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Fine-scale characteristics of the boundaries between annual patches and perennial patches in a meadow steppe

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Abstract

Context Boundaries are ubiquitous and may have crucial influence on the pattern, process, and dynamics of landscapes. However, there is little understanding of mechanisms that govern changes in the location and composition of boundaries. Especially, it is still uncertain whether there are definite relationships between vegetation and soil. At smaller scales, investigation of more detailed soil and vegetation characteristics can more clearly reveal the linkages between soil properties and vegetation patterns.

Objectives We studied fine-scale characteristics of boundaries between two physiognomically distinct patch types, annual patches and perennial patches, in a saline-alkaline grassland. The aims were to examine the relationship between vegetation patterns and soil properties, and to explore mechanisms that govern changes in the location and composition of boundaries.

Methods In a 50 ha grassland fenced for more than ten years and where a recovery process had been initiated and where annual grasses were dominating in most saline-alkaline areas, we quantitatively characterized the spatial gradients across the visually-identified physiognomic boundary (subsequently adjusted by hierarchical clustering approach) between the annual patches and perennial patches at a fine spatial scale (220 cm × 50 cm transects consisting of 11 quadrats). We statistically defined the boundaries by the Split Moving Window method based on soil and plant variables. We also applied Canonical Correspondence Analysis and Nonmetric Multidimensional Scaling to assess the relationship between the fine-scale functional

patterns and soil properties along the studied environmental gradient.

Results At fine scale, the vegetation and soil boundaries were well-defined and statistically characterized by a high rate of change, compared to the immediately adjacent areas. The plant characteristics were markedly influenced by soil properties. The alteration of salinity and alkalinity were the most important factors explaining the plant patterns across the patch boundaries. However, physiognomic vegetation boundaries did not fully coincide with the soil boundaries, nor with statistically-defined boundary in species richness and biomass. There were successional processes of colonization involved in perennials encroachment in the annual patches.

Conclusions Underlying soil properties primarily determine the plant patterns of the boundary; the plant succession caused by interspecific competition is superimposed on the plant-soil feedback loop maintaining soil nutrient conditions. These processes ultimately alter the characteristics and locations of patch boundaries in response to changing disturbance regimes. Our findings offer insight into the processes occurring at the boundary and how the boundary may respond to the changes of environmental conditions and drive landscape-level dynamics.

Keywords

Boundary characteristic · Patch · Meadow steppe · Saline-alkaline grassland · Fine-scale study · Plant-soil feedback

Introduction

Vegetation is commonly arranged in mosaics of patches with intervening boundaries, not only in the arid ecosystems but also in mesic regions (Aguiar and Sala 1999). Boundaries between different communities at macro- or meso-scales in forest-grassland and grassland-shrub land mosaics have been extensively studied (Nicholas et al. 2011; Müller et al. 2012). Looking more closely at grassland vegetation structure at finer scales (e.g., at 1-meter scale or less), discrete, functional-group based patches are easily observed within even seemingly continuous grasslands (Moore 2009). However, studies of boundaries between functional-type patches within one ecosystem at fine scales have been comparatively scarce. Yet, investigation of more detailed soil and vegetation characteristics could reveal the linkages between soil properties and vegetation patterns, and lead to a better understanding of dominant processes giving rise to landscape dynamics at larger scales. Such understanding is ultimately needed to make sounder management decisions.

Vegetation and soil patterns across boundaries are well known to be tightly coupled (Buxbaum and Vanderbilt 2007). Distinct floras usually coincide with edaphic disjunctions (Hobbs 1986; Buxbaum and Vanderbilt 2007; Nano and Clarke, 2008). The soil often imposes strong impacts on resources available to plants, so that the formation and dynamics of vegetation patterns are constrained by the underlying soil properties (Bestelmeyer et al. 2006; Conti et al. 2017). In turn, dynamic feedback may involve vegetation-induced changes in soil properties (Peters et al. 2006). Mason

et al. (2016) showed that the soils typically associated with grassland were found under present-day deciduous forest, after vegetation boundary between forest and grassland had shifted in the Midwestern United States. They also suggested that other environmental factors such as parent material, topographic setting, and soil hydrology were influencing the timescale of soil response to vegetation alteration. Alternatively, abrupt physiognomic (structural) boundaries between communities or vegetation types might not to be associated with edaphic changes (Read et al. 2006). Instead, they may be governed, to varying degrees, by other local abiotic environmental factors such as geomorphology and distance from the water table or distance from the boundary (Buxbaum and Vanderbilt 2007; Stine et al. 2011). Furthermore, besides the abiotic factors, biotic interactions (e.g. facilitation or competition) might shape boundary structure and could explain boundary dynamics (Peters et al 2006; Nicholas et al. 2011). On some occasions, changes in the intensity or frequency of disturbance, especially grazing or fire regime, or climate change, could operate to change the conditions for vegetation in boundaries (Allen and Breshears 1998; Hodgkinson 1998; Sankey et al. 2006).

The above controversy may be attributed to the different scales of the studies. Ecological phenomena possess an inherent scale at which the ecological processes or physical characteristics occur over the landscape, both spatially and temporally. Recognition of the scale-dependence and hierarchical structure of patchiness is crucial to understanding the dynamics and stability of ecological systems (Wu and Levin 1994; Wu and Louchs 1995). Boundaries can be considered as structures of biotic

communities that appear to be distinctly organized at different scales (Muñoz-Reinoso 2009). The macro-scale boundaries (hundreds to thousands of kilometers in space) are always determined by a few key factors, such as climate, topography, geology and hydrology (Parks and Mulligan 2010). The meso-scale boundaries (hundreds of meters in space) are usually assumed to result from a complicated interaction between a range of concurrent, overlapping environmental and disturbance factors such as topography, soil texture, and biotic interactions. The occurrence of different transition types are controlled by all correlated parameters, and potentially even their interactive effects, rather than single explanatory factors (Nano and Clarke 2008; Carlile et al. 1989; Müller et al. 2012). At these broader scales, the interactive effects of all constraints easily make it uncertain whether there are definite relations between vegetation and soil. However, at finer scales (centimeters to tens of meters), investigation of more detailed soil and vegetation characteristics in domains of relatively identical topography, slope transitions and groundwater table, etc., could more clearly reveal the linkages between soil properties and vegetation patterns. From the perspective of hierarchical patch dynamics, Wu and Louck (1995) asserted that the mechanistic explanation as to how the focal-level (e.g., mosaic of species association patches in grassland) processes operate must be sought at the next level down or, sometimes, at even finer scales. However, the scarcity of research at fine scales is obvious, limiting our insight into the boundary characteristics and dynamics.

Exploring physical and biological processes that regulate the position and structure of the boundary is an effective way of gaining understanding on boundary

dynamics (Fernandes et al. 2016). Boundary dynamics are controlled by structuring processes, each of which may operate at its own temporal and spatial scale; connections between pattern-process on the local stand and on landscape scale and their drivers result in the systematic change. Commonly, changes in the fine-scale processes within a defined area propagate to produce broad-scale responses. Therefore, studies at fine scales are most likely to provide the mechanistic understanding for behavior at a particular scale (Peters et al. 2007). For example, Montana (1992) elucidated vegetation dynamics of vegetated arcs in a Mexican desert. He found that a succession process of colonization occurred in the upslope fringes whereas senescence without new recruitment occurred in the downslope fringes, offering an example of succession in arid lands where two-phase mosaics existed.

Within the last century, extensive human disturbance of the vast steppe in northeastern China, mainly through overgrazing and frequent mowing, has led to soil salinization, resulting in a highly fragmented grassland landscape consisting of a mosaic of distinct patches characterized by different plant communities and visually abrupt boundaries. In the seriously degraded grasslands, the landscapes are populated by hierarchical and dynamic mosaic of vegetation patches of different sizes and successional stages.

These patchy grasslands provide excellent model systems for studying spatial micro-scale boundaries. They exemplify a hierarchical patch system where associations between individuals and their abiotic and biotic environment occur at a

micro-scale, driving fine-scale dynamics within patches and on the patch boundaries (Wu and Loucks 1994; Peters et al. 2006; Wu and David 2002). These fine-scale dynamics give rise to landscape-level patterns, manifested as a mosaic of patches of different sizes and at different successional stages. At the core of this landscape-level dynamics is the boundary dynamics of individual patches, determining how different patch types wax and wane in their total coverage within a fragmented landscape.

Boundaries (biotic transitions) could be defined at multiple spatial scales, including individuals, assemblages of species, and species associations (Peters et al. 2006). For this study, we focused on the boundaries (i.e., ecotones) between patches defined by adjacent species associations or plant communities. We investigated plant populations and the associated soil variables along fine-scale transects crossing annual patch/perennial patch boundaries in a degraded grassland. We aimed at addressing the following objectives: a. to quantify the fine-scale characteristics of patch boundaries and to examine the relationship between vegetation and soils, and b. to explore mechanisms that govern changes in the location and composition of boundaries.

Methods

Study area and patch characteristics

The study was conducted at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, China (44°45' N, 123°45' E), in the eastern region of the Eurasian continent. This area is characterized by a temperate,

semi-arid continental monsoon climate with cold and dry winters and hot and wet summers. Mean annual temperature ranges from 4.6 to 6.4°C, and mean annual precipitation is 280–400 mm, mostly occurring during the summer months (July–September). Annual potential evapotranspiration is extremely high, about three times the annual precipitation (Zhong et al. 2014). The main vegetation type is meadow steppe predominated by *Leymus chinensis* and *Stipa baicalensis* (Wang and Ba 2008). The main soils are chernozem, chestnut soil, meadow soil, and aeolian soil (Wang et al. 2009), most of them characterized by mixed salinity and being alkaline (pH value 7–10.5).

We conducted this study in a 50 ha grassland plot fenced for more than ten years to prevent grazing and human access. A recovery process has started in this plot where the plant communities are composed of different patch types in varying successional stages (Wang et al. 2015). At the earlier successional stages, salt-tolerant communities (e.g., *Chloris virgata* or *Suaeda glauca* communities), mostly the salt-tolerant annual grasses, tend to be lush in saline-alkaline stands, even on the bare ground (Fig. 1 a). The perennial communities (e.g., *L. chinensis* or *L. chinensis*+forb communities) flourish in fertile patches at the later successional stages. The encroachment of perennials frequently shows a clumpy pattern, forming patches embedded in the annual grass matrix (Fig. 1 b). These perennial patches vary in area from a few tens of square centimeters to several hundred square meters. The smallest patches (few tens of square centimeters) only contain one or two salt-tolerant species. With succession proceeding, the patch size and the species richness increase, and the adjacent patches

would meet and merge together to form larger but fewer patches. At the final stages, one or two perennial grasses such as *L. chinensis* should be dominant in these large patches (several hundred square meters) (Bai et al., 2015). Han et al. (1996) found that the variation of species number with increasing area of patch shows a humped relationship.

Sampling design and measurements

The dependence of boundaries on the scale of observation has important implications for empirically describing them. While the number of transects generally decreases with increasing scale, the length of each transect usually needs to increase. The number of transects may range from a few short transects for fine-scale studies (e.g., Hobbs 1986; Montana 1992; Müller et al. 2012: about 10 transects measuring some tens of meters), through few at intermediate scale (e.g., Dutoit 2007; Stine et al. 2011: three to five transects some hundreds of meters long), to just one long (>1 km) transect at larger-scale studies (e.g., Stein and Ludwig 1979; Buxbaum and Vanderbilt 2007; Muñoz-Reinoso 2009).

We have observed that, in our study area, the plant biodiversity in perennial patches of few square meters in area were usually high enough to include forbs, legumes, sedges, perennial grasses, and salt-tolerant annual grasses. In late July 2008, in order to investigate the spatial pattern and the relationship between plant and soil across the boundaries of these patches, we randomly selected 12 typical perennial community patches with a diameter of about 2 m, scattered in a matrix of continuous

annual communities. These patches contained forbs, perennial grasses and annual grasses, and their shapes were relatively regular, indicating that they had developed through gradual restoration succession, rather than through merging of patches. For each patch, a 2.2-m transect was set up, crossing the boundary perpendicularly; the boundary was identified visually, based on differences in the physiognomy of perennial and annual grass communities. Each transect was composed of 11 adjacent rectangular sampling quadrats of 20×50 cm with their long axis parallel to the boundary (Fig. 1b). The mid-quadrat, defined as 0 cm-quadrat of each transect, was located on the visually-identified boundary between the annual/perennial patches. Consequently, each transect had five quadrats in the annual grasses patch and five in the perennial patch. Quadrats at the same position relative to the visually-identified boundary were treated as independent replicates across the 12 replicate transects; the graphed values are means (with SD) across the replicates.

To avoid the subjectivity of visual determination, we applied a hierarchical clustering approach to adjust the visual boundaries by building an ultrametric functional dendrogram (functional tree; Mouchet et al. 2008) (UPGMA, function `hclust` in R) (Fig. S1), based on species abundance in 11 quadrats of each transect. 11 quadrats in each transect were divided into two distinct clusters, an annuals cluster, and a perennial cluster. The quadrat just next to the annuals cluster was defined as 0 cm. Results of clustering analysis showed that the visual determination of 0 cm-quadrats in most of the transects (9 of 12) was consistent with quantitative determination. In the remaining three transects, we redefined the original 20 cm-

quadrats as new 0 cm-quadrats, and adjusted the distances of the other quadrats accordingly. Therefore, these three transects contain only four (rather than five) perennial-patch quadrats.

Within each quadrat, the following samplings were made. First, the shoots were removed by cutting at the soil surface and identified to species level. Referring to group designations derived by Kindscher and Wells (1995) for tallgrass prairie sites in Kansas (USA) and classifications applied by Jackson (2005) for herbaceous species in open woodlands in north-eastern Queensland (Australia), we classified all plant species (39 species) into five functional groups based on their phenology and morphology, assuming that these characteristics are also related to the heterogeneity of the grassland: annual grasses (2 species), perennial grasses (7 species), sedges (1 species), forbs (24 species) and legumes (5 species). After measuring species numbers and tiller numbers of each species, the plants within each quadrat were dried in an oven at 70 °C for 48 h and weighed to obtain the dry weight; the values were then converted into grams per square meter to determine the biomass. Soil samples were taken at the center of each quadrat using a soil corer (4.0 cm in diameter, 15.0 cm in depth), stored in ziploc plastic bags, brought into laboratory, and hand-sorted to remove stones and roots before analysis (see below). Soil moisture (SM) was determined from the difference between the fresh and oven-dried weights (at 115°C for 12 h) of soil samples and calculating the percentage of the moisture lost. The rest of the soil samples were air-dried at room temperature for two weeks, crushed, and passed through a 2-mm mesh sieve for the following measurements. Soil pH value

(Shi and Wang 2005) and salinity (electrical conductivity, EC; Corwin and Lesch 2005) were measured from a soil/water (1: 5) paste; the pH was determined using a PHSJ-4A pH meter and EC was measured with a DDSJ-308A conductivity meter. Soil nutrient condition (soil organic matter, SOM; Ford et al. 2016) was calculated by measuring the total organic carbon in the soil by the dichromate oxidation method (Walkley and Black 1934) and converting to organic matter.

Descriptive metrics and data analysis

Several metrics were used for describing plant characteristics in each quadrat: species richness (number of species, S), Shannon-Wiener index, Pielou index, and functional type proportions. Shannon-Wiener index (H') was calculated as $H' = -\sum_{i \in S} (P_i \times \ln P_i)$ (where P_i is the proportional abundance of species i , summed over all S species); Pielou index (E) was calculated as $E = H' / \ln S$ (where S is the total number of species); functional type proportions were the ratios of species number of each functional group to the total species number recorded for a specific quadrat.

Montana (1992) suggested that the number of species would be expected to be spatially related in the presence of a successional process of colonization. We used geostatistics (Rietkerk et al. 2000) to explore the general sequence of species turnover by verifying whether the changes in plant species richness followed a regular trend or were spatially independent. If the data are spatially patterned, the semi-variogram will exhibit autocorrelation. These analyses were conducted using the program GS+ 5.0 (Gamma Design Software, Plainwell, MI) (Robertson 2000).

It would be desirable to be able to infer the dynamics of the spatial process based on a spatial snapshot taken from a sampling at a single time, without the need for long-term study of vegetation dynamics. Based on a study on a rising sea-shore where elevation could be used as a proxy of habitat age and successional change, Cramer and Hytteborn (1987) suggested that Canonical Correspondence Analysis (CCA) could be used to identify and separate distinct transitional pathways between two spatial configurations, with each in its own distinct phase of development. Accordingly, we performed CCA and Nonmetric Multidimensional Scaling (NMDS) to combine the analysis of floristic gradients with distance to explore whether the vegetation succession tracks the distance away from the boundaries. The NMDS was performed based on the Bray-Curtis dissimilarity index with the metaMDS function (Oksanen et al. 2012). The ordisurf function was employed to fit a smooth surface of the distance gradient and soil condition (pH, EC, SOM) onto the NMDS ordination. The CCA not only helped to detect relationships between the plant community composition and the distance from the boundary, but was also used to explore spatial patterns of functional groups along the soil gradients. Partial CCA partitioned the variance in functional group dispersions explained by environmental variables. All the CCAs were tested for significance with a Monte Carlo permutation test (999 permutations). All analyses were performed with software R version 3.5.1 (R Core Team 2018). The NMDS and CCA were applied considering each transect as a group of samples in which each individual quadrat represented one sample. Wang et al. (2015) also found that the spatial variability and spatial structure of several soil

variables (C, N, P, pH, and EC) were related to grassland plant species richness and diversity. We used distance and three soil indices (SOM, EC, pH) as the environmental variables, and used abundance of five functional groups as floristic variables. Soil moisture (SM) was excluded from these analyses because SM measured at a specific time may not be representative of conditions over longer time scales (across seasons) that are important for vegetation dynamics.

Statistically, a boundary can be defined as the location with the highest dissimilarity between adjacent samples (Ludwig and Cornelius 1987). To define the position of boundaries between neighboring communities and the width of the transition zone, we used the plant and soil attributes to define boundary using the Split Moving Window Boundary Analysis in which the Euclidean distance coefficient was plotted on the ordinate against the transect position on the abscissa (Muñoz-Reinoso 2009). We calculated the Euclidean distance coefficient using plant and soil mean value, treating 12 transects as independent replicates. In our analysis, a window width of four quadrats revealed a relatively smooth pattern of distance peaks; widths of less than four had greater sample-to-sample noise, whereas window widths from five to eight did not appreciably affect the interpretation of boundary locations.

Results

Spatial patterns of plant variables

Plant species richness, Shannon-Wiener index, evenness, and biomass

We investigated plant characteristics as plant diversity and above-ground biomass across the patch boundaries. Above-ground biomass, species richness, and Shannon-Wiener and Pielou indices all showed clear escalating trends from the annual patches to the perennials patches (Fig. 2); all these trajectories were significantly different from uniformity ($P < 0.0001$). Based on pair-wise comparisons of adjacent quadrats along the transects, there were no significant differences in above-ground biomass, plant species richness, or Shannon-Wiener and Pielou indices within the annual patches at quadrats -100 cm to -20 cm from the boundary, nor within the perennial patches from 60–100 cm from the boundary, whereas there were steep increases near and across the visually-identified boundary. Plant biomass, species richness, and Shannon-Wiener and Pielou indices at the quadrat 60 cm in the perennial patches were on average 7.0, 6.2, 14, and 4.2 times higher than at -20 cm in the annual patches, respectively (Fig. 2). There was a tendency for species richness and above-ground biomass to increase with distance from the boundary within the perennial patches, but this tendency was statistically significant only for quadrats more than 1–2 quadrats apart (Fig. 2a, b). Plant species richness in the perennial patches was far higher (up to more than ten species) than in the annual patches (1–2 species). Similarly, the mean biomass was much higher in the perennial patches (355 g/m² vs. 38.2 g/m² for annual patches).

The semi-variogram of plant species richness showed a significant positive spatial autocorrelation (Table 1, $P < 0.01$). A high ratio $C/(C+C_0)$ (i.e. >75%) means that a large part of the variance was introduced spatially, implying a strong spatial

dependency of the variable. The high R^2 (0.988) of the linear model with a sill indicated patchy structure.

The proportions of different plant functional types

Differences regarding the proportion of 5 plant functional types are evident along the studied gradients (Fig. 2e, f, g, and fig. S2). Annual grasses were ubiquitous in the annual patches (representing up to 92% of species) and scarce in the perennial patches (less than 10%). Within each patch type, the percentages of annual grasses did not significantly change along the transects, neither within the annual patches nor within the perennial patches. However, there was an abrupt change at the boundary, from -20 cm to 0 cm. Forbs showed the reverse tendency: there was a jump from a nearly complete absence in the annual patches to moderate–high species richness in the perennial patches containing on average 2–8 species; the maximum among all sampling quadrats was 14 species. Of all quadrats, only those near or on the boundary (from 0 cm to 20 cm in the perennial patches) had significant different proportions of forbs compared to the quadrants further in or out ($P < 0.0001$). The percentage of sedges and legumes in total species was no more than 12%. They all occurred in the perennial patches. The proportions of legumes within the perennial patches were greater than within the annual patches ($P < 0.0001$) (Fig. S2a). The proportions of sedges did not change along the transects ($P = 0.204$) (Fig. S2b).

Surprisingly, the proportion of perennial grasses showed a completely different pattern from other functional groups. The proportion of perennial grasses peaked in the boundary area where they reached absolute dominance (on average 68% vs. 22%

for annual grasses and 10% for forbs, respectively), with sharp declines away from the boundary in both directions (Fig. 2f). Perennial grasses were somewhat more abundant in the perennial patches than in the annual patches, but the differences were not significant for many comparisons.

The significant dissimilarities of the functional groups across the distance gradients were also confirmed by permutational multivariate analyses of variance and analyses of similarities (ANOSIM) ($R = 0.338$, $P = 0.001$; Fig. 4a). The plot of NMDS shows that, with increasing distance from the boundary within the perennial patches, the abundance of forbs, legumes, and sedges significantly increased, whereas the opposite is observed for the abundance of annuals.

Spatial patterns of soil properties

An examination of spatial patterns of soil properties indicated that dramatic changes occurred in soil variables across the patch boundary. Electrical conductivity (EC) and pH value showed sharp declines when moving from the annual patches to the perennial patches (Fig. 3a, b). EC dropped by 70% between -100 cm in the annual patches and 100 cm in the perennial patches. Changes in soil moisture (SM) across the boundary were similar to the changes in EC and pH (Fig. 3d); there was a 31% decrease in SM between -100 cm in the annual patches and 100 cm in the perennial patches. Conversely, soil organic matter (SOM) increased from about 1.0% to 2.8% when moving from the annual patches to the perennial patches.

Relationship between plant and soil properties

The axes extracted by CCA represent those directions of variation in the functional group composition that are related to environmental variables. The four environmental variables explain 44.3% of the variance in functional group distribution, with the first two axes accounting for 44.2% (Table S1, $P \leq 0.001$). The variation partitioning indicated that the four environmental variables had a significant pure effect ($P < 0.01$). pH had the greatest independent contribution (3.6%), followed by SOM (1.8%), EC (1.5%), and distance (1.1%) (Table S2). The results of the partitioning confirmed that a relatively large part of the explained variation was related to joint effects of the explanatory variables. The main direction of change for each of the environmental variables was illustrated by the arrows in the center of the biplot. The length of these arrows corresponded to the relative importance of these four variables in determining the floristic variation (Fig. 4b). The large obtuse angle between the vectors for EC and pH versus SOM and distance showed that these two variables were negatively correlated with SOM and distance. The small acute angle between EC and pH indicated they were positive correlated, as expected. The similar positive relation between SOM and distance were also shown by the small acute angle between them. With increasing distance from the boundary, forbs and legumes were abundant on lower pH, lower EC and higher SOM soils, whereas annual grasses were dominant on higher pH, higher EC and lower SOM soils.

Boundary description

Peaks or ridges generated by the moving split-window distance technique applied

to either plant characteristics or soil properties would indicate the locations of discontinuities along the gradient. Our results showed that abrupt shifts in the studied soil properties were evident, with a possible exception of soil pH (Fig. 5). The boundary for SM was situated at -10 cm in the annual patches, whereas the boundary for SOM and EC was situated at 10 cm in the perennial patches; the profiles for SOM and EC were very similar. By contrast, the more gradual shifts of biomass and richness were evident as wider peaks. The biomass peak straddled the annual patch/perennial patch boundary (-10 cm to 10 cm), whereas species richness peaked within the perennial patches (30–50 cm; Fig. 5). Thus, the Euclidean distance peaks suggest different boundaries for plant and soil variables.

Discussion

Although a number of studies have been conducted on exploring reasons for boundary structures at macro- and mesoscales, and interactions between the biotic and abiotic environment have been demonstrated, the directions of the interactions, that is causation, are not clear. Consequently, we have a low ability to predict boundary dynamics. By analyzing the relationship between herbaceous species distributions and spatial variation in soil parameters at smaller scales, we found that the plant assemblage transitions were affected by—but not completely coinciding with—the occurrence of distinct edaphic changes. Therein, underlying soil properties constrained plant pattern formation and dynamics. We suggest that this pattern can be explained by plant succession that was superimposed on the plant-soil feedback loop

maintaining soil conditions.

Spatial pattern of plant variables and soil properties

Our results indicate that boundaries occurred where the changes in both floristic and edaphic attributes with spatial position were abrupt. The simultaneously abrupt shifts implied a potential linkage between the changes in plants and soils. CCA analysis further revealed that all the plant functional groups were closely associated with SOM, pH and EC (Fig. 4b). These results are similar to most previous findings on the influence of soil properties on structural plant patterning across the boundaries such as grass-shrub boundaries (Hobbs 1986; Nicholas et al. 2011), mulga-spinifex boundaries (Nano and Clarke 2008), and savanna-forest boundaries (Staal and Flores 2015).

Figures 2 (e, f, g) and 4b clearly show that the annuals patches were covered by few halophilic plants or even salt-alkaline crusts, featuring salinization and alkalization (higher EC and pH) and poor nutrients (low SOM, less than approximately 1.5%). Only a few halophytes, such as *C. virgata* and *S. glauca*, are present, owing to their salinity tolerance (Yang et al. 2008; Niu et al. 2008; Li et al. 2009). Conversely, the perennial patches provide favorable soils with lower EC and pH but higher SOM for dominant species and forbs, such as *L. chinensis*, *Medicago ruthenica*, *Thalictrum simplex* and *Kalimeris integrifolia*, which are species demanding relatively rich nutrient and low alkaline-salinity stress levels. Here the higher richness could be interpreted mainly as an effect of abundant organic matter,

the limiting factors for plant biomass accumulation (Roem and Berendse 2000; Ford et al. 2016). Specifically, the clonal perennial grasses, *L. chinensis* and *P. australis*, can respond to habitat heterogeneity by shifting their morphology and architecture (Wang et al. 2017). They preferentially exploit both relatively favorable and higher-stress boundary areas just adjacent to annual patches (Zhang et al. 2014).

Furthermore, their physiological response to saline-alkaline stress may also enhance their ability to outcompete their neighbors (Shi and Wang 2005; Yang et al. 2007).

Moreover, our results of partial CCA of four environmental variables suggested that pH was the most important predictor to account for the variation in species richness. This result aligns with the view of Shi and Wang (2005) that salt-alkaline mixed stress was the dominant inhibitory factor in those saline-alkaline grasslands. Here high concentrations of exchangeable Na^+ in soil (higher EC and pH, Fig. 3 a, b), accompanied by the lack of organic matter (Fig. 3 c), not only destabilize the soil structure and lead to waterlogging (Fig. 3 d) and hypoxic conditions, but also negatively affect the plants during the germination, growth and fruiting stages; of these, seed germination and seedling growth are the most sensitive ones to salinity (Shi and Wang 2005, Ibrahim 2016). Consequently, soil patchiness occurring across the boundary seems to be a key determinant of spatial plant patterns.

Boundary description

Quantitative description of the boundaries by differential profiles is informative (Hobbs 1986). Abrupt changes in physiognomy are visually very evident in the

studied grassland, yet such abrupt changes were accompanied by the broad transitional zones in terms of plant species richness and biomass, which did not spatially fully coincide with each other nor with the physiognomic boundary. Narrow peaks in the profiles of environmental variables, indicating sharp soil boundaries (i.e., EC, SOM and SM), were evident and, apart from SM, were largely found to coincide with each other and the physiognomic boundary (Fig. 5). Hobbs (1986) proposed that less well-defined boundaries were produced by more gradual changes in species composition, and that well-defined boundaries occurred where the changes in species composition with spatial position were more abrupt than elsewhere in the area. For the degraded saline-alkaline grasslands, the soils are relatively stable and reflect long-term formation conditions. The plants, however, may be more sensitive to some disturbances and environmental changes. Moreover, different types of vegetation boundaries (species richness and biomass) reflect different responses to underlying environmental processes (Fortin et al. 1996). Plant communities are more changeable than soils, and the boundary locations dictated by different variables are quite different. Consequently, we suggest that stable soil parameters are suitable for determining ecologically sound boundaries.

Hierarchical patch dynamics

At the landscape level, the dynamics of a patch mosaic is determined by how new patches are formed, how patches may grow or shrink, and how they eventually may disappear (Levin and Paine, 1974). The growth and shrinkage of patches is manifested

as dynamic patch boundaries. In the studied grassland landscape, patch boundaries are strongly correlated, but not fully coinciding, with soil physical properties. The dynamic nature of the boundary is reflected by the successional pattern that is seen near the boundary. In particular, it appears that under the present disturbance regime (i.e., absence of overgrazing), perennial grasses are driving the encroachment of the perennial community into the annual patches, being the dominant functional group at the patch boundaries and penetrating into the annual patches, in contrast to forbs and legumes that are almost entirely confined to the perennial patches. In turn, within the perennial patches, succession dynamics favors forbs and legumes that get more abundant away from the boundary. Thus, soil properties are setting the stage for a competitive community where micro-scale interactions are eventually driving the patch boundaries and the landscape pattern.

Direction of vegetation change

Here we synthesize insights from earlier literature and the results reported here to outline our best interpretation of the processes that underlie the vegetation dynamics in the studied mosaic landscape. Figure 6 presents a conceptual model that summarizes our understanding, acknowledging that our data represent a snapshot that cannot conclusively resolve the proposed dynamics.

The documented snapshot reflects the transitional pathway between two patch types that differed in soil conditions and species composition as well as in their spatial correlation and interaction with each other. Fig. 4a, b shows that the direction of

floristic change was clearly related to environmental variable distance. This result means that distance had the profound influence on the distribution of species, suggestive of successive species replacement along an environmental gradient (Cramer and Hytteborn 1987). Our autocorrelation analysis of species numbers along successive quadrats also revealed that the changes in species richness were spatially-dependent variations (Table 1). According to Montana (1992), this indicates that there did exist a successional process of colonization. Fig. 4a showed the significant trend of floristic change in agreement with the trend of succession: annuals → perennial grasses → forbs + legumes + sedges. Thereby, in the restoration process occurring within the enclosure (indicated by the solid horizontal arrows in Fig. 6), the general sequence of species substitution in a saline-alkaline patch could be elicited as similar as this spatial sequence from the annual patches over the boundary to the perennial patches. By the same token, a degradation process (depicted by the dashed arrows in Fig. 6) could be inferred as the sequence forbs → perennial grasses → halophytes, along with the soil degradation, when grasslands are excessive disturbed (e.g., through overgrazing).

Fragmented grassland is a dynamic mosaic of patches in different successional stages. These patches might influence boundary dynamics for the system. In saline-alkaline grassland, saline-alkaline mixed stress is the primary limiting resource (Shi and Wang 2005). As discussed above, only alkali-tolerant halophytes (e.g. *C. virgate*, an annual gramineous species) can colonize bare alkaline patches as pioneer species (Li et al., 2009). Therefore, the patches of annuals are usually characterized by

consociation with single synusia consisting of a pure population. The subsequent de-alkalization and enrichment as well as concentration of nutrients are expected as additional soil property changes because of the plough-back effects (Gao et al. 1996). These processes create the conditions for the establishment of more-demanding species (i.e., perennial gramineal grasses and forbs). Recruitment of scattered perennial patches within the annual matrix starts stochastically at some locations (Gao et al. 1996). The whole succession is primarily characterized by elimination in which perennial grasses and forbs gradually exclude the halophytes by the competition mechanisms within the perennials patches featuring higher nutrient levels (Nicholas et al. 2011). Then the higher plant diversity favors organic matter accumulation in soil, especially by the nitrogen-fixing legumes (only existing in the perennial patches, Fig. S2b), a vital part of the functioning in the nitrogen limited meadow steppe of north-east China (Mulder et al. 2002; Wang et al. 2015). Changes to soil properties that are caused by plants, which in turn influence the performance of plants, result in plant–soil feedbacks. Among perennial species, perennial gramineal grasses, efficient colonizers in saline-alkaline grassland (Wang et al. 2014; Zhang et al. 2017), will exploit annual patches as marginal habitat. Their expansion over the perennial/annual boundaries may facilitate subsequent succession of forbs by improving soil conditions and reducing competition from annuals. In sum, different causes and mechanisms operate on different spatial scales, and create a hierarchical structure of patchiness, also induced dynamic boundaries. Abiotic constraints (primarily soil conditions) are largely responsible for the spatial configuration of patches, whereas species

interactions (i.e., interspecific competition) lead to succession within the patches.

Our finding that the locations or range of boundaries differed between floristic and edaphic properties represents a major deviation from some earlier studies that have suggested that vegetation zones strongly coincided with soil series zones (Nano and Clarke 2008; Nicholas et al. 2011). These findings might agree with the hypothesis that if vegetation was strongly patterned in relation to soil patterns, changes from past vegetation have not been great (Stein and Ludwig 1979). By contrast, transitions in saline-alkaline grassland appear far more dynamic if patterns or levels of disturbance change (Liu et al. 2015). According to the views of Peters et al. (2006) on patch and boundary dynamics, the perennial patches and the bare saline-alkaline patches (annual patches) are two end states, with a boundary between them. The location of the boundary as well as the spatial distribution of the end states may shift as the disturbance regime (e.g., enclosure vs. grazing) changes through time. Specifically, enclosures create favorable conditions for the perennial patches, whereas over-grazing creates conditions that favor annual patches (or even saline-alkaline patches). The boundary between perennial patch and saline-alkaline patch may shift back and forth spatially through time as grazing management changes. We hereby propose a conceptual framework trying to elucidate the mechanisms underlying boundary dynamics (Fig. 6). However, because the evidence that our study can provide is correlative, further disturbance-based experiments are needed to provide direct evidence for how disturbance can lead to changes in edaphic and vegetative parameters as the framework predicted.

Results of this study suggest that the mechanisms by which boundary dynamics are driven are different at different spatial scales. The configuration of patches is primarily determined by the underlying soil properties. The floristic composition is decided by species interactions within each type of patches. Then the plant-soil feedback profoundly contributes to plant succession and soil development. The boundaries are internally dynamic with inherent abiotic constraints reinforced by biotic feedbacks. These processes ultimately alter the characteristics and locations of patch boundaries in response to changing disturbance regimes, driving the landscape-level pattern of patch mosaics. These findings may provide insight into the processes occurring in the boundaries more generally and help to predict how the landscapes respond to these changes.

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Table legends

Table 1. Parameters of the optimal models of the transect semi-variograms of plant richness and soil attributes.

R^2 , coefficient of determination. C_0 , nugget variance. C_0+C , sill. The degree of spatial dependence $C/(C+C_0)$ determinates the proportion of the sample variance that is explained by spatial structure. If $C/(C_0+C)<0.25$, the variables have weak spatial autocorrelation; $0.25 < C/(C_0+C) < 0.75$ signifies medium spatial autocorrelation, and $C/(C_0+C) > 0.75$ significant spatial autocorrelation.

Figure legends

Fig. 1 Patchy landscape of the field site and spatial set-up of the sampling transects at the transition zone between perennial patch and annual matrix. a. degraded grassland consisting of vegetation patches (green) and extensive saline-alkaline bare areas (white); b. recovering grassland, with perennial communities (green) embedded in the annual grasses matrix (yellow). Rectangles denote 11 plant sampling quadrats along the sampling transect; the points illustrate the location of soil cores within each quadrat. Quadrat position is expressed relative to the border, with positive distances (20–100 cm) for quadrats inside the perennial patch and negative values outside

Fig. 2 Plant aboveground biomass (a), plant species richness (b), Shannon-Wiener index (c), Pielou index (d), proportions of annual grasses (e), perennial grasses (f), and forbs (g) along the gradient from annual patch to perennial patch. Values are means \pm S.E. Different lowercase letters indicate significant difference among neighboring sampling points ($P < 0.05$). The points sharing the same letter are not significantly different in pairwise comparisons

Fig. 3 Soil pH value (a), electricity conductivity (b), soil organic matter (c), and soil moisture (d) along the gradient from the annual patches to the perennial patches. Values are means \pm S.E. Different lowercase letters indicate significant difference among neighboring sampling points ($P < 0.05$). The points sharing the same letter are not significantly different in pairwise comparisons

Fig. 4 Two-dimensional ordinations using Nonmetric Multidimensional Scaling (NMDS) and Canonical Correspondence Analysis (CCA).

a. NMDS ordination of vegetation functional groups distribution associated with distance from boundaries, based on Bray-Curtis dissimilarity distance. The red contours show the smooth response surface of the distance gradients. The triangles represent the functional groups. The effect and direction of three soil parameters are superimposed by arrows. The low stress values imply the minimal loss of information for the reduction of the data into two dimensions.

b. CCA ordination of vegetation functional groups with four environmental variables. Red biplot vectors represent the functional groups. Black ones represent the major explanatory environmental variables. SOM: soil organic matter; EC: electricity conductivity.

EC, electrical conductivity; SOM, soil organic matter

Fig. 5 Euclidean distance coefficient of the floristic richness and soil attributes in transition zone from annual to perennial patches. The peak of the curve corresponds to the greatest change along the transect, i.e. the statistically-identified boundary for a given metric

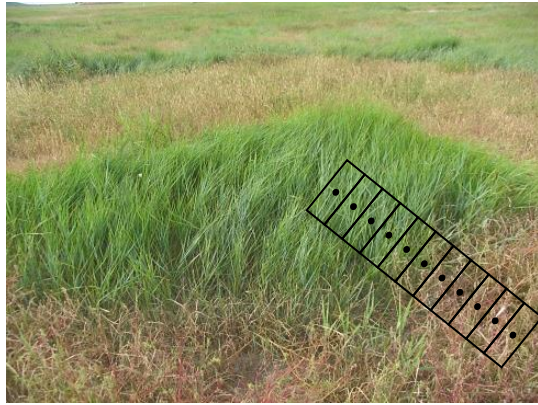
Fig. 6 Conceptual framework of the boundary dynamics between annual patches and perennial patches

Fig. 1



- Plants sampling quadrat
- Soil sampling location

a



b

Fig. 2

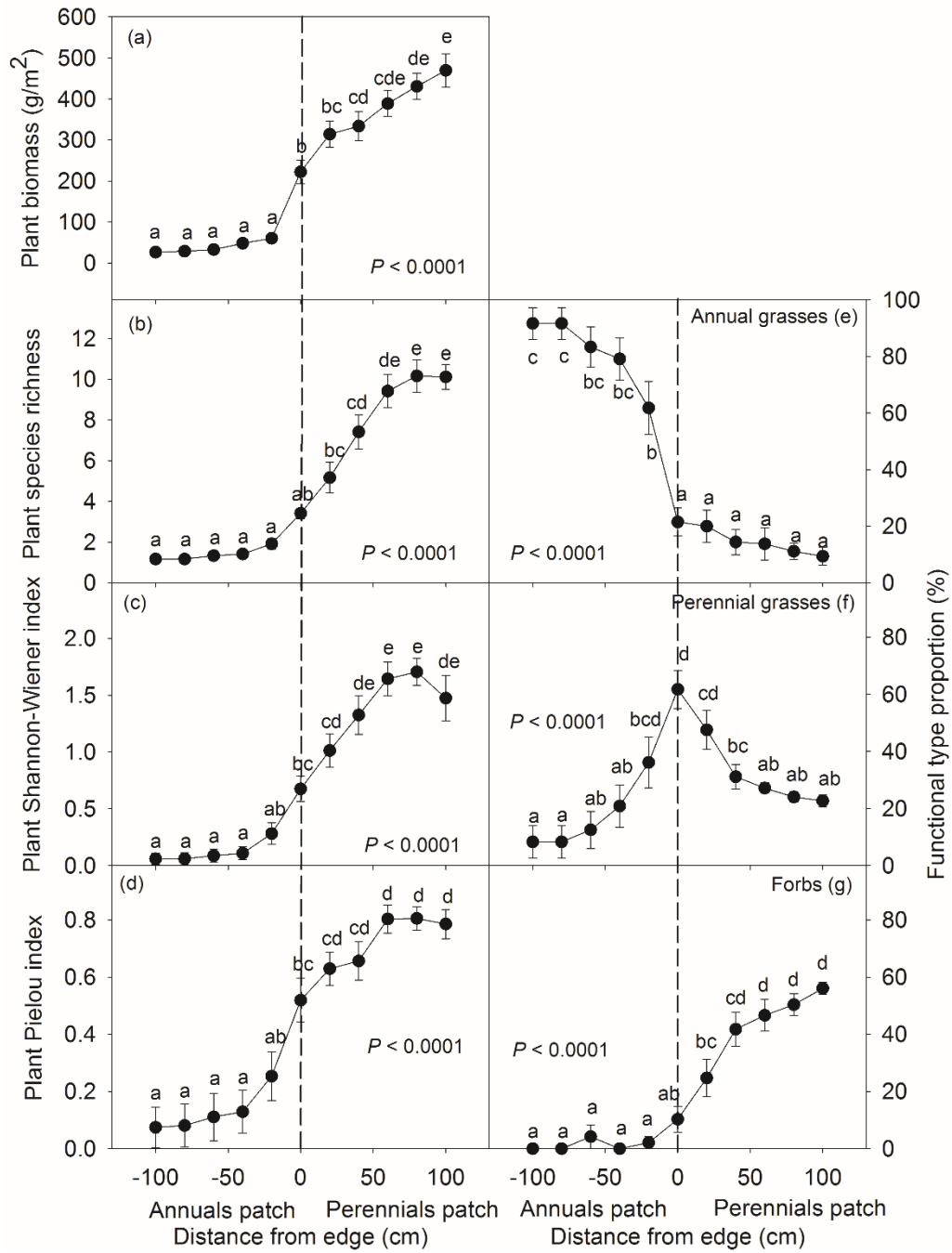


Fig. 3

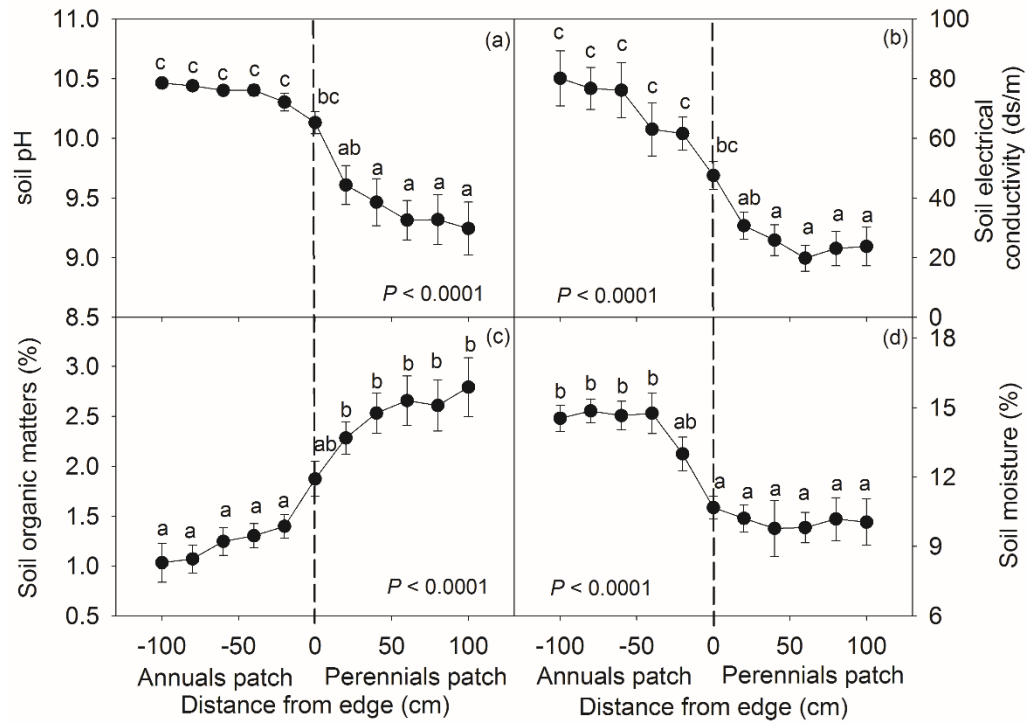


Fig. 4

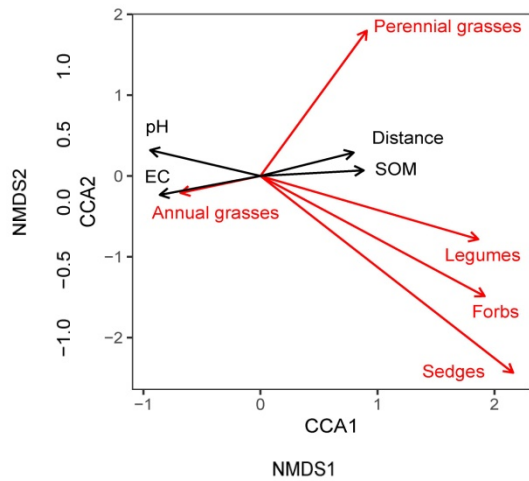


Fig. 5

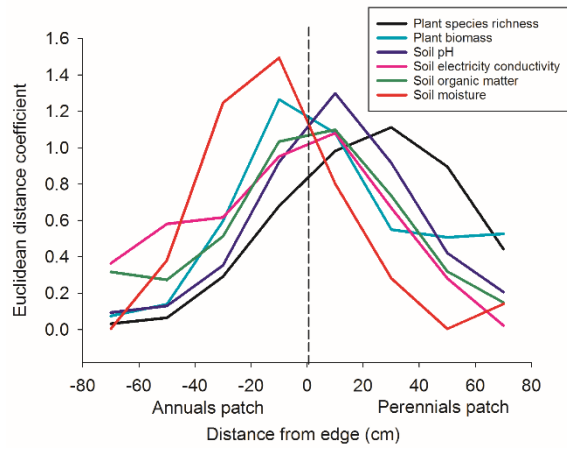


Fig. 6

