper, we report on changes in plant community composition in three Mongolian ecozones over 20 yr, using field data from 1994, 1995, and 2013, and relate these changes to

spatial gradients in grazing intensity and changes in climate over this period. We synthesize our findings into state-and-transition models of vegetation change, contributing to our understanding of ecological dynamics in relation to management and environmental change, and the development of tools for resilience management (Briske et al. 2008, Bestelmeyer et al. 2010, Kachergis et al. 2013). Before describing our methods, we briefly review the concept of state-and-transition models and their application to resilience management and summarize existing research about the effects of grazing, climate and grazing-climate interactions on Mongolian steppe plant communities.

Westoby et al. (1989) proposed the state-and-transition model (STM) approach to describing and managing ecological change based on alternate state theory. State-and-transition models reflect the idea that plant communities may undergo reversible shifts in plant composition (i.e., community pathways) and irreversible transitions between ecological states (Bestelmeyer et al. 2003). According to alternate state theory, biotic and abiotic components drive ecosystem dynamics and feedback mechanisms associated with persistent or transitional states (Briske et al. 2005, Kachergis et al. 2012). Resilience is the tendency of a system to return to its reference state following disturbance, whereas resistance is the ability of an ecosystem to withstand change (Gunderson 2000). A diverse plant community, relatively intact ecological processes and ecosystem services, self-regulating feedbacks, and capacity for recovery following disturbances characterize the reference state (Briske et al. 2005).

State-and-transition models are increasingly applied as a resilience-based rangeland management tool worldwide, in the USA (Bestelmeyer et al. 2003, Briske et al. 2005, Kachergis et al. 2013), Mongolia (NAMEM, and MEGDT 2015), South America (López et al. 2011, Oliva et al. 2016), Africa (Milton and Hoffman 1994), and Australia (Suding and Hobbs 2009). State-and-transition models are a potentially valuable tool to manage for rangeland resilience, because they synthesize existing knowledge of vegetation dynamics, depict known ecological states and plant communities for a given system, and identify factors that drive transitions between states.

When informed by long-term monitoring data, management experiments, and local experiential knowledge, STMs can help managers to identify which states may be vulnerable to undesirable transitions and the potential for recovery after a transition. State-and-transition models thus serve as a valuable tool for rangeland assessment (determining what proportion of the landscape exists in each state), monitoring (determining meaningful indicators and how to interpret them in relation to current and potential states), and management (setting realistic goals and determining which actions to avoid or take to achieve them). Various approaches to developing data-driven STMs (Bartolome et al. 2009, Bagchi et al. 2012, Kachergis et al. 2012), and hybrid STMs incorporating multiple knowledge sources (Knapp et al. 2011, Kachergis et al. 2013, Bruegger et al. 2016), have been advanced, although in practice many STMs rely primarily on the knowledge of experienced professionals (Twidwell et al. 2013), or are based on data from a single point in time using a space for treatment substitution design (e.g., Targetti et al. 2010, Miller et al. 2011, Kachergis et al. 2012). Here, we present data-driven, generalized STMs for three ecological zones, combining a space for treatment design with repeated measurements and three-time intervals. These generalized models may serve as a basis for developing detailed site-specific models that incorporate additional local and professional knowledge and research.

In resource-limited semi-arid rangeland systems such as Mongolia's steppe ecosystems, scarce water, nutrients, management practices and disturbances drive community composition and cause switches between alternate states. To place our study in context, we briefly review past research on the effects of livestock grazing, weather and climate, and interacting grazing and climate effects on Mongolian ecosystems and similar regions. Broadly, the effects of livestock grazing on Mongolia's plant communities are well studied, with fewer studies of climate change impacts, or the combined and interacting effects of climate and grazing.

Observational (Fernandez-Gimenez and Allen-Diaz 1999, 2001, Sasaki et al. 2008, 2011, Sergelekhhuu et al. 2012) and experimental (Lkhagva et al. 2013) studies of grazing impacts on species composition in Mongolia show that plant

communities generally shift from palatable perennial species, and a greater proportion of grasses, to unpalatable or ruderal annual species, and a greater proportion of forbs, as grazing intensity increases in the steppe (ST) and mountain steppe (MS), but not the desert steppe (DS) (Fernandez-Gimenez and Allen-Diaz 1999, 2001). Jamsranjav et al. (*In press*) found that grazing plays a more important role in determining vegetation composition in the ST zone compared to other zones. These findings from Mongolia's MS and ST zone mirror those from similar systems globally, including the STs of Inner Mongolia (Zhang et al. 2004, Li et al. 2015) and Tibet, China (Dorji et al. 2014, Wang and Wesche 2016), and the northern mixed-grass prairie near Cheyenne, Wyoming (Porensky et al. 2016), which also show species richness and composition changes with heavy grazing. Overall, these results from previous studies support the non-equilibrium theory of rangeland dynamics (Ellis and Swift 1988, Fernandez-Gimenez and Allen-Diaz 1999), which predicts that biotic factors such as grazing have a relatively greater effect in more mesic environments, where the conditions for plant growth are constant, whereas precipitation is the primary driver of community composition in more arid and variable systems. However, others observed similar plant compositional changes in the DS (Sasaki et al. 2008, 2011, Sergelenkhuu et al. 2012), contrary to the predictions on non-equilibrium theory. Sasaki et al. (2013) found that the removal of grazing did not result in recovery after 5 yr, suggesting that a biotic threshold was crossed in the ST and DS study sites.

Several observational and experimental studies have documented climate change effects on rangeland vegetation in Mongolia. Changes in the amount and timing of precipitation could cause compositional change (Spence et al. 2016), and warming may reduce flower production, particularly in graminoids (Liancourt et al. 2012), without affecting productivity. Vegetation composition is influenced more by timing of rainfall than rainfall amount in this semi-arid region (Spence et al. 2016). Observational studies (Ni 2003, Yan et al. 2015) in Inner Mongolia and Tibet, as well as in similar regions (Walker et al. 2006), report shifts in species composition, including increases in shrubs with declining

precipitation (Ni 2003) and warming (Walker et al. 2006). Climate change studies show that (1) precipitation timing is more important to plant community composition than precipitation amount (Spence et al. 2016) and, (2) precipitation (Ni 2003, Yan et al. 2015, Spence et al. 2016) and temperature (Walker et al. 2006, Klein et al. 2007), both influence species composition shifts.

Few studies investigated interacting grazing and climate change effects on plant communities in Mongolia and in similar systems around the World. Wesche et al. (2010) found strong effects of inter-annual precipitation variability on plant species diversity, community composition, flower production and biomass productivity and slight but significant differences between grazed and ungrazed treatments after eight years in an experimental grazing enclosure study in southern Mongolia. They concluded that grazing effects are small compared to climate effects (Wesche et al. 2010). Cheng et al. (2011) investigated how rainfall variability and grazing influence vegetation composition and species richness across six sites in two different ecological zones of Mongolia for two different precipitation years. They found that precipitation had more influence than grazing pressure on vegetation changes in drier areas with high rainfall variability, confirming predictions of non-equilibrium theory (Ellis and Swift 1988, Fernandez-Gimenez and Allen-Diaz 1999). In the DS zone, species richness was lower in the drier year but did not vary with grazing pressure. In the ST zone, species richness varied significantly with grazing pressure but did not vary between years (Cheng et al. 2011). Wan et al. (2015) examined how plant community structure responds to individual and combined effects of grazing intensity, selective grazing, and precipitation patterns over 6 yr in an experimental study in semi-arid typical steppe of Inner Mongolia. They found that palatable species, mainly forbs, were most severely damaged and spatial heterogeneity of above-ground biomass and species composition peaked at intermediate levels of grazing intensity. Cold season precipitation positively correlated with the abundance of C₃ grasses and negatively correlated with subdominant forbs and C₄ plants. They concluded that diet selection of grazing animals is an important factor in semi-arid grasslands (Wan et al. 2015). In an experiment, Klein

et al. (2007) showed that warming, not grazing, decreases rangeland quality on the Tibetan Plateau. These studies suggest that both inter-annual variability in rainfall and climate warming affect rangelands more strongly than grazing. However, plant community responses vary along a precipitation and productivity gradient.

In this observational study of plant community change over 20 yr, we synthesize our results into generalized state-and-transition models for each ecological zone and use the resulting models to evaluate the resilience and resistance of each ecological zone to combined grazing and climate change pressures. Our overarching research questions are as follows: (1) How has plant community composition changed over the past 20 yr in three different ecological zones? (2) What abiotic and biotic factors, including grazing intensity and climate, are most associated with observed changes in community composition and function? (3) Do ecological zones differ in their resistance and resilience to interacting grazing and climate change? Based on previous research, we expected that the MS would be more resilient because it is more productive and diverse. We expected that the DS would be more resistant to change, because grazing would not shift competitive dynamics within the plant community, as it does in the mesic MS, and precipitation is the primary driver of community composition. We expected that climate and grazing would both influence community change in the MS and ST.

MATERIALS AND METHODS

Study sites and sampling design

We sampled in the MS, ST (Bayan-Ovoo district) and DS (Jinst district) zones of Bayankhongor Province, Mongolia, in 1994, 1995, and 2013 (Fig. 1). Study sites are located in between 45°15' N and 46°30' N latitude and 100° E and 100°40' E longitude and fully described in Fernandez-Gimenez and Allen-Diaz (1999). We used distance from high livestock impact sites, such as wells and water sources, as a proxy for grazing intensity. This space for treatment substitution observational approach is well established and has been widely used where experimental control of livestock densities is impossible (Stump et al. 2005, Sasaki et al. 2008, Manthey and Peper

2010). We randomly selected five replicate plots within each of three different distances from water source categories at each site: <500 m from water (the highest grazing intensity, coded as 1), 500–2000 m (moderate grazing, coded as 2), >2000 m from water (light grazing, coded as 3). We used 1994–1995 plot center coordinates to relocate plots in 2013, as the original transects were not permanently marked. We used a systematic plot layout in place of the randomly located transects of 1994–1995 and centered our 50 × 50 m plots on the original plot centers. Five 50-m transects were systematically placed at equal intervals along a 50-m baseline.

Data collection

We recorded plant species cover every half meter along each transect using the line point intercept method (Herrick et al. 2005). Nomenclature follows Grubov (1982). When individual species cover was insufficient for analysis or consistency in species identification was in doubt, we lumped species by genus. We classified species into five plant functional types based on life history and growth form: perennial grasses, sedges, perennial forbs, annual forbs, and shrubs.

We clipped standing biomass separately for grasses, sedges, forbs, and shrubs, in five 1 × 1 m quadrats in each DS plot and five 0.50 × 0.50 m quadrats in the ST and MS. For consistency with the 1994–1995 sample, shrub biomass was not included in this analysis and we combined grass and sedge biomass. We oven-dried biomass samples at 60°C for 48 h and weighed them. Because we did not use utilization cages, standing biomass estimates reflect biomass under grazed conditions.

We sampled soils at each plot center in 2013. In order not to disturb the transect vegetation cover, we dug a soil pit at least one meter distant from the nearest transect mid-point. Each soil pit was excavated at least to the C horizon, or approximately 75 cm deep. We described each soil horizon's depth, texture (coded 1–24: 1—finest and 24—coarsest soil particle size), value (coded 0–10: 0—absolute black soil and 10—absolute white soil), rock fragments (%), clay content (%), effervescence (coded 1–5: 1—non-effervescent and 5—violently effervescent), according to USDA NRCS protocol (Schoeneberger et al.

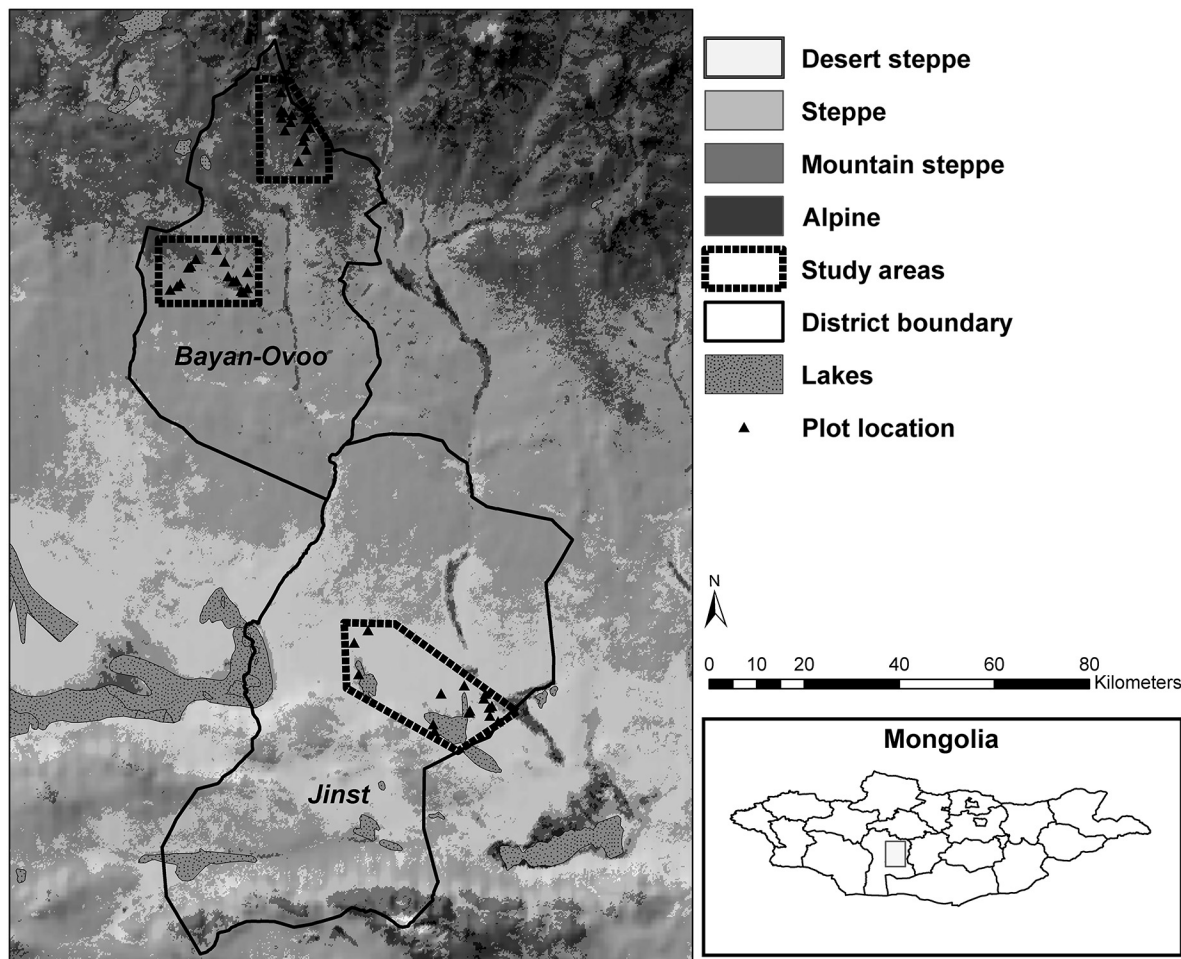


Fig. 1. Location of study sites in Jinst and Bayan-Ovoo districts, Bayankhongor Province, Mongolia.

2012). We recorded site characteristics including aspect, slope, landform, slope position, and elevation at each plot. Aspect measured in azimuth degrees was transformed into numerical values according to Beers et al. (1966).

Climate variables include the standardized precipitation evapotranspiration index (SPEI), annual temperature, and annual precipitation. For each of our sample plot locations, we extracted the SPEI data from the Global SPEI database (<http://sac.csic.es/spei/database.html>; Vicente-Serrano et al. 2010a, b, 2013, Beguería and Vicente-Serrano 2014), and precipitation and temperature from the CPC Unified precipitation dataset (Chen et al. 2008) and the Global Historical Climate Network temperature dataset (Lawrimore et al. 2011). Because our focus was on the influence of longer-

term trends in climate rather than inter-annual variation, we used the five-year running average prior to and including the sampling year for annual average temperature, total annual precipitation, and SPEI. The SPEI index incorporates the role of precipitation and evapotranspiration, thus can identify climate change processes related to alterations in precipitation and/or temperature (Vicente-Serrano et al. 2010a, b).

Data analysis

We used a combination of cluster analysis, analysis of variance (ANOVA), classification and regression trees (CART), and ordination to identify distinct plant communities, changes in community composition over time, and associated drivers of change. We used species cover data

measured in 1994, 1995, and 2013 from 15 different plots each in the DS, ST and MS zones and treated each plot by year combination as a separate sample unit in the analysis. We tracked the movement of plots over time in multivariate species space to understand changes in community composition. Static abiotic factors, including aspect, slope, elevation, soil clay content, rock fragments, soil depth, and effervescence, as well as dynamic biotic factors (grazing distance) and dynamic abiotic factors (climate variables), were used in CART and ordination analysis to identify drivers of plant community composition and change. To characterize communities, we also calculated species richness, diversity (Shannon-Wiener index: $SWI = -\sum [p_i \times \ln(p_i)]$, where p_i —the portion of cover of the i th species) and evenness (Gini Coefficient: $G = 1 - \sum p_i^2$) (Gotelli and Ellison 2013).

First, we identified potential plant communities using agglomerative hierarchical cluster analysis of plant species cover data in PC-ORD (version 6; McCune and Mefford 2011). We included all species (rare and common) in the analysis, unless there was a problem with sampling consistency and species identity (Cao et al. 1998, Poos and Jackson 2012). We used the Sorensen (Bray-Curtis) distance measure to calculate plot dissimilarity and the flexible beta linkage method (beta^{1/4} 0.25) because this space-conserving method is compatible with Sorensen (Bray-Curtis) distance (McCune and Grace 2002). Indicator species analysis, which generated an indicator value between 1 and 10 based on the faithfulness and exclusiveness of species to groups of plots, was used to prune the cluster dendrogram (Dufrêne and Legendre 1997). We selected the number of groups with the most significant indicator species (lowest average P value for species based on a randomization test with 4999 randomizations), which will be the most ecologically meaningful number of groups (McCune and Grace 2002). According to these classifications, we entered the grouping variables into our environmental variables matrix. Then, we used ANOVA post hoc analysis (Tukey's honest significant difference method) for multiple comparisons to determine which variables significantly differed between groups. Statistical tests were considered significant at $P < 0.05$ and performed using SPSS statistics 24 (IBM 2016) and R

software (version 3.3.2) using the `lm`, `cld` tests, and `car` and `lsmeans` packages (R Core Team 2016).

Second, we conducted Pearson's correlation analysis on environmental variables in each ecozone and removed highly correlated variables. The following variables from each zone with correlation coefficients >0.6 were eliminated from the environmental matrix for ordination and CART analysis. In the MS, latitude, longitude, clay percent at soil horizon-2, and mean annual precipitation were removed. In the ST, latitude, longitude, value at soil horizon-1, mean annual precipitation, soil texture at horizon-1 and horizon-2, rock fragments at soil horizon-1, clay percent at soil horizon-2, and mean annual temperature were removed. In the DS, latitude, longitude, mean annual precipitation, soil texture at horizon-1 and horizon-2, elevation, and rock fragments at soil horizon-1 were eliminated.

Third, we compared the species cover composition among groups identified using cluster analysis using pair-wise multiresponse permutation procedure (MRPP) on the Sorensen (Bray-Curtis) distance with a Bonferroni correction in PC-ORD (version 6). Multiresponse permutation procedure tested the hypothesis of no differences among potential communities (Mielke 1984, Mielke and Berry 2001, McCune and Grace 2002) using species cover data. Groups that differed significantly were retained as distinct communities and considered potential states.

Fourth, we used non-metric multidimensional scaling (NMS), the most generally effective ordination method for ecological communities (McCune and Grace 2002), to describe the relationship between plant species composition and environmental variables. Non-metric multidimensional scaling runs were performed from random starts with medium thoroughness settings for autopilot mode in PC-ORD (version 6) using same Sorensen (Bray-Curtis) distance method. We also used CART (Breiman et al. 1984) to explore our species group relationships to environmental variables and cross-check the results of NMS analysis. Classification and regression trees is used in ecology most often to classify vegetation types in relation to environmental variables (McCune and Grace 2002). We looked for patterns and relationships in each of our categorical and continuous environmental variables (input variables) as they

related to our ecological community groups (target variable). We used IBM SPSS Modeler 18 software (IBM 2016) for CART analysis. The Gini splitting criterion was used to grow the tree, because it provides the best classification accuracy. Minimum records in parent branch are 2% and in child branch 1%.

Finally, we developed state-and-transition models to synthesize findings into a single diagram for each ecozone that illustrates the potential communities and states, transitions and drivers. To determine community resistance and resilience, and reversibility of transitions, we tracked each sample unit to determine whether it changed membership from one community to another over time. Communities or states where sample units (plots) stayed within the same community/state in all three sampling periods were inferred to be resistant. Plots that transitioned and then returned to the original community were inferred to be resilient. Plots that transitioned and did not return were neither resilient nor resistant. We compared plant functional type composition among potential states using pair-wise MRPP on the Sorensen (Bray-Curtis) distance with a Bonferroni correction in PC-ORD (version 6) to test whether our communities are distinct states or community phases within states. In this analysis, we used MRPP to test the hypothesis of no differences among potential states using plant functional type data.

We conducted an initial classification of the 1994 data from all plots in all ecological zones together. This classification resulted in three clear groups corresponding with the three different ecological zones (Fig. 2); therefore, we analyzed data from each ecological zone independently in our subsequent analyses. At the end of this process, we conducted a classification and ordination of data from all plots in all years, to further assist in interpreting observed changes within each ecological zone, and to determine whether there was evidence that plant communities that were clearly associated with one zone in 1994 had become more similar to communities in other zones over the past 20 yr (Appendix S1: Fig. S1).

RESULTS

In the following sections, we first present the results of the community classification, then the

relationship of the identified potential communities to static and dynamic environmental drivers, and the potential alternate states. In each of these sections, we present the results from each ecological zone separately, with the final classification and ordination across all zones at the end.

Community classification

Mountain steppe.—Eighty-four species were included in the MS classification, and seven community groups were identified. We named groups by their dominant species, which had the highest absolute covers in each group (Appendix S1: Table S1). According to pair-wise MRPP tests on species cover, all potential community groups were significantly different ($P < 0.05$) from each other in this zone except group five. Group 5 had only two plots and therefore was excluded from the analysis.

1. *Mountain steppe group 1: Carex duriuscula–Koeleria* included plots ($n = 7$) sampled in 1994 ($n = 3$), 1995 ($n = 2$) and 2013 ($n = 2$). Common perennial grasses occurring in this community were *Agropyron cristatum*, *Koeleria*, and *Festuca* species and a sedge *Carex duriuscula*. Perennial forbs were *Arenaria capillaris*, *Potentilla bifurca*, and *Potentilla* species. Subshrubs included *Artemisia frigida* and *Artemisia lactiniata* (Appendix S1: Table S1). Mean species richness, diversity, Gini coefficient (equal to group 4), shrub cover, and elevation were the highest in this community group compared to the other groups (Appendix S1: Table S2).
2. *Mountain steppe group 2: Festuca–Koeleria–Ag. cristatum* included plots ($n = 12$) from 1994 ($n = 8$) and 1995 ($n = 4$) and was dominated by the typical MS grasses such as *Festuca* and *Koeleria* species. Other common perennial grasses were *Ag. cristatum* and *Stipa krylovii*. Perennial forbs included *Pot. bifurca* and subshrubs included *Art. frigida* (Appendix S1: Table S1). Mean perennial forb, total forb cover, annual precipitation, and annual SPEI were the highest in this community group (Appendix S1: Table S2).
3. *Mountain steppe group 3: Festuca–Koeleria–S. krylovii* included plots ($n = 13$) from 1994 ($n = 4$) and 1995 ($n = 9$). The main difference between communities 2 and 3 was the lower

Festuca cover in community group 3 and greater cover (by 3–4%) of perennial grasses *Poa attenuata* and *S. krylovii*. Common perennial grasses were *Ag. cristatum*, *Poa attenuata*, *S. krylovii*, *Festuca*, and *Koeleria* species. Common sedges included *Carex duriuscula*, perennial forbs included *Ar. capillaris*, and subshrubs included *Art. frigida* (Appendix S1: Table S1). Mean total annual forb cover was the highest in this community group (Appendix S1: Table S2).

- species. *Heteropappus hispidus* was the common annual forb in this community group (Appendix S1: Table S1). None of the other community groups had common (100% frequency) annual forbs; however, groups 2, 3, 6, and 1 had *He. hispidus* 92, 85, 75, and 71%, respectively. The common shrub was *Artemisia laciniata*. Mean monocot biomass, total herbaceous biomass, Gini coefficient (equal to group 1), slope, depth of soil horizon-1, soil texture at horizon-1, and clay percent at horizon-1 and horizon-2 were the highest in this community group compared to the other groups (Appendix S1: Table S2).
- Mountain steppe group 5: Carex duriuscula*–*Artemisia adamsii* ($n = 2$) included only two plots sampled in 2013, which were dominated by grazing-tolerant and ruderal species. A perennial grass, *Ag. cristatum*, a sedge, *Carex duriuscula*, perennial forbs, *Art. adamsii*, and *Pot. bifurca* were common in this community

(Appendix S1: Table S1). *Artemisia adamsii* is an unpalatable and grazing-tolerant species. *Artemisia adamsii*, *Carex duriuscula*, and *Pot. bifurca* are all indicators of heavy grazing (Hilbig 1995). Mean sedge, monocot, total herbaceous foliar and total foliar cover, dicot biomass, mean annual temperature, and depth of soil horizon-2 were the highest in this community group (Appendix S1: Table S2).

6. Mountain steppe group 6: *Stipa krylovii*–*Carex duriuscula* ($n = 4$) included only plots sampled in 2013. Common perennial grasses occurring in this community were *Ag. cristatum*, *S. krylovii*, *Koeleria*, and *Festuca* species and a sedge *Carex duriuscula*. Perennial forbs included *Pot. bifurca* (Appendix S1: Table S1). Mean soil texture at horizon-2 and rock fragments at soil horizon-1 and horizon-2 were the highest in this community group (Appendix S1: Table S2).
7. Mountain steppe group 7: *Stipa krylovii*–*Ag. cristatum*–*Carex duriuscula* ($n = 4$) included only plots sampled in 2013. Common perennial grasses occurring in this community were *Ag. cristatum*, *S. krylovii*, *Koeleria*, and *Festuca* species, and a sedge *Carex duriuscula*. The common perennial forb was *Ephedra* species (Appendix S1: Table S1). Mean grass cover, distance value at soil horizon-1 and horizon-2, and effervescence at soil horizon-1 were the highest in this community group compared to the other groups (Appendix S1: Table S2). Effervescence at soil horizon-2 was same for all groups.

Steppe.—Fifty-five species were included in the classification analysis for the ST, and five potential communities were identified (Appendix S1: Table S3). According to pair-wise MRPP tests on species cover, all potential community groups were significantly different ($P < 0.05$) from each other in this zone. We removed group 2 from MRPP analysis due to low sample number ($n = 2$).

1. *Steppe group 1: Artemisia adamsii*–*Ag. cristatum* included plots ($n = 24$) from 1994 ($n = 11$), 1995 ($n = 11$), and 2013 ($n = 2$). *Agropyron cristatum* and unpalatable forb *Art. adamsii* were common in this community group (Appendix S1: Table S3). Mean

effervescence at soil horizon-1 and value at horizon-1 were the highest in this community group compared to the other groups (Appendix S1: Table S4).

2. *Steppe group 2: Koeleria macrantha*–*S. krylovii* ($n = 2$) comprised a single plot sampled in 1994 and 1995. Common perennial grasses occurring in this community were *Ag. cristatum*, *K. macrantha*, *S. krylovii*, and *Poa attenuata*. Perennial forbs were *Ptilotrichum canescens*, *Ar. capillaris*, *Allium*, *Astragalus*, *Potentilla*, and *Scorzonera* species. Shrubs included *Art. frigida*, *Thymus gobicus*, and *Caragana* species (Appendix S1: Table S3). Mean grass, shrub cover, species richness, diversity and Gini coefficient and annual precipitation, annual SPEI, slope, elevation, distance, and rock fragments at soil horizon-2 were the highest in this community group (Appendix S1: Table S4).
3. *Steppe group 3: Allium*–*Art. adamsii* included plots ($n = 8$) from 1994 ($n = 2$), 1995 ($n = 2$), and 2013 ($n = 4$). *Stipa krylovii*, a grazing and drought tolerant perennial grass, *Carex duriuscula*, a grazing-tolerant sedge, and *Art. adamsii*, an unpalatable, disturbance indicator were common in this group (Appendix S1: Table S3). Mean perennial forb cover, soil depth of horizon-1 and horizon-2, value, and effervescence at soil horizon-2 were the highest in this community group compared to the other groups (Appendix S1: Table S4).
4. *Steppe group 4: Stipa krylovii*–*Carex duriuscula* included plots ($n = 8$) sampled in 2013 only. Perennial grasses *Ag. cristatum* and *S. krylovii* and a sedge *Carex duriuscula* were the common species in this community group (Appendix S1: Table S3). Mean sedge, monocot cover, monocot biomass, mean annual temperature, and clay percent at soil horizon-1 and horizon-2 were the highest in this community group (Appendix S1: Table S4).
5. *Steppe group 5: Chenopodium*–*Achnatherum splendens* ($n = 3$) comprised a single plot sampled each year. Fernandez-Gimenez and Allen-Diaz (2001) describe this plot as an outlier located at highly disturbed site near heavily used well. In 1994 and 1995, the plot supported eight species, but only two were present in 2013 (Appendix S1: Table S3). Mean annual forb, total forb, total

herbaceous foliar cover, total foliar cover, dicot biomass, total herbaceous biomass, soil texture at horizon-1 and horizon-2, and rock fragments at soil horizon-1 were the highest in this community group compared to the other groups (Appendix S1: Table S4).

Desert steppe.—Forty-eight species were included in the classification analysis for the DS, and seven potential plant communities were identified (Appendix S1: Table S5). According to pair-wise MRPP test on species cover, all potential community groups were significantly different ($P < 0.05$) from each other in this zone. We removed group 5 from MRPP analysis due to low sample number ($n = 2$).

1. *Desert steppe group 1: Stipa gobicalglareosa–Elymus* ($n = 3$) included a single plot sampled each year. The common species were perennial grasses *S. gobicalglareosa* and *Elymus* species, perennial forbs *Convolvulus ammannii*, *Iris bungei*, and *Scorzonera* species, and shrubs *Eurotia ceratoides*, *Caragana bungei*, and *Caragana leucophloea* (Appendix S1: Table S5). Mean perennial and total forb, mean annual temperature (equal to group 6), elevation, value at horizon-2 clay at soil horizon-2, and rock fragments at soil horizon-2 were the highest in this community group compared to the other groups (Appendix S1: Table S6).
2. *Desert steppe group 2: Stipa gobicalglareosa–Cleistogenes songorica* ($n = 5$) included plots from 1994 ($n = 1$), 1995 ($n = 3$), and 2013 ($n = 1$). *Stipa gobicalglareosa* together with subdominant C4 grass *Cl. songorica* was the common perennial grasses, and *Artemisia xerophytica* was the common shrub in this community (Appendix S1: Table S5). Mean sedge cover and soil depth at horizon-2 were the highest in this community group (Appendix S1: Table S6).
3. *Desert steppe group 3: Stipa gobicalglareosa–Art. xerophytica–Allium polyrrhizum* ($n = 16$) included plots from 1994 ($n = 3$), 1995 ($n = 7$), and 2013 ($n = 6$). Perennial grass *S. gobicalglareosa* was the dominant taxa in this community group (Appendix S1: Table S5). The average Gini coefficient was the highest in this community group (Appendix S1: Table S6).
4. *Desert steppe group 4: Stipa gobicalglareosa–Art. xerophytica–I. bungei* ($n = 13$) included plots from 1994 ($n = 8$) and 2013 ($n = 5$). *Stipa gobicalglareosa* was the dominant grass, and *Allium mongolicum* was the common perennial forb (Appendix S1: Table S5). Mean grass, monocot cover, total herbaceous foliar cover, total foliar cover, monocot biomass, and soil texture at soil horizon-2 were the highest in this community group compared to the other groups (Appendix S1: Table S6).
5. *Desert steppe group 5: Stipa gobicalglareosa–Artemisia schischkinii* ($n = 2$) comprised a single plot sampled in 1994 and 1995. *Stipa gobicalglareosa* was the dominant grass, and *Iris tenuifolia* and *Haplophyllum dauricum* were the common perennial forbs. Shrubs included *Art. schischkinii*, *Ajanía* species, *Oxytropis aciphylla*, and *Cara. leucophloea* (Appendix S1: Table S5). Mean dicot biomass, mean annual precipitation, annual SPEI, distance, clay at soil horizon-1, effervescence at soil horizon-1 and horizon-2, soil texture at horizon-1, value at soil horizon-1, and rock fragments at soil horizon-1 were the highest in this community group (Appendix S1: Table S6).
6. *Desert steppe group 6: Caragana bungei–Atraphaxis pungens* ($n = 3$) included a single plot sampled each year. *Stipa gobicalglareosa* was the common grass, and *I. bungei* was the common perennial forb. *Atraphaxis pungens*, *Cara. bungei*, *Cara. leucophloea*, *Convolvulus gortschakovii*, and *O. aciphylla* were common perennial shrubs in this community group (Appendix S1: Table S5). Mean annual forb, shrub, total herbaceous biomass, species richness, diversity and annual temperature (equal to group 1), and soil depth of soil horizon-1 were the highest in this community group (Appendix S1: Table S6).
7. *Desert steppe group 7: Stipa gobicalglareosa–Art. xerophytica–Cl. songorica* ($n = 3$) included plots from 1995 ($n = 2$) and 2013 ($n = 1$). Common perennial grasses occurring in this community were *S. gobicalglareosa* and *Cl. songorica*. *Allium polyrrhizum* was the common perennial forb, and *Cara. leucophloea* was the common perennial shrub (Appendix S1: Table S5). Slope was the highest in

this community group compared to the other groups (Appendix S1: Table S6).

Non-metric multidimensional scaling ordination, CART, and state-and-transition models

Non-metric multidimensional scaling revealed important relationships between plant species composition and environmental variables. In the MS, plant species composition was strongly correlated with annual SPEI ($r = 0.88$) and distance from water source ($r = 0.60$), where greater distance from water indicates lower grazing intensity (Fig. 3). Classification and regression trees analysis indicated that after elevation, distance had the greatest effect, followed by SPEI in the MS (Fig. 4).

In the ST (Fig. 5), plant species composition was most strongly correlated with grazing distance ($r = 0.63$) and annual SPEI ($r = 0.50$). Classification and regression trees analysis indicated that SPEI is the strongest driver of community composition in the ST followed by distance (Fig. 6).

In the DS (Fig. 7), plant species composition was associated with depth of soil horizon-1 ($r = 0.81$) and value at horizon-2 ($r = 0.43$). Classification and regression trees could not find a solution for the DS. We constructed STMs for each zone from the classification and NMS results, which represent a synthesis and interpretation of these combined results (Figs. 8–10;

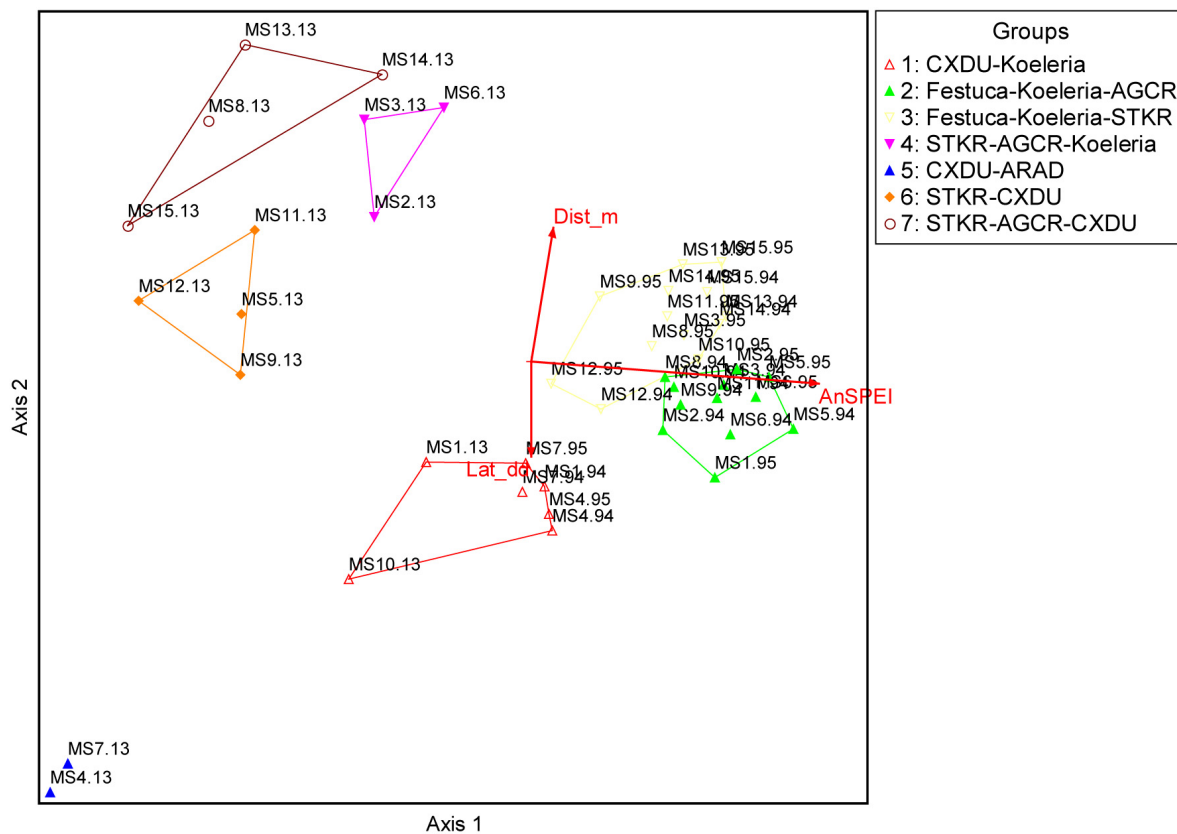


Fig. 3. Non-metric multidimensional scaling (NMS) graph for the mountain steppe (MS). Groups refer to the potential plant communities identified using cluster analysis (see text for complete names and descriptions). Arrows depict abiotic and biotic variables most highly correlated with the NMS axes, which explain most of the variation in species composition. Standardized precipitation evapotranspiration index (SPEI) is correlated with axis 1 ($r = 0.88$) and increases with the direction of the arrow, indicating wetter and cooler conditions. Grazing distance is correlated with axis 2 ($r = 0.60$), and relative grazing intensities decline with the direction of the arrow as distance from water increases.

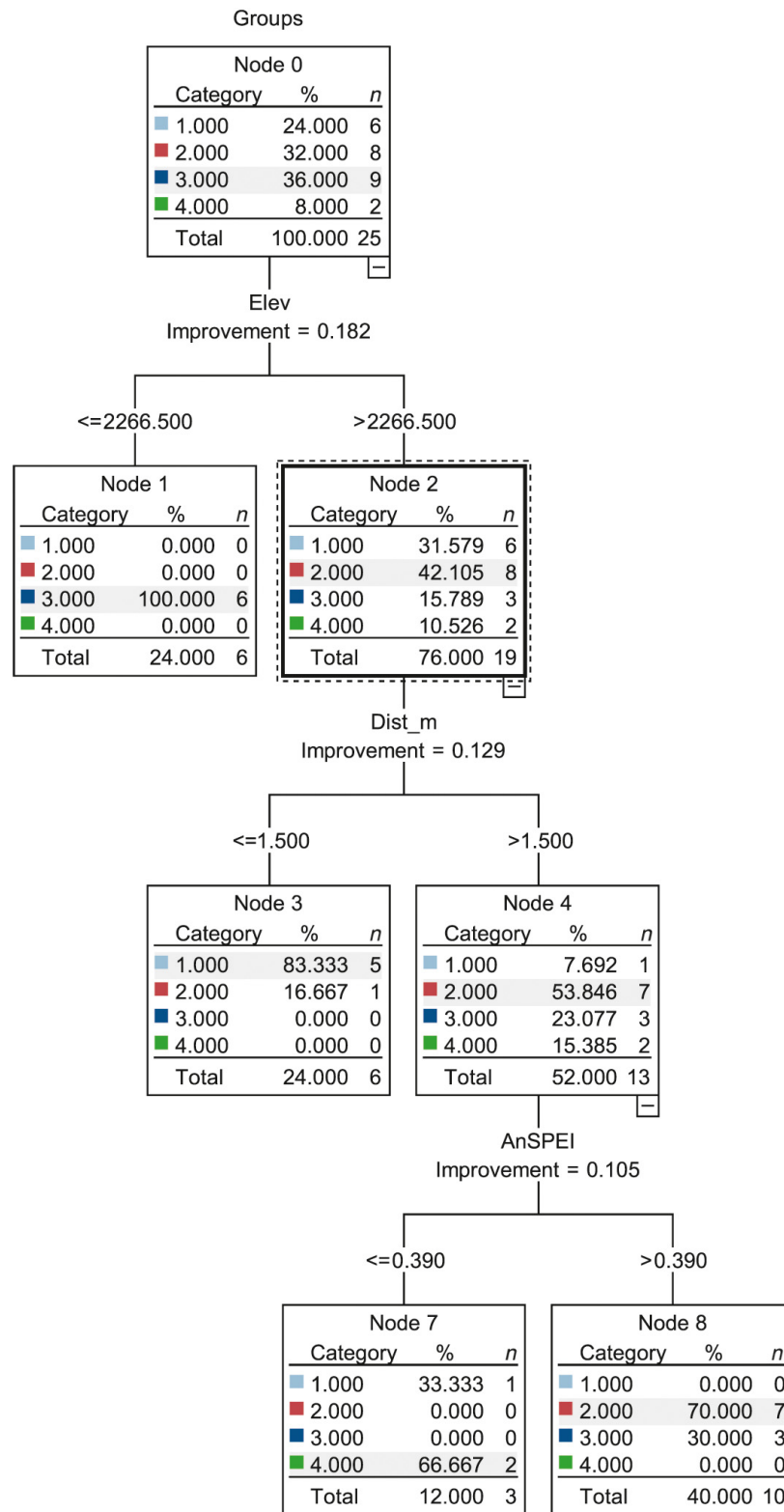


Fig. 4. Classification and regression tree diagram for the mountain steppe (MS) zone. AnSPEI—annual

(Fig. 4. Continued)

standardized precipitation evapotranspiration index. Dist_m—grazing gradient distance where 1 = <500 m, 2 = 500–2000 m, and 3 = >2000 m. Elev—elevation in meters. Aspect_T—aspect measured in azimuth degrees was transformed into numerical values according to Beers et al. (1966).

Appendix S1: Figs. S2–S4). In the following sections, we describe the states and dynamics depicted in each model.

Mountain steppe.—A pair-wise MRPP test on plant functional type cover indicated that all pairs of potential states differed significantly ($P < 0.05$) except for groups 1 and 6 ($P = 0.06$) and groups 3 and 4 ($P = 0.08$). Therefore, we grouped communities 1 and 6 and communities 3 and 4 together as one potential state each containing two distinct potential plant communities.

Communities 2 *Festuca-Koeleria-Ag. cristatum* and 3 *Festuca-Koeleria-S. krylovii* represent potential reference communities for this system and were most vulnerable to change. Eight plots transitioned out of community 2, and seven plots transitioned out of community 3 over the 20-yr study period. In 2013, no plots measured in 1994 or 1995 remained in the same community (2 and 3). All transitioned to communities 1, 4, 5, 6, or 7, suggesting that these *Festuca*-dominated communities are becoming rarer in this system. Transitions from reference communities (2 and 3) to communities 4, 6, and 7 were related to warming and reduced moisture (inversely related to SPEI). One sample unit (MS1) moved back and forth between communities 2 and 1, potentially

indicating resilience (Fig. 8; Appendix S1: Fig. S2). Two sample units moved from community 1 to community 5, the most highly disturbed site with the lowest SPEI. Overall, only one plot transitioned but returned to its original community, 14 out of 15 plots transitioned permanently, and none of the plots remained in the same community in 2013. Classification and regression trees analysis in MS indicated that grazing distance was the most important dynamic factor driving species composition in the MS, followed by SPEI. Classification and regression trees also suggests that lightly grazed communities were more affected by moisture variability (SPEI).

Steppe.—Multiresponse permutation procedure tests on plant functional type cover indicated that all pairs of potential states differed significantly ($P < 0.05$) except for communities 1 and 4 ($P = 0.34$) and communities 3 and 5 ($P = 0.07$). We removed group 2 from the MRPP analysis due to low sample size ($n = 2$) but included it in the state-and-transition model. The final STM includes three states, two of which include two communities. The community most influenced by grazing, 5. *Chenopodium-Ac. splendens*, was stable across the three sampling periods and resisted further change (Fig. 9; Appendix S1: Fig. S3). The

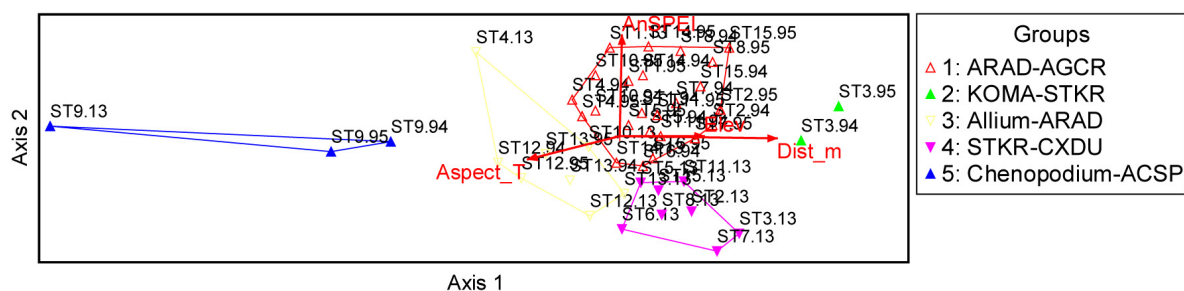


Fig. 5. Non-metric multidimensional scaling (NMS) graph for the steppe (ST) zone. Numbered groups refer to the potential plant communities identified using cluster analysis. Arrows depict abiotic and biotic variables most highly correlated with the NMS axes, which explain most of the variation in species composition. Grazing distance is correlated with axis 1 ($r = 0.63$) and increases with the direction of the arrow indicating decreasing relative grazing intensity with increasing distance from water. Standardized precipitation evapotranspiration index (SPEI) is correlated with axis 2 ($r = 0.50$) and increases with the direction of the arrow representing wetter and cooler conditions.

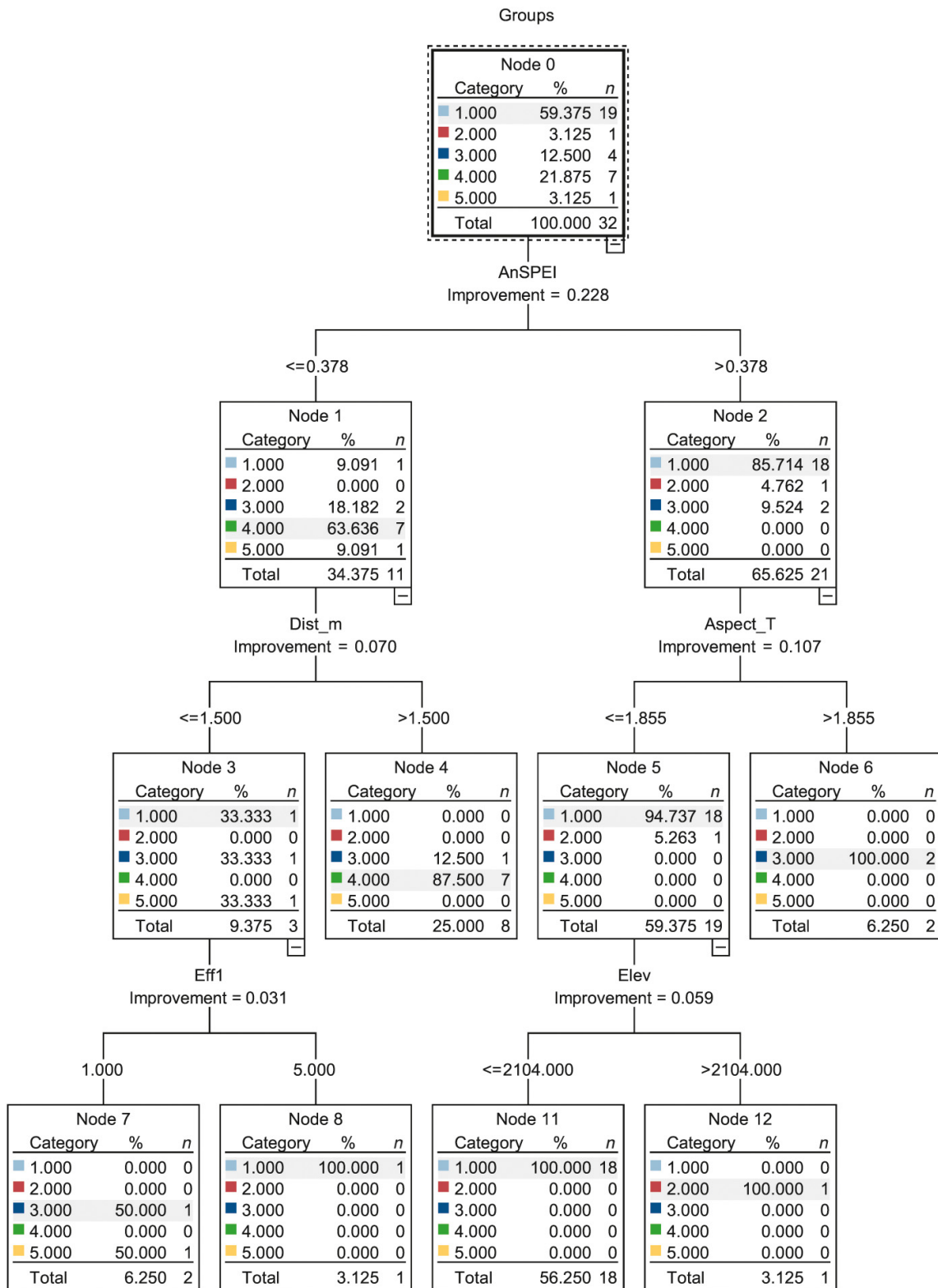


Fig. 6. Classification and regression tree diagram for steppe zone. AnSPEI—annual standardized precipitation

(Fig. 6. Continued)

evapotranspiration index. Dist_m—grazing gradient distance where 1 = <500 m, 2 = 500–2000 m, and 3 = >2000 m. Aspect_T—aspect measured in azimuth degrees was transformed into numerical values according to Beers et al. (1966). Elev—elevation in meters. Eff1—effervescence at horizon 1, where non-effervescent = 1, very slightly effervescent = 2, slightly effervescent = 3, strongly effervescent = 4, violently effervescent = 5.

potential reference community, 1. *Artemisia adamsii*–*Ag. cristatum*, was most vulnerable to change. Seven plots transitioned from this community to community 4. *Stipa krylovii*–*Carex duriuscula*, due to warming and declining moisture (decreasing SPEI) and two transitioned to community 3 *Allium*–*Art. adamsii* due to both climate and grazing (decreasing SPEI and higher grazing intensity). No sample units returned to the reference community. Overall, five plots out of 15 remained in the same community over all three sampling periods, 10 plots transitioned permanently, and none transitioned and then returned to the original community. Overall, plant community composition was more strongly correlated with grazing intensity ($r = 0.63$) than SPEI ($r = 0.50$). However, the majority of long-term shifts (documented in 2013) in community composition were most strongly associated with declining moisture (SPEI). Classification and regression trees analysis in the ST

shows SPEI was the most important driving factor. In the ST, grazing intensity had a greater influence on drier and warmer sites and abiotic environmental factors had a greater effect on cooler wetter sites. Generally, SPEI and grazing were important drivers of community composition in both eco-zones, but grazing had a greater influence on drier sites in the ST and moisture had a greater influence on lightly grazed sites in the MS.

Desert steppe.—Multiresponse permutation procedure tests on functional group cover indicated that all pairs of potential states differed significantly except the communities 2 and 3. We removed community 5 ($n = 2$) from the MRPP analysis due to small sample size, but included it in the state-and-transition model. In the DS, three plots remained in the same community over the 20-yr period, six fluctuated but returned to their original community, and six changed communities permanently. Standardized precipitation

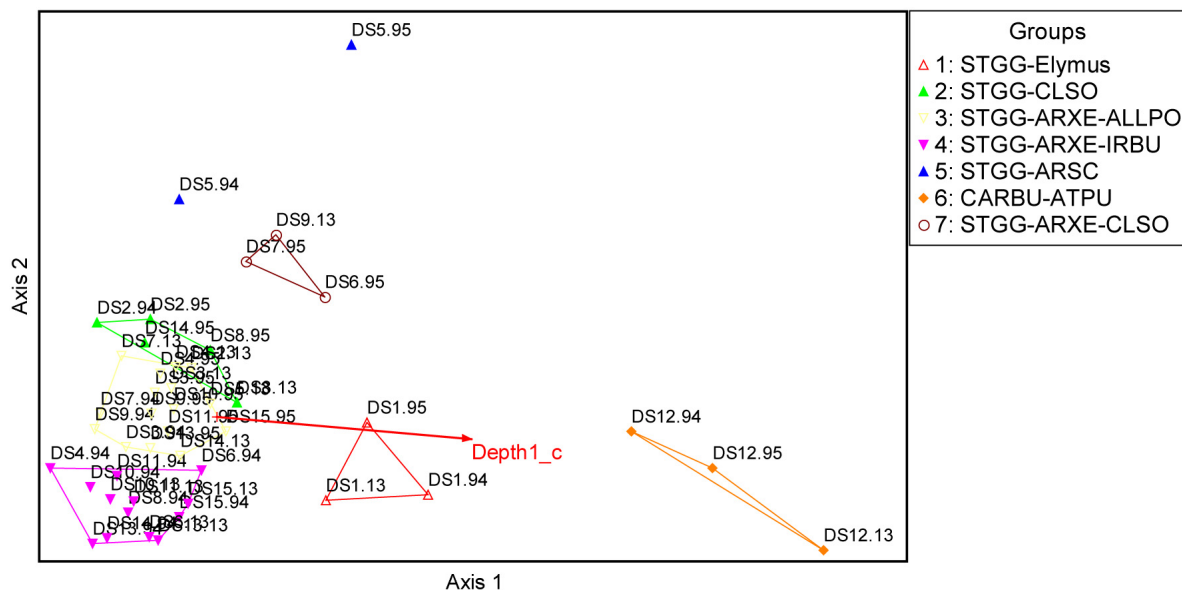


Fig. 7. Non-metric multidimensional scaling (NMS) graph for the desert steppe (DS) zone. Numbered groups refer to the potential plant communities identified using cluster analysis. Arrows depict abiotic and biotic variables most highly correlated with the NMS axes, which explain most of the variation in species composition. Soil depth at horizon-1 was strongly correlated with axis 1 ($r = 0.81$) and increases with the direction of the arrow.

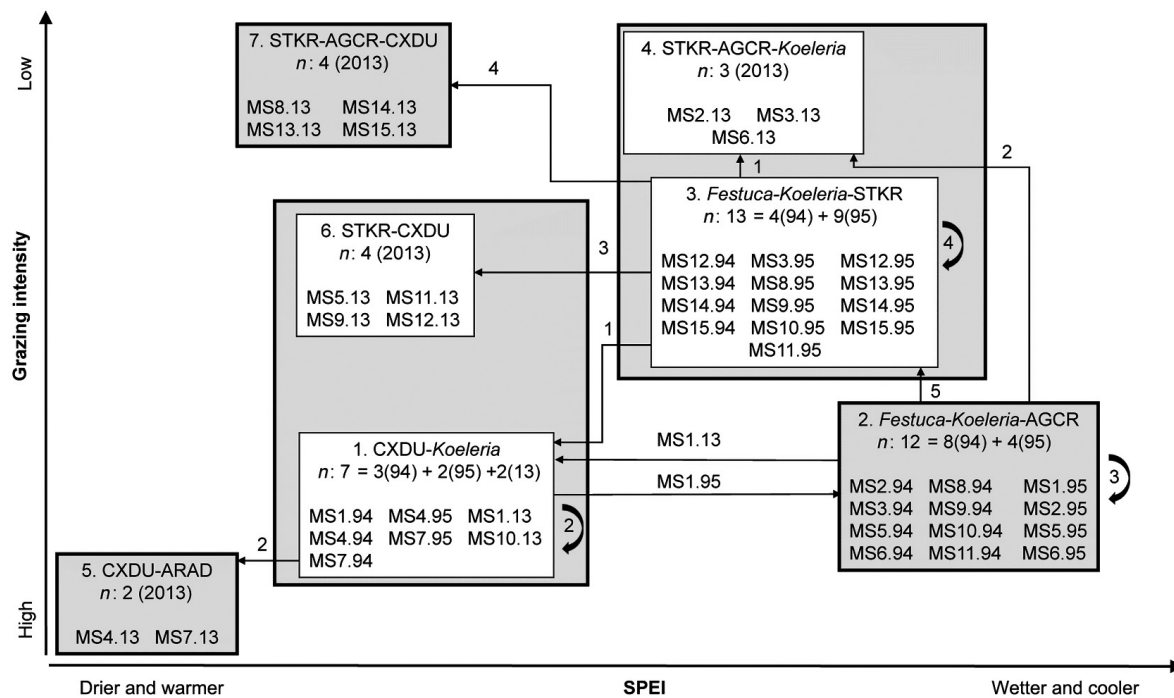


Fig. 8. Mountain steppe (MS) state-and-transition model. Each numbered box indicates a potential plant community and n = the number of sample units in that community in each sampling year (94, 95, and 13, respectively). White boxes indicate potential plant communities that differ in species composition but not function. Gray boxes with bold outlines represent potential alternate states that differ in both species composition and functional attributes. Arrows between boxes indicate transitions between communities and the numbers beside each arrow denote the number of sample units that shifted from one community to another. Numbers inside curved arrows denote the number of sample units that stayed in this potential community group between sampling periods. Sample units that shifted back and forth between communities are labeled by sample unit code that indicates ecological zone, plot id, and sampling year (MS1.95 = MS plot 1, sampled in 1995). The axes represent the major drivers of community composition identified in non-metric multidimensional scaling graph (Fig. 3). Species codes are in Appendix S1: Table S7.

evapotranspiration index and grazing did not affect community composition in this region. Community composition was driven by site-specific environmental characteristics such as soil depth at horizon-1 ($r = 0.81$) and value at soil horizon-2 ($r = 0.43$), but not related to the SPEI and grazing (Fig. 10; Appendix S1: Fig. S4), unlike the other two ecological zones.

Classification and ordination of all plots and all years

Classification of all plots in all years revealed three groups, corresponding with the three ecological zones, as was the case for 1994 plots alone (Fig. 2). However, 13 plots classified as MS in 1994 and 1995 transitioned to the ST group in 2013

(Appendix S1: Fig. S1). Plots classified as DS and ST remained in the same group across all time periods in this analysis. However, one plot that was classified as DS in the analysis of 1994 data alone, was classified as ST in all three sampling periods in this combined analysis of all ecological zones.

DISCUSSION

As depicted in the MS STM (Fig. 8; Appendix S1: Fig. S2), which synthesizes the classification and ordination results, plant species composition in the MS was more strongly associated with decreasing SPEI ($r = 0.88$) than grazing intensity ($r = 0.60$). All MS plots transitioned over the course of our 20-yr study, 14 of them

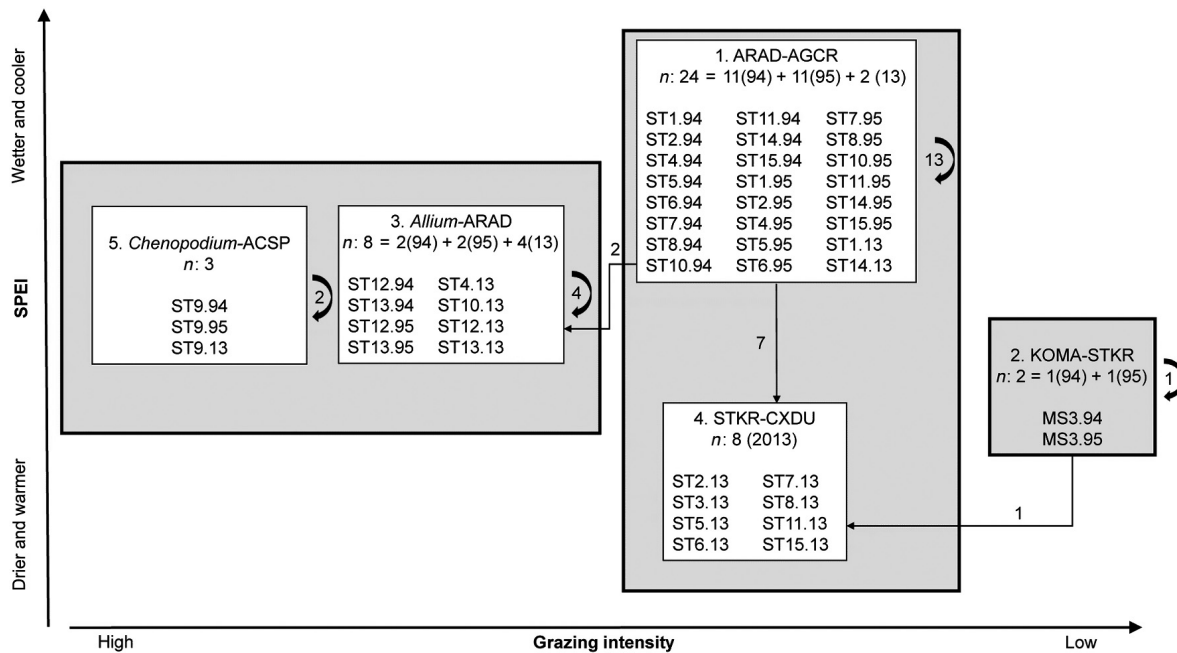


Fig. 9. Steppe (ST) zone state-and-transition model. Each numbered box indicates a potential plant community and n = the number of sample units in that community in each sampling year (94, 95, and 13, respectively). White boxes indicate potential plant communities that differ in species composition but not function. Gray boxes with bold outlines represent potential alternate states that differ in both species composition and functional attributes. Arrows between boxes indicate transitions between communities, and the numbers beside each arrow denote the number of sample units that shifted from one community to another between sampling periods. Numbers inside curved arrows denote the number of sample units that stayed in this potential community group between sampling periods. The axes represent the major drivers of community composition identified in non-metric multidimensional scaling graph (Fig. 5). Species codes are in Appendix S1: Table S7.

permanently. In the MS, declining SPEI drove more than half of the transitions between communities; however, grazing also played a role. As the final analysis of all plots in all years shows (Appendix S1: Fig. S1), composition of MS plant communities increasingly resembles the ST. Our results support the hypothesis that climate change is having a greater impact than grazing on plant community composition in the MS. However, our results also indicate that long-term grazing does influence plant community composition in the MS, as prior studies have shown (Fernandez-Gimenez and Allen-Diaz 1999, Zemmrich et al. 2010, Khishigbayar et al. 2015). Spence et al. (2014) found that *Festuca lenensis*, a dominant species in MS communities 2 and 3, declined significantly with both experimental warming and grazing, supporting our interpretation that both climate change and grazing contributed to the

disappearance of *Festuca*-dominated communities over 20 yr from our sampling sites. Our results in this region are consistent with previous findings that climate variability (Wesche et al. 2010) and climate change (Klein et al. 2007, Cheng et al. 2011) effects in Mongolian and other high latitude and altitude rangelands are stronger than grazing influences. Our findings also align with predictions for Mongolia that the MS will experience more extreme and earlier shifts in species composition due to climate change (Angerer et al. 2008, Ojima et al. 2013).

In the ST, plant species composition was most strongly associated with grazing intensity ($r = 0.63$) and decreasing SPEI ($r = 0.50$) in NMS. Classification and regression trees indicated that SPEI is an important predictor that conditions ST community response to grazing, with grazing affecting drier sites more strongly than wetter

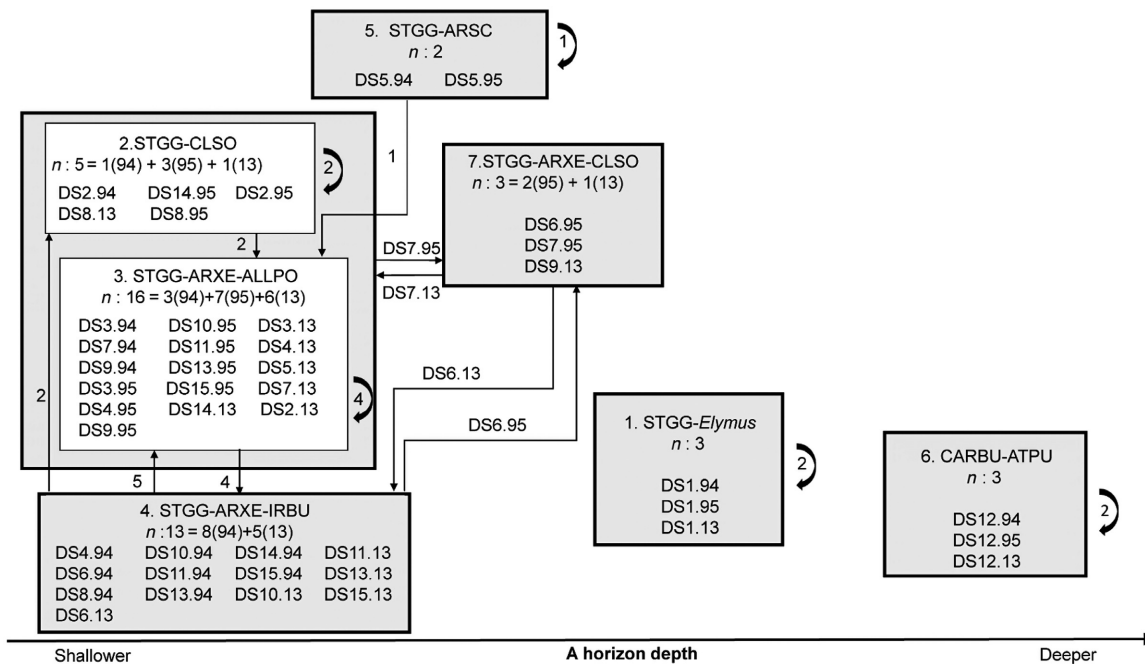


Fig. 10. Desert steppe (DS) state-and-transition model. Each numbered box indicates a potential plant community and n = the number of sample units in that community in each sampling year (94, 95, and 13, respectively). White boxes indicate potential plant communities that differ in species composition but not function. Gray boxes with bold outlines represent potential alternate states that differ in both species composition and functional attributes. Arrows between boxes indicate transitions between communities, and the numbers beside each arrow denote the number of sample units that shifted from one community to another. Numbers inside curved arrows denote the number of sample units that stayed in this potential community group between sampling periods. Sample units that shifted back and forth between communities are labeled by sample unit code that indicates district, plot id, and sampling year (DS6.95 = DS plot 6, sampled in 1995). The axis represents the major driver of community composition identified in non-metric multidimensional scaling graph (Fig. 7). Species codes are in Appendix S1: Table S7.

sites. Five ST plots remained stable over the study period and did not shift between communities. Ten of the 15 plots demonstrated long-term transitions. The majority of long-term shifts in plant community composition were associated with declining SPEI, indicating that climate change is affecting ST plant communities, as CART results show. Our results are consistent with Jamsranjav et al.'s (*In press*) findings that grazing plays a more important role in determining plant species composition in the ST compared to other zones. In the ST, several communities associated with higher grazing intensities existed in 1994 or 1995 (Fig. 9; Appendix S1: Fig. S3) and remained stable over 20 yr, indicating that grazing-induced changes had already occurred at the beginning of the study period.

In contrast to the MS and ST, DS plant communities were not affected by climate and grazing and were mainly controlled by abiotic factors such as soil depth of the first horizon ($r = 0.81$) and value of horizon-2 ($r = 0.43$), which indicates soil organic matter content. In contrast to the MS and ST, fewer than half of the DS plots (six of 15) experienced long-term transitions over the 20 yr of the study. Our findings are consistent with Milchunas et al. (1988) and Cingolani et al. (2005) assertions that vegetation in arid regions with a long evolutionary history of grazing is moderately resistant to grazing. However, the lack of association with SPEI was surprising, since past work has shown that DS vegetation dynamics are largely driven by precipitation or soil moisture (Fernandez-Gimenez 1999, Wesche

et al. 2010, Zemmrich et al. 2010). Our use of a 5-yr moving average SPEI in this study in order to understand the influence of longer-term trends in climate rather than inter-annual variability may have masked potential effects of inter-annual rainfall variation on species composition. However, the precipitation in two of the three sampling years (1995 and 2013) was similar (Khishigbayar et al. 2015). Thus, even if inter-annual variation is a key driver, our data included limited variation in this driver.

Some plots in the MS (1) and DS (6) shifted back and forth between communities, indicating the resilience of those communities, and some plots in the ST (5) and DS (3) did not transition at all (stayed at the same community group all three sampling years), indicating resistance of these communities to change (Figs. 8–10; Appendix S1: Figs. S2–S4). For example, ST community 5. *Chenopodium–Ac. splendens* ($n = 3$) included one plot measured in three years. This plot was already disturbed by grazing in 1994 and resisted further change, indicating a stable degraded community under continuous heavy grazing. Only experimental removal of heavy livestock use (such as with an exclosure) would reveal whether this state could recover to a more diverse plant community with greater composition of perennial grasses. Similarly, DS communities 1. *Stipa gobica*/*glareosa–Elymus* and 6. *Caragana bungei–At. pungens* each comprised one plot measured across three years. Because static soil properties accounted for most of the variability in species composition in the DS, we suspect that these communities represent distinct ecological sites, where soils, landform, and climate give rise to a distinct kind and amount of vegetation (Brown 2010). Our results support the hypothesis that the DS is more resistant (three out of 15 plots did not move, and only six experienced long-term transitions), and resilient (six plots fluctuated and returned to their original state) to climate change and grazing than the MS or ST. The MS showed some resilience (one of 15 plots fluctuated) but not resistance to change (none of the plots stayed at the same community for all three sampling years, and 14 transitioned permanently). Some ST plots were resistant (five out of 15 plots did not move) but not resilient (none of the plots fluctuated and returned to its original state).

Although recent nation-wide rangeland assessments (NAMEM and MEGDT 2015) and observational studies (Jamsranjav et al. *In press*) have shed light on the current status of Mongolia's rangelands, little long-term monitoring exists across ecological zones to clarify the interacting effects of grazing and climate change on these systems. This 20-yr observational study of plant community composition and change helps distinguish states that are associated with heavy grazing, and which have persisted for over 20 yr (e.g., ST communities 3 and 5), from those that represent potential reference conditions (e.g., ST communities 1 and 2), and have shifted in composition due to increasing temperature, declining moisture for plant growth (SPEI), high grazing intensity, or a combination of these factors. In the MS, for example, the reference communities (MS communities 2 and 3) sampled in 1994 and 1995 did not appear at all in the 2013 sample (Fig. 8; Appendix S1: Fig. S2). The STMs for the MS and ST reveal how community composition is changing in response to these factors, and in some cases, describe communities that potentially did not exist, or were rare, in the sampled landscapes in the early 1990s, and which have now become more prevalent (e.g., MS communities 1, 4, 5, 6, and 7; Fig. 8; Appendix S1: Fig. S2).

By describing and illustrating these potential states, communities, and drivers of transitions, these STMs provide a valuable tool for both government land managers and pastoralists to interpret current conditions and possible future changes. State-and-transition models suggest what changes may be expected, even in the absence of heavy grazing, as the climate continues to warm, as well as changes that may be induced by the interaction of grazing and climate change, or heavy grazing alone. State-and-transition models also suggest that within some ecological zones, climate conditions community responses to grazing, with warm dry sites more affected by grazing in the ST. Interestingly, it appears that some communities heavily influenced by grazing are the most stable and unresponsive to climate change (e.g., ST 3 and 5; Fig. 9; Appendix S1: Fig. S3). We cannot know whether such stability indicates that a biotic threshold was crossed without an opportunity to observe how these sites respond to grazing reduction or removal.

We emphasize that these generalized STMs for the three ecological zones are a starting point, rather than a final product, and acknowledge several limitations of our study, including its observational nature, inclusion of only three monitoring periods in a 20-yr time span, and limited sample size. Because our study is observational rather than experimental, our conclusions are based on correlations between static (e.g., soil texture, slope) and dynamic (e.g., climate, grazing) environmental factors and plant community composition over time. However, the use of grazing gradients (a space for treatment substitution design) and repeated sampling over time helps to isolate grazing from climate change effects, especially given that precipitation levels in 2013 at all sites were very similar to those in 1995. The limited number of monitoring periods precluded a more nuanced understanding of inter-annual variation and short-term, potentially reversible, transitions. We recommend that these models be further refined with local and professional knowledge and made site specific with additional monitoring data stratified by ecological site and collected at more frequent intervals, and experimental research to (1) determine recovery potential of apparently persistent states that transitioned due to heavy grazing and (2) verify observed correlations among climate, grazing intensity, and plant community composition (Kachergis et al. 2013).

CONCLUSIONS AND IMPLICATIONS

Our analysis and synthesis of long-term monitoring data into generalized STMs for three Mongolian ecological zones provides insights into the combined effects of grazing and climate change across three steppe regions. As hypothesized, community composition in the DS was unrelated to either grazing intensity or climate change, and persistent DS communities may represent distinct ecological sites. In the MS, community composition overall was most strongly associated with climate, and transitions from one community to another were associated with climate change or combined climate and grazing effects. Mountain steppe communities appear to be shifting in composition to more closely resemble the ST, a predicted outcome of climate change (Angerer et al. 2008, Ojima et al. 2013). In the ST, grazing intensity was the strongest influence on

overall community composition in NMS, but transitions between communities from the early 1990s to 2013 were primarily associated with climate change, and SPEI was the strongest predictor in CART. The ST included grazing-induced stable communities, already heavily modified by grazing in 1994 and 1995, which resisted further change over the study period.

Our findings suggest that plant communities in the MS and ST are especially vulnerable to climate change, as others have predicted (Angerer et al. 2008, Ojima et al. 2013). Communities already significantly altered by heavy grazing may be more resistant to climate-induced change than lightly grazed reference communities. These findings indicate potential resilience of grazing-induced degraded communities. Climate-induced changes to lightly grazed MS reference communities may be unavoidable consequences of a warming climate, and rangeland managers, including pastoralists, must consider how to adapt to rather than mitigate these changes.

If these MS communities are indeed growing rarer across Mongolia, they may be appropriate conservation targets where current and future climatic conditions can support them. Further fieldwork is needed to determine trends in and current distribution of these communities. Resampling other long-term research plots located in MS regions may help to determine whether trends observed at these Khangai Mountain study sites are occurring elsewhere in the Khangai and other Mongolian MS regions. Plant distributions may change due to changes in habitat due to land conversion or fragmentation, dispersal processes, or environmental characteristics (Doxford and Freckleton 2012). In our Khangai study sites, we observed no land conversion, fragmentation, or alterations in dispersal processes, leading us to infer that changes in environmental factors, namely climate change and livestock grazing, are more likely responsible for changes in plant community prevalence. The nature of these threats in combination with the largely intact Khangai Mountain landscape suggests integrated plant community conservation approaches (Loss et al. 2011) may be an appropriate strategy, including in situ protection of existing rare mountain plant communities, conservation of sites where future climatic conditions may support these communities (Gitlin et al. 2006), and potentially, assisted

migration and ex situ genetic conservation (Loss et al. 2011). Finally, as recent studies have highlighted, the loss of rare plants and plant communities may have important implications for ecosystem functions (Mouillot et al. 2013), pointing to the need for future research on biodiversity–ecosystem function relationships in these potentially vulnerable Mongolian mountain plant communities.

Our findings illustrate the utility of STMs as a means to synthesize and visually depict plant community composition and change in relation to dynamic climate and management factors. The data-driven approach we used provides further validation of the data-driven modeling methods applied by Kachergis et al. (2012, 2013) and Bruegger et al. (2016) and illustrates the value of repeated monitoring data in understanding patterns and drivers of plant community distribution and change along grazing gradients. These STMs also highlight communities and associated indicator species that warrant prioritization for monitoring and management, such as potentially declining reference communities and MS grasses in the MS, and communities and associated species that may indicate transitions toward a grazing-induced or grazing \times warming-induced alternate states, such as *Stipa krylovii* or *Carex duriuscula*-dominated states in the MS. Given the relative paucity globally of experimental and observational data on the combined effects of grazing and climate change on rangeland plant communities, our findings provide a basis for further research and adaptation planning. Specifically, our results provide fodder for future cross-system comparative studies and meta-analyses and suggest hypotheses to test in distributed experiments across multiple grassland types. Finally, our results offer empirical evidence of climate- and grazing-driven changes in community composition across multiple rangeland ecological zones, illustrating which zones and communities are most (ST and MS) and least (DS) likely to shift compositionally in response to the individual or combined effects of these stressors.

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