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RESEARCH ARTICLE

Climate and native grassland vegetation as drivers of the community structures of shrub-encroached grasslands in Inner Mongolia, China

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Abstract Shrub encroachment in grasslands will lead to a mosaic landscape with shrub patches interspaced with grass patches and thus alters local and regional water and heat balance. Syntheses on effects of the climate and native grassland community on the shrub-encroached grassland (SEG) are very limited at a large scale. In this study we examined the variation of their community characteristics in the Inner Mongolian grasslands, using 192 SEG plots data from field survey during 2012–2013. Our results indicated that shrub cover and patch size exhibit a significant increase with longitude, but showed a hump-shaped latitudinal pattern. Shrub patch density and herb abundance were negative associated with latitude and longitude, whereas plant height showed an opposite trend. Such geographical patterns were likely co-determined by climate and native vegetation. Precipitation was the major controller for shrub cover and patch size, and temperature was the primary factor influencing shrub height and patch density. Consequently, shrub cover and patch size were greater at dry and warm habitats than at moist and cool sites. In addtion, native vegetation also significantly influenced the variations in that of shrub patches. Diverse habitats with tall vegetation were likely more resistant to shrub encroachment. Furthermore, although we did not fully evaluate the effects of soils on SEGs, the discussion on the soil-SEG relationship suggests an important role of soils in characterizing SEG structures. Our study provides the first regional assessment on the variations of SEG structures, and has an implication in the regional shrub expansion management and control.

Keywords Arid and semi-arid area · Climate · Community structure · Geographic pattern · Grassland · Shrub encroachment · Shrubby grassland · Shrubland

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Introduction

Shrub encroachment into grassland and the thickening of woody plant cover in savannas are widely reported in arid and semi-arid areas (Van Auken 2000; Jackson et al. 2002; Knapp et al. 2008; Maestre et al. 2009). In the United States about 330 million ha of non-woodland area are estimated to be undergoing shrub encroachment in the xeric western states (Houghton et al. 1999; Knapp et al. 2008). In South Africa almost 13 million ha of savanna have been subject to thorn bush encroachment (Eldridge et al. 2011). Similar phenomena have also been reported in Australian and in Eurasian steppe ecosystems (Rivest et al. 2011; Gomez-Rey et al. 2013). In China, more than 5.1 million ha of grassland have been encroached by *Caragana microphylla* in the Inner Mongolian grasslands (Zhang et al. 2006; Peng et al. 2013). Shrub encroachment into native grasslands worldwide will alter species interaction, which in turn may promote a loss of biodiversity and influence various aspects of ecosystem functioning. Thus, shrub encroachment is believed to affect more than two billion people across the world (Throop and Archer 2008; Eldridge et al. 2011; Gomez-Rey et al. 2013).

Shrub encroachment usually leads to a mosaic landscape with shrub patches interspaced with grass patches (Fig. 1), which is defined as shrub-encroached grassland (SEG) in this study. Although intensive studies have been conducted on the impacts of shrub encroachment on ecosystem structure and functioning (Eldridge et al. 2011), few studies have treated SEG as a whole to explore its community characteristics in relation with climate and native vegetation at a large scale. Shrub patches and grass patches in the interspaces have significant differences in community structure and nutrient cycling, making SEG clearly differ from the pure grassland or shrub land (Meyer et al. 2009; D'Odorico et al. 2012). Exploring the spatial patterns of community characteristics of SEG across space will help understand the encroachment process that regulate SEG structure and their interplay with environmental drivers.

Climate is the major factor influencing the large-scale patterns of community structure and ecological attributes in grassland and savanna ecosystems (Bai et al. 2008). For example, in temperate grasslands, the richness and productivity of community will be significantly influenced by precipitation (Vicca et al. 2007; Bai et al. 2008; Ma et al. 2010; Xia et al. 2010). Likewise, variation in rainfall is also the most important driver of both herbaceous and woody layer dynamics in savanna, i.e., woody density, height of canopy, density of regenerative stems, and woody area significantly increased along rainfall gradient in Australia and South Africa savanna system (Williams et al. 1996; Shackleton and Scholes 2011). However, the role of climate in shaping SEG community structure remains unknown.

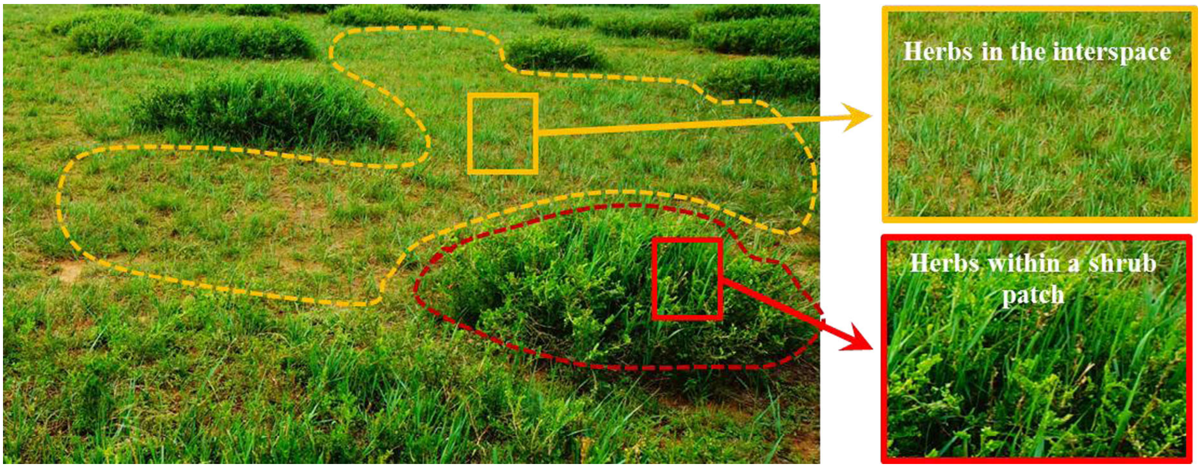

Fig. 1 Schematic diagram of shrub patches interspaced with grass patches in shrub-encroached grasslands (SEGs). The *red dotted line area* indicates a shrub patch and *orange dotted line area* indicates an interspaced grass patch. We define "native grassland vegetation" as the herbs in the interspace

In addition to climate, the shrub expansion in grassland is largely dependent on the interaction between shrub patches and native vegetation. Therefore, native vegetation may also influence the community characteristics of shrub patches in SEG (Arenas et al. 2006). In this study, we define "native grassland community" and "native vegetation" as the grass patch in the interspace. Previous studies demonstrated that the native grassland with higher species richness and functional diversity has high resistance to the invasion of exotic species (Wardle et al. 2008; Altieri et al. 2010; Reisner et al. 2013). But how characteristics of native vegetation affect the encroachment of indigenous shrubs remains largely unknown.

Therefore, this study was designed to explore the community characteristics of SEG in relation to climatic factors and native vegetation based on a data set of 192 plots sampled at 48 sites across the Inner Mongolian grasslands. We specifically examined the following questions: (1) what are the general community characteristics of SEG and what are the differences between various SEG types? (2) what is the geographical patterns of SEG communities? (3) how does shrub encroachment change along with both climatic gradients and native vegetation characteristics? and (4) how do plant species richness and the composition of herbs within shrub patches change along with both climatic factors and shrub patch characteristics?

Materials and methods

Study area

The study was conducted in the grasslands of Inner-Mongolia, China, a central part of the Eurasian steppe (Bai et al. 2008). An east–west transect of shrub-encroached grasslands (SEGs) was established including 48 sites along a precipitation gradient, which runs from 38.67 to 44.91°N in latitude and 108.28 to 119.02°E in longitude (Fig. 2). The mean annual temperature (MAT) of the study area ranges from 2.1 to 8.6 °C and mean annual precipitation (MAP) is between 157 and 362 mm (Table S1 in supplementary materials). Soil types include dark chestnut, typical chestnut, calcic brown and light brown soils. The vegetation was dominated by *Leymus chinensis, Stipa krylovii*, and *Stipa klemenzii*, corresponding to the different community types (Bai et al. 2012) (Table S1). All study sites were selected far from villages to avoid anthropogenic disturbances and grazing impacts.

Field investigation

We conducted field surveys at 48 sites during the growing season (early July to early September) in 2012 and 2013. To avoid biases from community heterogeneity, we set up four plots at each site. Both shrub and grass patches were sampled by a systematic sampling design. The 20 × 20 m shrub plots (400 m^2 in total) were divided into four 10 × 10 m subplots. The shrub patch was surveyed in two diagonal subplots. We established two 1 × 1 m quadrats within a shrub patch and in the interspace in one of the four subplots, respectively, to investigate the number of herb species. To avoid the influence of shrubs, the quadrat used for measuring interspace plant populations was at least 2 m away from the nearest shrub. Also, we divided the 1 m^2 quadrat into four 0.25 m^2 small quadrats and investigated the characters of herb community in one of the 0.25 m^2 small quadrats.

We pursued the plot investigation as below. First, we recorded the geographical coordinates and elevation of each plot. Second, for the shrub patch, we recorded the shrub names, shrub cover and the number of stems of each shrub patch and measured the crown diameters and height of all shrub patches in two of the four sub plot. Because most of the shrubs sent forth many branches from the roots instead of an apparent main stem, we did not measured the basal diameter of shrubs. Third, for the herb layer, we recorded the species names in two 1 m^2 herb quadrats. We also measured the mean cover, height, and density of each vascular species appearing in the 0.25 m^2 small quadrats.

Climatic variables

Mean monthly air temperature (MMT, °C) and mean monthly precipitation (MMP, mm) of our plots from 1982 to 2010 were obtained from the National Meteorological Information Center of the China Meteorological Administration (http://www.nmic.gov.cn). Using MMT and MMP, we estimated MAT (°C), MAP (mm) and annual potential evapotranspiration (PE, mm). PE was calculated using the method of Thornthwaite and Hare (1995). Using MAP and PE,

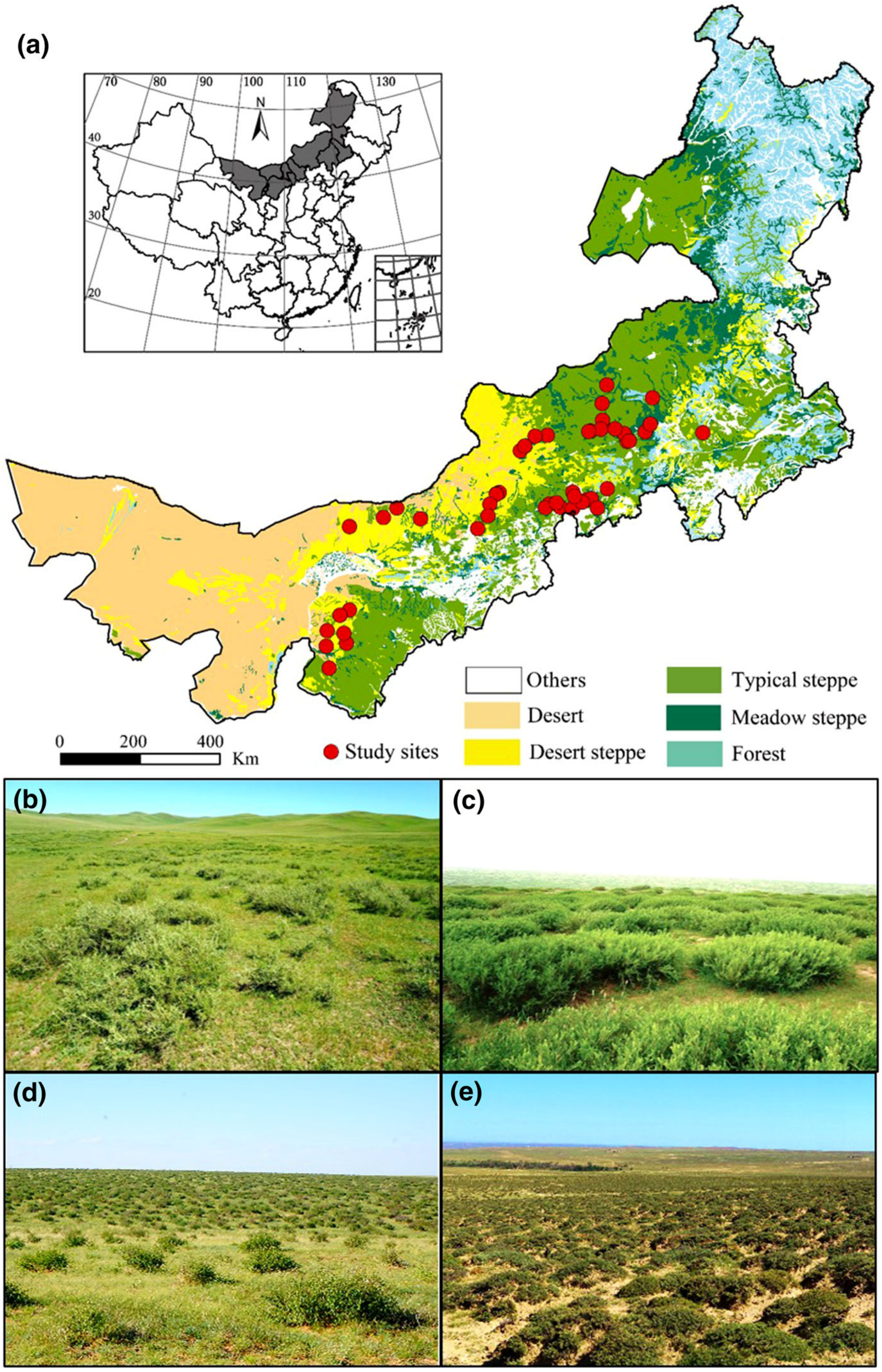

Fig. 2 Study sites and typical landscapes of SEG in Inner-Mongolia. **a** Location of study sites, **b** *Caragana microphylla* in meadow steppe, **c** *C. microphylla* community in typical steppe, **d** *Amygdalus pedunculata* community in desert steppe, and **e** *C. tibetica* community in desert steppe

we calculated the aridity index (AI) of each plot using Eq. (1) (Zheng et al. 2010):

$$\text{Aridity index (AI)} = \text{PE/MAP} \quad (1)$$

The AI of the plots ranged from 1.5 to 3.8, indicating all of our plots were located in semi-arid areas (Zheng et al. 2010). To compare the community structural characteristics between different SEG types, we classified 192 plots into three types based on the aridity index (AI) of the plots as shown in Eq. (2):

$$\begin{cases} \text{Type} = \text{I} & \text{if AI} \leq 1.8 \\ \text{Type} = \text{II} & \text{if } 1.8 < \text{AI} < 2.8 \\ \text{Type} = \text{III} & \text{if AI} \geq 2.8 \end{cases} \quad (2)$$

Data analysis

Statistical analyses were performed using SPSS Statistics 20 (IBM SPSS, Chicago, IL, USA). We used an ANOVA to compare the different structural characteristics among three types of SEGs. The structural characteristics are defined as biological and ecological attributes that can influence the community structure, including shrub cover, shrub patch size, and vascular plant richness, shrub height, shrub patch density, shrub richness, and herb height, richness and abundance within a shrub patch and in the interspace. Shrub patch size was calculated as follows: shrub patch size = π/4 × long crown diameter × short crown diameter.

To evaluate the relationships between geographical/climatic factors (latitude, longitude, MAT, MAP) and community structures across 192 plots, we conducted an ordinary least square (OLS) regression. The model R^2 was used to compare the explanatory power of different geographic and climatic variables. Then we used a forward stepwise regression method to explore the effects of both climatic factor and native vegetation characteristics on shrub patch structure. The percentage of sum squares (SS %) of each variable in this model indicated the explanatory power of this variable. The model included MAT, MAP, height, richness, abundance of herbs in the interspace as independent variables, and shrub cover, shrub size, height and shrub patch density as dependent variables. The same method was also used to examine the effects of both climatic factors and shrub patch community characteristics on herb community characteristics. In this model, climatic variables (MAT and MAP), plot-level shrub characteristic variables (shrub cover, shrub patch size, shrub height) and individual shrub variables (cover, patch size and height of the individual shrubs in which herb quadrat was set) were used as independent variables, and plot-level height, richness, abundance of herb within shrub patches were used as dependent variables.

Results

Species composition of the shrub-encroached grasslands

Six shrubs were encroached into grasslands in the study area (Table 1). Five of them (*Caragana microphylla*, *C. stenophylla*, *C. intermedia*, *C. tibetica*, and *C. pygmaea*) belong to the family, Leguminosae, and one (*Amygdalus pedunculata*) belongs to the family, Rosaceae (Table 1). *C. microphylla* had the highest frequency (70.83 %) and cover (12.97 %) across our study sites. Although *C. stenophylla* and *C. pygmaea* had relative high frequencies (33.85 and 16.15 %), their mean covers were only 3.56 and 0.51 %, respectively. In contrast, *C. tibetica* and *A. pedunculata* had relative low frequencies (12.50 and 6.25 %) but high coverages (11.28 and 8.01 %, respectively).

In addition, 123 herb species were recorded in shrub-encroached grasslands (SEGs) habitats (Table 1, see Table S2 for the full list of species in supplementary materials). *Cleistogenes squarrosa, Agropyron michnoi, Carex korshinskyi, Leymus chinensis* and *Stipa krylovii* were the most frequently found perennial herbs in all the plots and *L. chinensis, Carex korshinskyi, Potentilla tanacetifolia, Enneapogon borealis,* and *Agropyron michnoi* are the most abundant perennial herbs in the SEG community.

Overall structural characteristics

Overall, the shrub cover in SEG sat the plot level was about 12.8 %, with a range (defined as the 2.5 and 97.5 % quantiles) of 0.9–39.1 % (Table 2). About 82.3 % of the plots had less than 20 % shrub cover (Fig. 3a). The shrub patch size at the plot level was about 1.22 m^2 with a range of 0.11–4.23 m^2 (Table 2). Across all shrub patches, shrubs patch size was less than 1.25 m^2 for 83.1 % of shrub patches (4,706 individuals), and 9.4 % (about 531 individuals) was between 1.25 and 2.5 m^2 (Fig. 3b). Total vascular plant species of the SEG were 8–23 species/100 m^2. Across all plots, the height, patch density and richness of shrubs were about 28.3 cm, 6,468 clump/ha, and 1.5 species/100 m^2, with ranges of 8.0–51.8 cm, 250–38,574 clump/ha and 1.0–3.0 species/100 m^2, respectively. We estimated the community characteristics of herbs within shrub patches and in the interspaces separately. Overall, the height, richness and abundance of herbs within shrub patches were 18 cm, 7 species/m^2 and 328 individuals/m^2, and were 10.1 cm, 11 species/m^2 and 467 individual/m^2 in the interspace, respectively (Table 2).

Structural characteristics by SEG type

Generally, type I SEG is composed of meadow steppe and part of the typical steppe located in relatively

Table 1 A list of shrub species and major herb species (frequency >10 %) in all 192 plots

Species	Frequency (%)	Type of SEG	Cover or abundance
Caragana microphylla	70.83	I, II, III	12.97
Caragana stenophylla	33.85	II, III	3.56
Caragana pygmaea	16.15	II, III	0.51
Caragana tibetica	12.50	II, III	11.28
Caragana intermedia	11.46	II, III	3.61
Amygdalus pedunculata	6.25	III	8.01
Carex korshinskyi	54.07	I, II, III	93
Leymus chinensis	51.74	I, II, III	135
Stipa krylovii	50.58	I, II, III	15
Allium tenuissimum	47.09	I, II, III	13
Artemisia frigida	46.51	I, II, III	8
Salsola collina	45.93	I, II, III	27
Setaria viridis	43.02	I, II, III	92
Artemisia annua	40.70	I, II, III	51
Eragrostis minor	40.12	I, II, III	79
Convolvulus ammannii	37.21	I, II, III	37
Allium mongolicum	36.05	I, II, III	10
Euphorbia humifusa	36.05	I, II, III	45
Astragalus galactites	33.72	I, II, III	4
Melilotoides ruthenica	30.81	I, II	4
Corispermum chinganicum	29.65	I, II, III	14
Stipa klemenzii	29.65	II, III	20
Chenopodium aristatum	28.49	I, II, III	40
Cleistogenes songorica	27.91	II, III	12
Enneapogon desvauxii	24.42	I, II, III	56
Heteropappus altaicus	23.26	I, II, III	8
Allium bidentatum	23.26	I, II, III	23
Neopallasia pectinata	20.35	I, II	81
Chenopodium glaucum	17.44	I, II, III	14
Allium ramosum	16.28	I, II	16
Asparagus dauricus	16.28	I, II, III	6
Stipa breviflora	15.70	I, II, III	6
Tribulus terrestris	15.70	I, II, III	14
Iris tenuifolia	14.53	I, II, III	4
Potentilla bifurca	12.79	I, II	53
Kochia prostrata	12.79	I, II	18
Lappula myosotis	11.05	I, II	4
Bassia dasyphylla	10.47	I, II	23
Lespedeza davurica	10.47	I, II, III	4

Frequency (%) is defined as the number of times for a plant species occurring in 192 plots. Mean cover and mean abundance of each species in all the plots where they appeared are listed for shrubs and herbs, respectively

Table 2 Overall structural characteristics of shrub-encroached grasslands in Inner-Mongolia

Variable	No. of plots[a]	Mean	Range	SD
Overall				
Shrub cover (%)	192	12.8	0.9–39.1	10.3
Shrub patch size (m^2)	192	1.22	0.11–4.23	1.15
Vascular plant richness (/100 m^2)	192	15	8–23	4
Shrubs				
Mean height (cm)	192	28.3	8.0–51.8	12.4
Patch density (individual/ha)	192	6,468	250–38,574	11,580
Shrub richness (/100 m^2)	192	1.5	1.0–3.0	0.8
Herbs				
Herb height within shrub patch (cm)	172	18.0	4.9–43.3	9.0
Herb height in the interspace (cm)	172	10.1	3.4–22.7	4.6
Herb richness within shrub patch (/m^2)	172	7	2–15	3
Herb richness in the interspace (/m^2)	172	11	6–18	3
Herb abundance within shrub patch (/m^2)	172	328	20–1,243	78
Herb abundance in the interspace (/m^2)	172	467	81–1,392	94

[a] No herbs can be found within shrub patch in some plots. For herbs analyses, we only include 172 plots with herbs both within shrub patch and in the interspace

humid areas. Type II SEG is mainly composed of part of the typical steppe located in relatively arid areas and in the transition zone from typical steppe to desert steppe, and type III is composed by desert steppe.

In general, shrub cover and shrub patch size varied among three SEG types: the highest occurred in type I (17.2 % and 1.88 m^2), followed by type II (12.6 % and 1.27 m^2), and type III (8.8 % and 0.55 m^2) (Table 3). Both shrub and herb height followed the same pattern as these two variables: the highest was in type I (35.6 ± 10.9 cm for shrub; 14.5 ± 4.7 cm for herbs), followed by type II (27.7 ± 11.3 cm for shrub; 12.6 ± 5.1 cm for herbs), and type III (22.1 ± 11.2 cm for shrub; 10.6 ± 3.9 cm for herbs) ($P < 0.001$) (Table 3, Fig. 4).

In contrast, shrub patch density varied in an opposite trend by more than an order of magnitude across vegetation types: 1,169 ± 790 clump/ha for type I, 5,791 clump/ha for type II and 12,154 ± 15,954 clump/ha for type III ($P < 0.001$).

Species richness varied among SEG types and growth forms. Shrub richness was highest in type III (2 ± 1 species/100 m^2), and lowest in type I (1 ± 0.2 species/100 m^2). In contrast, herb richness was highest in type I (16 ± 4 species/m^2), and lowest in type III (11 ± 3 species/m^2). Herb abundance followed the pattern of richness (Fig. 4).

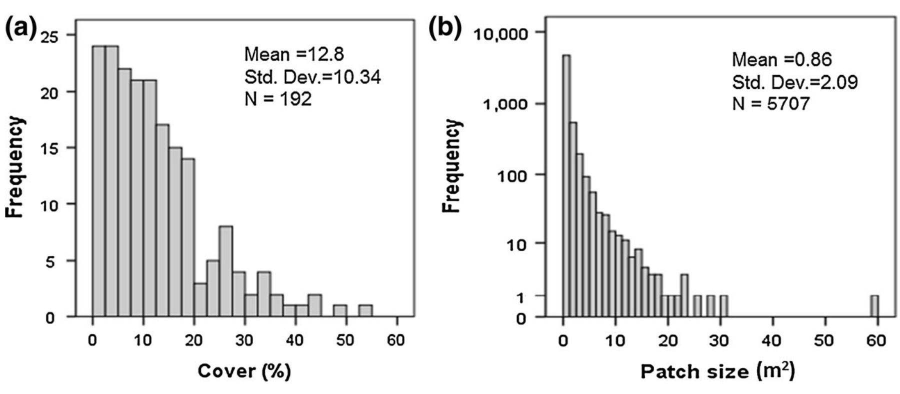

Fig. 3 Frequency distribution of **a** shrub cover (%) at the plot level and **b** individual shrub patch size (m^2)

Table 3 Structural characteristics of different shrub-encroached grasslands (SEGs) in Inner-Mongolia

Community structure	No. of plots	Mean	Range	SD
Overall				
Shrub cover (%)				
Type I	60	17.2	2.6–46.6	11.9
Type II	68	12.6	0.5–37.5	10.9
Type III	64	8.8	1.8–19.8	5.4
Shrub patch size (m^2)				
Type I	60	1.88	0.38–4.72	1.23
Type II	68	1.27	0.07–4.26	1.18
Type III	64	0.55	0.11–1.50	0.47
Vascular plant richness (/100 m^2)				
Type I	60	17	9–23	4
Type II	68	15	8–24	4
Type III	64	12	7–19	3
Shrubs				
Height (cm)				
Type I	60	35.6	18.9–56.9	10.9
Type II	68	27.7	7.9–48.0	11.3
Type III	64	22.1	7.8–43.0	11.2
Patch density (clump/ha)				
Type I	60	1,169	250–2,852	790
Type II	68	5,791	183–34,965	9,267
Type III	64	12,154	1,022–47,134	15,954
Shrub richness (/100 m^2)				
Type I	60	1.0	1–2	0.2
Type II	68	1.4	1–3	0.6
Type III	64	2.1	1–4	1.0

Geographical and climatic patterns of community characteristics

Geographically, shrub cover did not show a significant longitudinal trend, but showed a hump-shaped relationship with latitude (Fig. 5). A similar hump-shaped relationship was also found between shrub patch size and latitude. Patch size increased significantly with increasing longitude. Shrub height significantly increased with both increasing latitude and longitude ($P < 0.001$, Fig. 5). Geographical trends in the shrub patch density showed opposite patterns. Shrub patch density generally decreased with increasing altitude and longitude. For herbs within shrub patches, herb height significantly increased with increasing latitude and longitude (Fig. 6). Longitudinal trends in herb richness and abundance showed different patterns. Both herb richness and abundance showed hump-shaped longitudinal pattern ($R^2 = 0.07$, $P = 0.009$ and $R^2 = 0.30$, $P < 0.001$, respectively) (Fig. 6).

As expected, variations of community structure along with temperature and precipitation were similar to geographical patterns. Shrub cover and patch size increased with increasing MAP. Shrub patch size decreased with increasing MAT. Shrub height decreased with increasing MAT but increased with increasing MAP (Fig. 5). In contrast, shrub patch density increased with increasing MAT but decreased with increasing MAP. For herbs, height and abundance of herbs within a shrub patch decreased with increasing MAT but increased with increasing MAP. The richness of herbs within a shrub patch also

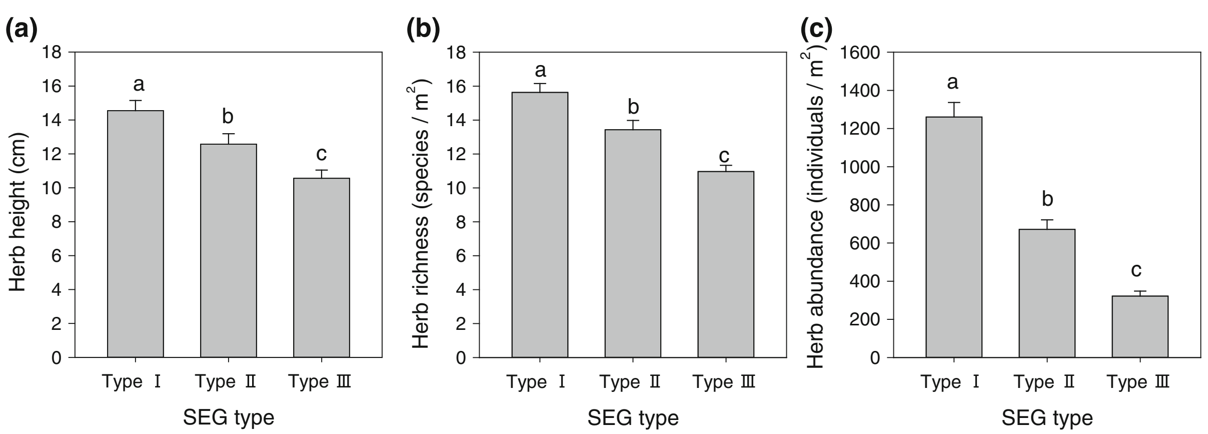

Fig. 4 Structural characteristics of grass patches in different SEG types. **a** height, **b** richness, and **c** abundance. *Different letters* indicate significant differences according to post hoc multiple comparisons of means in ANOVA

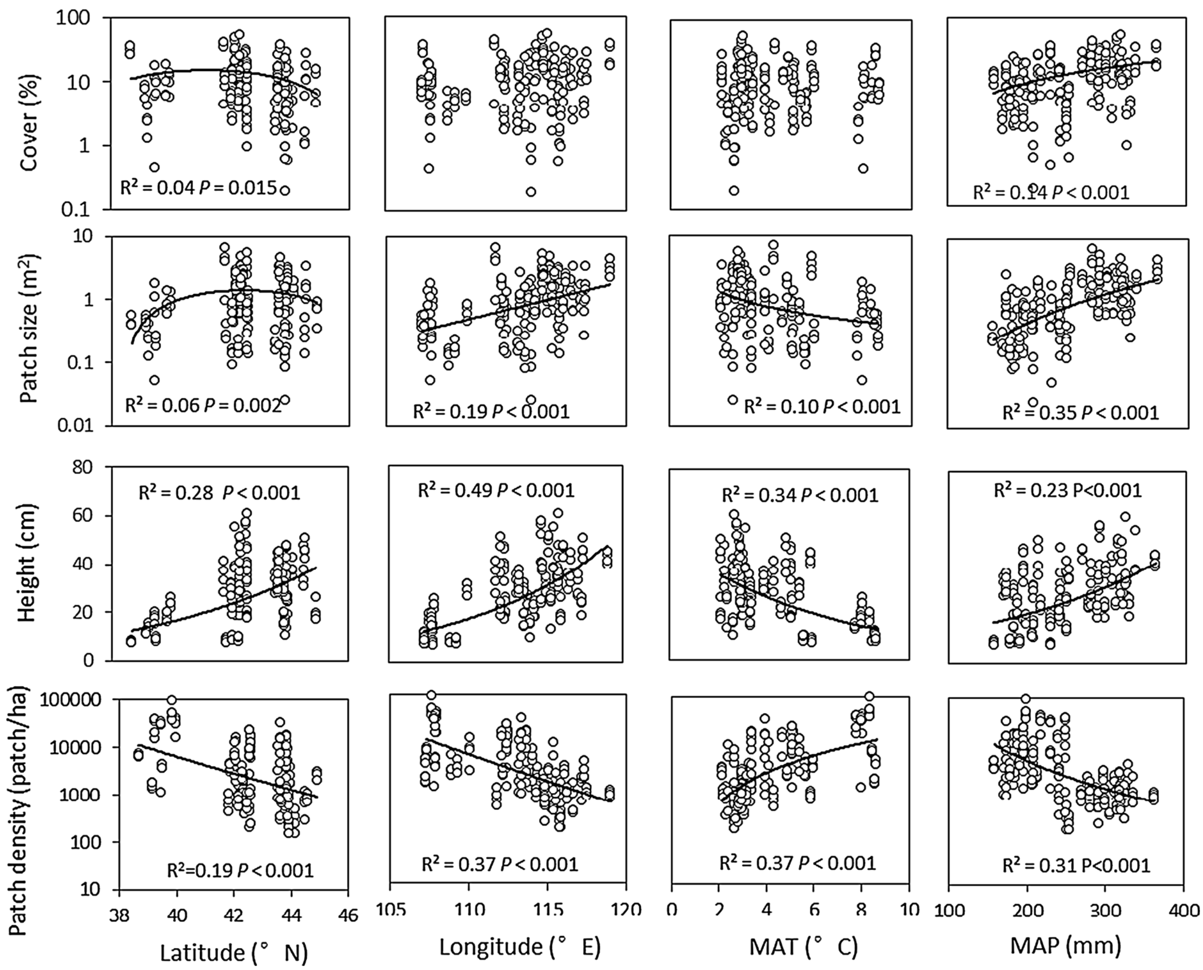

Fig. 5 Changes in structural measurements of shrub patches with latitude, longitude, mean annual temperature (MAT) and precipitation (MAP). The structural measurements include shrub cover, patch size, shrub height, and patch density

showed a positive relationship with MAP, but did not have a significant correlation with MAT (Fig. 6).

Combined effects of climate and native vegetation on shrub structures

Climatic variables could explain 12.4 % of the total variance in shrub cover, 23.5 % in patch size, 36.7 % in shrub height, and 30.9 % in shrub patch density (Table 4). Precipitation was the major factor influencing shrub cover and patch size, and temperature was the primary factor for determining shrub mean height and shrub patch density. In addition, native grassland community characteristics significantly influenced variations in shrub structure. In comparing the models with only climatic variables as independent variables, adding native grassland structure variables could improve the explanatory power for shrub cover, shrub height and shrub patch density (12.4 % vs. 16.4 % for cover, 29.5 % vs. 36.7 % for height and 31.1 % vs. 33.5 % for density). None of the native vegetation characteristics had significant effects on shrub patch size. According to the stepwise regression, there were negative correlations between herb height and shrub cover, herb richness and shrub height, herb abundance and shrub patch density.

Impacts of climate and shrub characteristics on herb within shrub patches

We conducted the stepwise regression to analyze the effects of climatic factors and shrub characteristics on

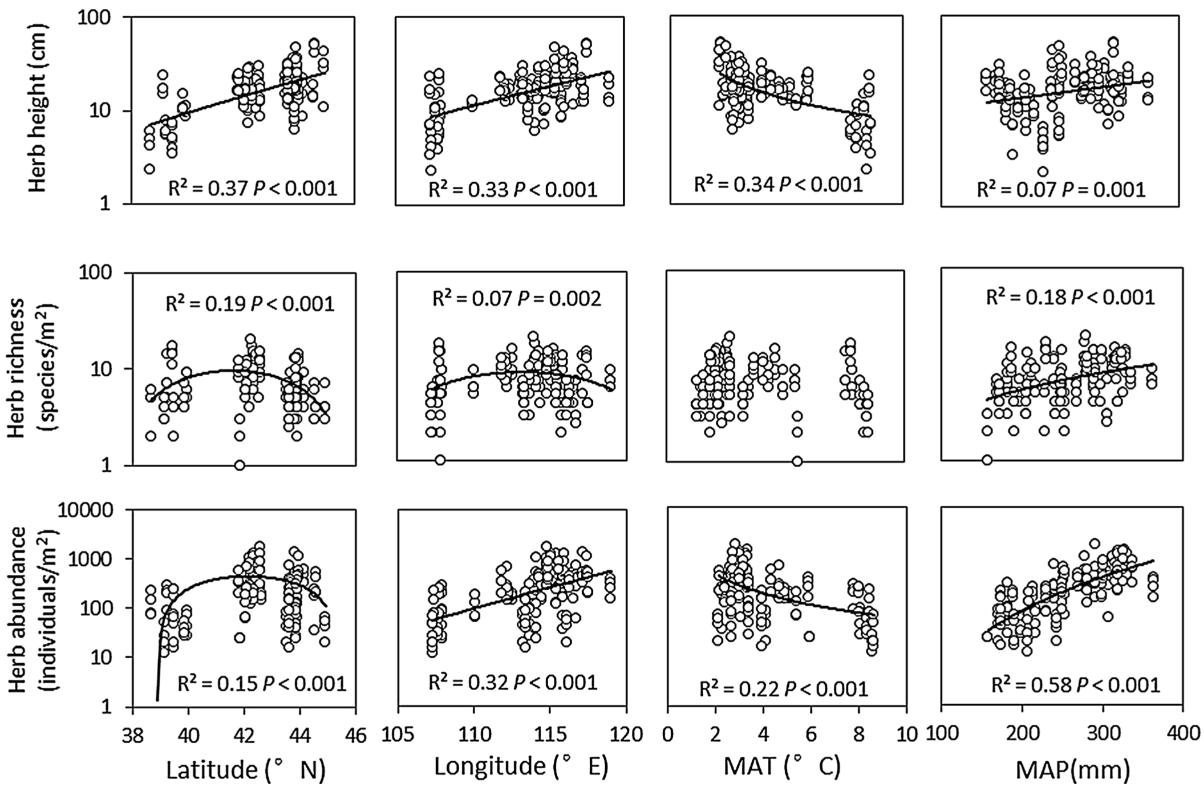

Fig. 6 Changes in structural measurements of herb within shrub patch with latitude, longitude, mean annual temperature (MAT) and precipitation (MAP). The structural measurements of herbs include mean height, richness, and abundance

community structures of herbs within shrub patches. The results indicated that climatic variables could explain 4.4 % of total variance in herb height, 26.6 % in herb richness, and 47.0 % in herb abundance, whereas individual shrub height could account for 24.2 % of total variance in herb height and 3.9 % in herb richness (Table 5). MAP was confirmed to be the major factor influencing herb richness and abundance within shrub patches. However, other than climatic variables, individual shrub height was the primary factor influencing herb height within shrub patches.

Discussion

Examining the patterns of community structures and how climate and the native grassland community shape the patterns would improve our understanding of plant ecological strategies (Cleland et al. 2004; Moles et al. 2009). Our study provided the first regional quantification of the impact of climate and native grassland community on shrub-encroached grasslands. In synthesizing both climatic and native vegetation community effects, we propose a conceptual framework of shrub encroachment patterns in different scenarios (Fig. 7). Compared those at the dry and warm sites, shrub cover and patch size were larger and patch density was lower at the moist and cool habitats. Also, diverse and tall native herb vegetation is likely more resistant to shrub encroachment than less diverse habitats and shorter herbs.

Consistent with previous studies, our results showed that climate is a major factor influencing the structural measurements of shrub-encroached grassland (SEG). For example, mean annual precipitation (hereafter referred to as "precipitation") is the primary factor determining the variation of shrub cover and patch size, two crucial characteristics for shrub-encroachment grassland. Positive relationship between shrub cover, patch size and precipitation is consistent with previous studies (Yao et al. 2006; Duniway et al. 2010; Throop et al. 2012; Li et al.

Table 4 Effects of climate and native grassland vegetation on structural characteristics of shrub patches

Variables	DF	Coefficient	SE	MS	*p*	SS %
Shrub cover						
Intercept	1	–0.71	3.73	3.48	0.849	
MAP	1	0.07	0.01	2,747.07	<0.001	12.4
Herb height	1	–0.47	0.16	794.48	0.004	4.1
Residuals	169			95.29		83.5
Patch size						
Intercept	1	–1.323	0.37	19.95	0.001	
MAP	1	0.01	0.001	70.14	<0.001	23.5
Residuals	170			1.06		76.5
Shrub height						
Intercept	1	26.52	4.85	2,601.80	<0.001	
MAT	1	–2.45	0.39	3,359.21	<0.001	29.5
MAP	1	0.08	0.01	2,449.84	<0.001	7.2
Herb richness	1	–0.72	0.23	852.45	0.002	3.4
Residuals	168			87.10		59.9
Patch density						
Intercept	1	–4,077.02	2,378.05	2.77×10^{8}	0.088	
MAT	1	3,024.33	400.83	5.63×10^{9}	<0.001	31.1
Herb abundance	1	–5.22	2.17	6.01×10^{8}	0.017	2.4
Residuals	165			9.75×10^{7}		66.8

Climatic indices include mean annual temperature (MAT) and mean annual precipitation (MAP), and the characteristics of native grassland vegetation include herb height, richness, and abundance. These climatic and herb variables are first applied to a stepwise regression to drop non-significant ones before they are included into the general linear models (GLMs). The degrees of freedom (DF), estimated regression coefficients (coefficient), standard error of regression coefficients (SE), mean square (MS), significant level (*p*) and percentage of sum squares explained (%SS) are reported for each variable

2013), suggesting water is the limiting factor for shrub expansion in arid and semi-arid areas. Additionally, the negative relationship between the shrub patch density and precipitation, but positive relationship with temperature contrasted with previous finding that woody density are significantly increased along rainfall gradient in savanna (Williams et al. 1996; Shackleton and Scholes 2011). This difference might arise because the precipitation gradient in our study sites are much narrower than those in savanna systems included a mesic locality with about 1,200–1,500 mm precipitation. The focused encroached woody species in our study sites are shrubs instead of trees in savanna ecosystem. In addition, such a pattern also resulted from the variation in species composition of shrubs along precipitation gradient. In type I SEG (with relative higher precipitation), *C. microphylla* is the only shrub species. Whereas *C. intermedia* and *C. tibetica* are the major shrubs in type III SEG (with relative lower precipitation). Compared to these two short shrubs, *C. microphylla* is larger and taller in size (Zhao 2005; Zhang et al. 2011). Consequently, compared those at dry and warm sites, shrub cover and patch size were larger and patch density was lower at moist and cool habitats.

In addition to climate, characteristics of the native grassland community provide additional crucial elements influencing the colonization and expansion of a plant species. For many species, expansion is variable in time and space as a result of the fine-scale interactions between invading plants and resident ecosystems (Godfree et al. 2004). In general, species-rich communities experience lower levels of exotic species invasion than species-poor communities (Tilman 1997; Ruijven et al. 2003; Belote et al. 2008; Vicente et al. 2010). For indigenous shrub encroachment, the native grassland community could control the shrub demography in a similar way because of the

Table 5 Effects of climate and shrub patches on herbs within shrub patches

Variables	DF	Coefficient	SE	MS	*p*	SS %
Herb height						
Intercept	1	16.51	3.41	1,543.73	<0.001	
Individual shrub height	1	0.21	0.05	958.77	<0.001	24.2
MAT	1	–1.22	0.45	486.17	0.007	4.4
Residuals	120			65.70		71.4
Herb richness						
Intercept	1	5.22	2.00	66.08	0.01	
MAP	1	0.03	0.01	236.71	<0.001	23.8
MAT	1	–0.56	0.18	97.46	0.002	2.8
Individual shrub height	1	–0.05	0.02	67.64	0.009	3.9
Residuals	124			9.65		69.5
Herb abundance						
Intercept	1	–402.55	149.33	7.78×10^5	0.008	
MAP	1	3.43	0.44	4.93×10^6	< 0.001	44.7
MAT	1	–30.19	12.95	3.24×10^5	0.021	2.3
Residuals	125			6.50×10^4		53.0

Climatic indices include mean annual temperature (MAT) and mean annual precipitation (MAP), plot-level shrub characteristic variables are shrub cover, patch size, and height, and individual shrub variables are cover, patch size and height of the individual shrub in which the herb quadrat was set. These climatic and shrub characteristics are first applied to a stepwise regression to drop non-significant ones before they are included into the general linear models (GLMs). The degrees of freedom (DF), estimated regression coefficients (coefficient), standard error of regression coefficients (SE), mean square (MS), significant level (*p*) and percentage of sum squares explained (%SS) are reported for each variable

overlap in the resource needs of grasses when compared to juvenile shrubs (i.e. water content in the upper soil layer) (Cipriotti et al. 2012). But surprisingly, very little work has been reported on the relationship between native vegetation condition and shrub encroachment (Peters et al. 2006; Cipriotti et al. 2012). In our study sites, the structures of interspaced grass patch including richness, abundance and herb height had no significant difference from those in the control grassland where there is no woody vegetation (richness: 11 ± 4 species/m^2 in control grassland vs. 11 ± 3 species/m^2 in the interspaced grass patch; density: 470 ± 54 individual/m^2 in control grassland vs. 422 ± 48 individual/m^2 in the interspaced grass patch; height: 11.09 ± 0.80 cm in control grassland vs. 10.83 ± 0.56 cm in the interspaced grass patch). Consequently, we used the grass patch in the interspace to stand for native grassland community. Our General Linear Model (GLM) results indicated that herb height could explain 4.1 % of total variation in shrub cover, herb richness could explain 3.4 % of total variation in shrub height, and herb abundance explained about 2.4 % of total variation in shrub patch density. Our results suggested that diverse and robust native vegetation in some extent is more resistant to shrub encroachment than in other habitats. In the native grassland community, shrubs are bound to compete with herbs for limiting resources (i.e., water, nutrients, and light) to increase their cover and abundance. Native grassland communities with higher grass abundance and height will reduced the light and water available for juvenile shrubs, thereby hindering the long-term development of shrub encroachment in the grassland.

In addition, soils are considered as important aspects in affecting shrub encroachment (Davis et al. 2000; Davis and Pelsor 2001).Variation in soil moisture and nutrient availability contributes to the increase in shrub early establishment rate (Cipriotti et al. 2012). We used the soil dataset published in previous studies (Ma et al. 2010; Yang et al. 2010, 2014) to evaluate the effects of soils on community structures of different grassland types (Types I, II and III). The previous soil dataset contains 396 soil profiles

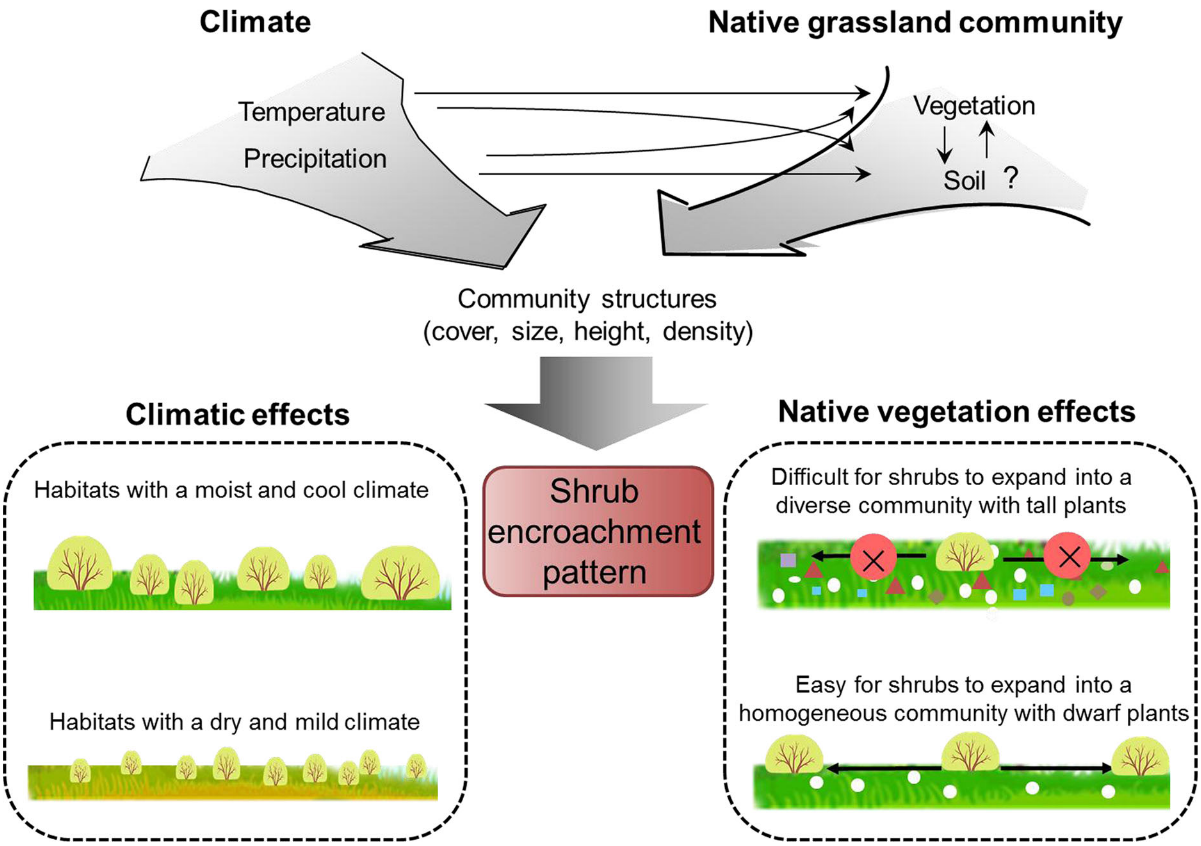

Fig. 7 A conceptual framework of combined effects of climate and native grassland community on shrub encroachment pattern. Compared with dry and warm climates, shrub cover and patch size were greater and patch density was lower at the moist and cool habitats. In addition, diverse and tall native grassland vegetation is likely more resistant to shrub encroachment than less diverse habitats and shorter herbs

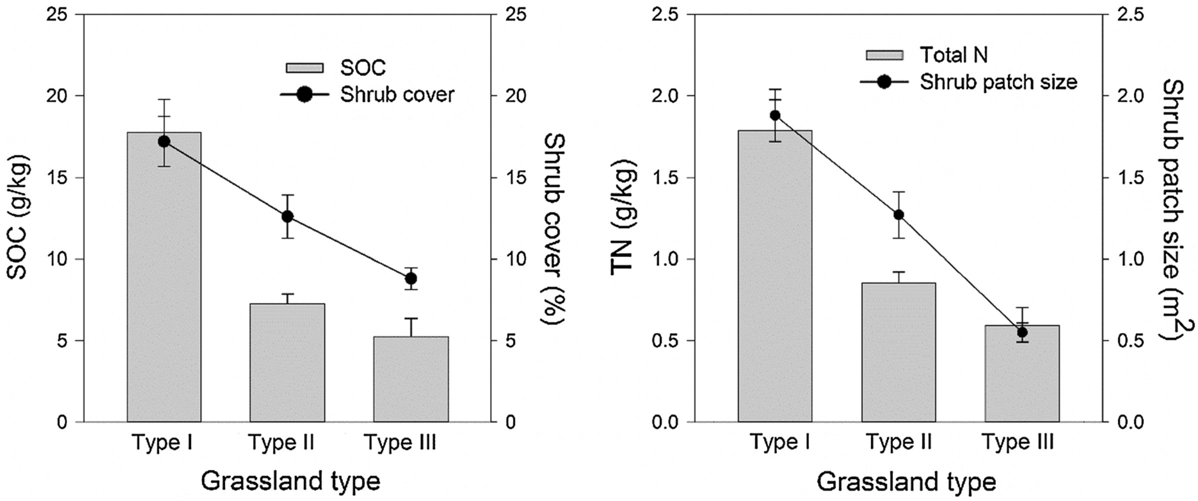

Fig. 8 A comparison of topsoil soil organic carbon (SOC), total nitrogen content (TN), shrub cover, and shrub patch size of three different grassland type

from 132 sites in the Inner Mongolian grasslands, of which 60 sites are near our study sites (Ma et al. 2010; Yang et al. 2010). Based on these 60 sites, we found that soil organic carbon (SOC) and total nitrogen (TN) in type I were significantly higher than those in types II and III (Fig. 8). The similar positive relationships between soil nutrient content and precipitation implied that shrub patch size and cover might have the positive relationships with soil nutrients (e.g. SOC, TN and TP). Further study should be conducted to directly explore the relationship between soil attributes (e.g., nutrients, water availability, and secondary metabolite content) and shrub community characters.

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