Divergent responses of above- and belowground ecosystem functioning to shrub encroachment in the Tibetan semi-arid alpine steppes

Jingxue Zhao[1], Awei Ji-Shi[1], Guangpeng Qu[2], and Gao-Lin Wu[3]

[1]Lanzhou University State Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems
[2]State Key Laboratory of Hulless Barley and Yak Germplasm Resources and Genetic Improvement
[3]Chinese Academy of Sciences and Ministry of Water Resources State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau

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Abstract

Semi-arid alpine ecosystems on the Tibetan Plateau are experiencing rapid climate change and extensive anthropogenic activity, concomitant with the encroachment of shrubs. Shrub encroachment leads to changes in both the structure and functioning of semi-arid alpine steppes. Yet, the encroaching impacts of shrubs on the above- and belowground ecosystem functioning of the semi-arid alpine steppes remains uncertain. To quantify shrub encroachment impacts on ecosystem functioning of the semi-arid alpine steppes, two shrub encroached alpine steppe sites are investigated, with one site encroached by a leguminous shrub (*Caragana spinifera*) and another site encroached by a non-leguminous shrub (*Dasiphora fruticosa*). Results showed that following both Leguminosae and Non-Leguminosae shrub encroachment, not only do these alpine steppes greatly increase the individual ecosystem functions but that this included significant enhancing of the ecosystem multifunctionality (EMF). We concluded that the main impacts of shrub encroachment were to facilitate belowground EMF (BEMF) rather than aboveground EMF (AEMF) in alpine steppes. Our findings also highlight that soil nutrients play critical roles in driving ecosystem functioning responses to shrubs encroachment. These findings further our understanding of shrub encroachment impacts on ecosystem functioning of the Tibetan semi-arid alpine steppes.

Introduction

Grassland is a central component of the terrestrial ecosystem, playing a prominent role in maintaining the world's ecological balance (Gravuer et al., 2019; Prommer et al., 2020). Grasslands across arid and semi-arid regions are currently undergoing widespread shrub encroachment, which were described as the rise in dominance and abundance of shrubby plants in grasslands (Stevens et al., 2017; Aguirre et al., 2021). These ecosystem transformations may be caused by combinations of climatic variation and anthropogenic processes, including large increases in precipitation, air temperature, nitrogen deposition, as well as grazing disturbances (Formica et al., 2014; Pistón et al. 2016). Shrub encroaching into grasslands often caused abrupt variations in biodiversity, vegetation productivity, hydrological properties, carbon dynamics, and soil nutrients (Liu et al., 2021; Broadbent et al., 2022). These changes are closely linked with alterations in not only the overall but also above- and belowground ecosystem functioning (Eldridge et al., 2011; Valencia et al., 2015).

Alpine ecosystem on the Tibetan Plateau has undergone rapid climate changes and intensity anthropogenic activities in recent decades (Kuang et al. 2016), which are also associated with substantial structural and functional variations of alpine ecosystems, particularly the prevalently ecological process known as shrub encroachment (Wu et al., 2021; Zhao et al., 2023). In general, compared with herbaceous species, shrub species with greater aboveground and root biomass can provide more organic matter input soils (Zhou et al. 2017; Cui et al., 2023) and enhance the accumulations of soil carbon and nitrogen (Li et al., 2019; Zhao et al., 2023). Shrub encroached into alpine grassland ecosystems can increase biodiversity, soil fertility, soil infiltration processes, ultimately attributing to strengthen ecosystem functioning (Butterfield et al., 2016; Cai et al., 2020). Nevertheless, neutral or even negative ecosystem individual and multiple functioning response to shrub encroachment also existed in alpine ecosystems (Zhang et al., 2022; Yang et al., 2023). Thus, the ecological impacts of shrub encroachment are expected to affect biodiversity and even lead to the shifts of ecological functioning in alpine ecosystems, which depend on a variety of factors, including shrub traits, edaphic condition, and local climate (Brandt et al., 2013; Collins et al., 2020).

In semi-arid alpine grasslands, increasing evidence suggesting that shrub encroachment can have the potential positive effects on the ecosystem functions, including plant diversity, soil hydrological, and soil fertility (Noumi et al., 2016; Wang et al., 2023). Nevertheless, the degree by which shrub encroachment caused variations in the ecosystem functioning could vary with the traits of encroaching shrubs (e.g., Leguminosae or Non-Leguminosae species). In semi-arid regions, Leguminosae shrubs can overcome drought stress and nutrients constraints to promote species richness, vegetation productivity, and carbon accumulation (Saixiyala et al., 2017; Ale et al., 2023). However, the encroachment of Leguminosae shrubs was differently associated with the ecosystem functioning than that of none-leguminous shrubs (Li et al., 2016; Zhao et al., 2023). Nevertheless, their wider positive impacts on belowground ecosystem functioning, and the underlying mechanisms and the changes magnitude of the ecosystem functioning of the semi-arid alpine steppes induced by shrub encroaching, remain poorly understood.

Much less attention has been given to recent widespread encroachments of shrubs in semi-arid alpine ecosystems, such as leguminous shrub (*Caragana spinifera*) and none-leguminous shrub (*Dasiphora fruticosa*). These encroaching shrubs was expected to provide favorable habitat for herbaceous plants due to increased shrubs abundance and sprawling canopy that provide increased ultraviolet radiation protection and buffering of extreme soil temperatures and drought stress, as well as an increase in soil nutrients availability (Cui et al., 2023; Zhao et al., 2023), which are associate with strengthening ecosystem functioning. These dwarf shrubs may be associated with different above- and belowground effects, including increased vegetation productivity and increased soil nutrient contents. We tested two hypotheses. First, we hypothesized that encroachment of both Leguminosae and non-Leguminosae shrubs had beneficial effects on the ecosystem functioning of the semi-arid alpine steppes, which was associated with increased vegetation productivity and higher soil nutrient availability. Second, we hypothesized that above- and belowground ecosystem functioning of the semi-arid alpine steppes responded differently to shrub encroachment, with the belowground ecosystem functions increased greatly than the aboveground ecosystem functions.

Here two shrub encroached alpine steppe sites of the central Tibetan Plateau were surveyed, with one site encroached by a leguminous shrub (*Caragana spinifera*) and the other site encroached by an none-leguminous shrub (*Dasiphora fruticosa*) . The changes in the individual and multiple ecological functions of the semi-arid alpine steppes following the encroachments of leguminous shrub and none-leguminous shrub were assessed. The aims of our study were to (1) quantify the impacts of encroached by leguminous shrub and none-leguminous shrubs on above- and belowground ecosystem functioning of semi-arid alpine steppes, and (2) identify the underlying mechanisms of encroaching shrubs induced variations in ecosystem functioning in the semi-arid alpine steppes.

Materials and methods

Site description

The study sites were located in the Damxung County, Xizang Autonomous Region, China (Fig. 1). The area has a continental semi-arid climate. The average annual temperature in the region is -0.8 and the annual precipitation is 403 mm (Ma et al., 2023). Alpine steppe is one of the major grassland types in this region, which were dominated by *C. parvula* and *S. capillacea* (Table S1). Other coexisting species included mainly *A. szechuanensis* , *A. wellbyi* , *M. sikkimensis* , *P. saundersiana* , and *P. nivea* . *C. spinifera* and *D. fruticosa* are native shrubs that widely distributed on the central Tibetan Plateau, which is becoming more abundant at alpine ecosystem in recent years (Zhao et al., 2023).

Experimental design

In Mid-August of 2021, field data were collected in two sites of the Tibetan semi-arid alpine steppe, Shrub encroachment has been prevalent in both the two sites, with one site encroached by a leguminous shrub (*C. spinifera*) and the other site encroached by an none-leguminous shrub (*D. fruticosa*). At each site, alpine steppe and shrub encroached alpine steppe were selected (Fig. 1a-d). At each of the AS and AS_{SE} treatments, a 30 m x 30 m grassland plot was set, with the paired grassland plot and shrub encroached grassland plot separated by approximately 30 m. Within each plot, five 0.5 m x 0.5 m quadrats were sampled. Totally, 20 quadrats (2 shrub types x 10 quadrats) were sampled.

Vegetation survey and soil property measurement

Within each sampling quadrat, we measured plant height, percentage coverage, aboveground biomass (AGB), and belowground biomass (BGB) of herbaceous species at August 2020 according to the standard filed vegetation survey method (Zhao et al., 2023). Following the vegetation sampling, soil samples (0–10 cm in depths) were collected from each quadrat for measuring soil property. soil organic carbon (SOC), soil total nitrogen (STN), soil inorganic nitrogen (NH_4^+-N and NO_3^--N), soil microbial biomass carbon (MBC) and nitrogen (MBN). Soil organic carbon (SOC) and soil total nitrogen (STN) contents were measured determined by an elementary analyzer (Vario EL III, Elementar, Germany). Soil inorganic nitrogen ($NO_3^{—}$N and NH_4^+-N) contents were measured using auto-analyzer (Auto Analyzer 3, Bran Luebbe, Germany). The soil microbial biomass carbon (MBC) and nitrogen (MBN) contents were measured by the chloroform fumigation-extraction method.

Data analysis

The ecosystem multifunctionality (EMF) indexes of alpine steppes with and without shrub encroachment were calculated by five plant functions (Cover, Height, *SR* , AGB, and BGB) and seven soil functions (SW, SOC, MBC, STN, MBN, NO_3^--N and NH_4^+-N), which were also reclassified into aboveground ecosystem multifunctionality (AEMF) index and belowground ecosystem multifunctionality (BEMF) index. These indexes were calculated as follows:

$$EMF = \frac{1}{N}\sum_{i=1}^{N} \text{Zij}$$

where N represents the total number of functions evaluated andZij is the standardization (Z-score) of the i th ecosystem function in the j th plot.

We further used the relative interaction intensity (RII) to estimate the changes magnitude of the ecosystem functioning in semi-arid alpine steppes induced by shrub encroaching. The RII index was calculated as:

$RII=(V_{SE}-V) / (V_{SE} + V)$

where V_{SE} and V are the values of ecosystem individual functions in shrub encroached and non-encroached alpine steppes, respectively. The RII values >0 indicating a positive impact shrub encroachment on the individual and multiple ecosystem functioning.

The independent sample *t* -test was used to test the differences in vegetation characteristics, soil variables and the EMF indexes between alpine steppes with and without shrub encroachment. Two-way analysis of variance (ANOVA) tested the impacts of shrub type and shrub encroachment, and their interactions on the individual and multiple ecosystem functioning. We further used the Pearson correlation to explore the relationships among the individual ecosystem functions as well as the ecosystem multifunctionality indexes.

Results

Variations in plant characteristics and soil properties

Shrub encroachment had differential effects on above and below-ground ecosystem functions of semi-arid alpine steppes (Table S2). The cover of herbaceous tended to increase following shrub encroachment (Fig. 2a and Fig. 3). However, the encroachments of both Leguminosae and Non-Leguminosae shrubs had no significant impacts on plant height, species richness, above and below-ground biomass of herbaceous species (Fig. 2b-e and Fig. 3). The SOC, STN, and NO_3^--N contents rather than soil water content greatly increased following shrub encroachment (Fig. 2f-h and Fig. 3). The MBC and MBN contents significantly increased after encroached by non-Leguminosae shrub rather than by Leguminosae shrub (Fig. 2i-j and Fig. 3). However, the NH_4^+-N only significantly enhanced after Leguminosae shrub encroachment (Fig. 2j).

Variations in ecosystem functions following shrubs encroachment

Shrub encroachment strengthened ecosystem functioning of the semi-arid alpine steppes, with the mean EMF indexes greatly increased after shrub encroachments (Fig. 4a and Table S3). The BEMF index also significantly increased following the encroachments of both Leguminosae and Non-Leguminosae shrubs (Fig. 4b). However, the BEMF index had neutral trends after shrubs encroachment (Fig. 4c and Table S3). The RII indexes further indicated greater facilitative effects of both Leguminosae and non-Leguminosae shrubs on the EMF and BEMF of the semi-arid alpine steppes (Fig. 4d-e). In pooled all data together, we found that shrub encroachment increased the belowground ecosystem functioning greater than the aboveground ecosystem functioning, with the BEMF and AEMF increased by 295% and 50%, respectively (Fig. 7).

Controls of the variations of individual and multiple ecosystem functions following shrub encroachment

Plant cover, species richness, AGB and BGB were significantly related with SW, NO_3^--N and NH_4^+-N contents (Fig. 5). The SOC and STN contents also had significant relationship with BGB, SW, NO_3^--N and NH_4^+-N. In pooled all data together, we found that SR, AGB, SW, STN, MBC, and NO_3^--N had significant relationships with the overall and above- and belowground ecosystem multifunction indexes of the alpine steppes (Fig. 5). We further found that the RII indexes of plant productivity, soil microbial biomass, and soil nutrients had positive relationships with that of the ecosystem multifunction indexes (Fig. 6), suggesting that plant productivity, soil microbial activity, and soil nutrients play critical roles in driving ecosystem functioning responses to shrubs encroachment (Fig. 7). However, the RII index of EMF indicated that there were no significant relationships between EMF and that of SR and SW (Fig. 6). For different apart of the ecosystem functions, the RII indexes of AEMF and BEMF both yielded positive and significant relationships with that of the plant cover, AGB, BGB, SW, SOC, and NO_3^--N (Fig. 6).

Discussion

In semi-arid alpine regions of the Tibetan Plateau, climatic warming and increased precipitation are expected to cause widespread shrub encroachment into alpine grassland ecosystems (Lu et al., 2022; Wang et al., 2022).Shrubs encroaching will promote plant growth, increase vegetation productivity, and lead to accumulation of soil carbon and nutrients in water-limited alpine grasslands (Pistón et al., 2016; Cui et al., 2023), and, in turn, results in the strengthen of ecosystem functioning (Wang et al., 2023). Consistent with these findings, our study also found that shrub encroachment enhanced ecosystem multifunctionality index of the Tibetan semi-arid alpine steppes (Fig. 4a). Nevertheless, our finding also revealed divergent above- and belowground ecosystem functioning responses to both Leguminosae and Non-Leguminosae shrubs encroachment in semi-arid alpine steppes, with the BEMF index rather than AEMF index increased following shrub encroachment (Fig. 4b-e). Briefly, our results further suggest that shrub encroachment had neutral effects on aboveground ecosystem functions, specifically plant cover, species richness, and below-ground plant biomass (Fig. 2a-e and Fig. 3). However, shrubs encroached into semi-arid alpine steppes generally tend to enhance the belowground ecosystem functions, that is, higher soil nutrients, and soil carbon and nitrogen stocks (Fig. 2f-l and Fig. 3).

The encroaching shrubs of *C. spinifera* and *D. fruticosa*are generally drought tolerant and nutrient rich. These encroaching shrubs can create a microhabitat favoring growth of herbaceous plants through buffering of extreme soil temperatures and drought stress and increasing in soil nutrients availability, contributing to the increase of biodiversity and ecosystem functioning (Cui et al., 2023; Zhao et al., 2023). However, species richness, diversity, and productivity of herbaceous plants in the encroached areas also could be lower due to the encroaching shrub species competing for soil nutrients and shading light resources (Zhang et al., 2022). Therefore, the net impacts of shrub encroaching on biodiversity and ecosystem functioning often depend greatly on its facilitation and inhibition effects. In the present study, we found that encroaching of both shrubs tended to increase coverage of the herbaceous plants, but had neutral effects on the diversity and production of herbaceous plants (Fig. 2 and Fig. 3). Thus, the finding indicated that plant diversity and vegetation productivity are an unlikely major mechanism for the shrubs encroaching induced facilitation impacts on ecosystem functioning of the semi-arid alpine steppe.

The availability of soil water and nutrients mainly limited plant growth in alpine steppes (Sun et al., 2020; Cheng et al., 2022). With the encroachment of shrubs, soil organic matter and nutrients gradually accumulate in the soil, creating the "fertile islands" effects of shrubs (Valencia et al., 2015), which is conducive to the increase of BEMF and EMF. In addition, shrub encroachment could enhance the soil water availability under the shrub canopy by reducing evaporation under the shrub canopy (Iyengar et al., 2017; Liu et al., 2020). It was noted that shrub encroaching induced mitigation of soil water and nutrient deficiencies was the major reason for the abrupt facilitation of ecosystem functioning (Ale et al., 2023; Wang et al., 2023). However, former studies indicated that soil nutrient rather than water availability mainly mediated the encroaching of shrubs caused facilitation impacts on the ecosystem functions of semi-arid alpine grasslands (Cui et al., 2023; Zhao et al., 2023), which is also well reflected by our finding that showed the increased EMF following shrub encroachment (Fig. 4). In the present study, despite the significant relationships between soil water content and species richness of herbaceous plants were showed after encroachment by the tow shrubs, we found that both encroaching shrubs had no significant effects on the SW (Table 3), suggesting that water availability might not be the major reason for the changes of ecosystem functioning of the semi-arid alpine steppes.

Previously have been emphasized that the traits of encroaching shrubs (e.g., Leguminosae or non-Leguminosae species) could affect the degree of their effects on the ecosystem functioning (Eldridge et al., 2011). In semi-arid alpine ecosystems, Leguminosae shrubs, compared with non-Leguminosae shrubs, have great potential to alleviate nutrient limitations and often to facilitate species richness, vegetation productivity, soil microbial activities, and carbon accumulation as well as ecosystem functioning under their canopies (Iyengar et al., 2017; Ale et al., 2023). Our findings showed that the encroaching of both Leguminosae and non-Leguminosae shrubs enhanced ecosystem functions of semi-arid alpine steppes. Nevertheless, the encroachment of both Leguminosae and non-Leguminosae shrubs had significant positive impacts on the belowground ecosystem functioning rather than aboveground ecosystem functioning in semi-arid alpine steppes. This may be because the climate in this region is relatively dry, and shrub encroachment-induced increase in soil nutrients may just slightly promote the growth of herbaceous plants in the semi-arid alpine steppes. In addition, in semi-arid region, most of these herbaceous plants with a shallow root system might be more sensitive to water rather than nutrients availability, and the shallow roots also makes them less advantageous in competing for water and nutrient resources with the deep-rooted Leguminosae shrub (Zhang et al., 2022). Such mechanisms also could explain why there was a neutral response of the AEMF in semi-arid alpine steppes after the encroaching of both shrub species.

Nevertheless, it is critical to note that our study was conducted primarily in the water-limited region on the Tibetan Plateau, and these semi-arid alpine steppes were highly responsive to changes in precipitation and soil water conditions (Zhao et al., 2019). Our findings based on observations highlight that the encroaching of both leguminous and none-leguminous shrubs has the potential to substantially strengthen ecosystem functioning of the semi-arid alpine steppes on the Tibetan Plateau. These findings have important and broadly applicable implications for developing management measures and better maintenance of alpine ecosystems given the vast expanse of alpine steppes across the Tibetan Plateau. Such changes to alpine grasslands ecosystem functioning resulting from shrub encroachment should be adequately considered in predictions of climate changes and anthropogenic activities impact because they could challenge our understanding of how alpine grasslands function.

Conclusion

Our study concluded that the encroachment of both Leguminosae and Non-Leguminosae shrubs had the overall facilitation impacts on ecosystem functioning of the semi-arid alpine steppe. However, our finding showed divergent above- and belowground ecosystem functioning responses to both Leguminosae and Non-Leguminosae shrubs encroachment in the Tibetan semi-arid alpine steppes, with the BEMF index rather than AEMF index of semi-arid alpine steppes increased following shrub encroachment. We highlight the role of shrub encroachment induced enhancements in resources availability, such as increased soil nutrients, maybe of more importance for determining their impacts on ecosystem functioning in semi-arid alpine steppes. Our findings could help provide new insights for the further understanding of alpine ecosystem transformations, and are beneficial for scientific management and utilization of semi-arid alpine steppes.

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Data Availability Statement

All data used for this manuscript are available when manuscript be accepted for publication.

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Figure captions

Figure 1 Landscape site at Damxung County on the central Tibetan Plateau and the pictures of the alpine steppes encroached (a) by a leguminous shrub (*Caragana spinifera*) and (b) by an none-leguminous shrub (*Dasiphora fruticosa*).

Figure 2 Differences in (a) vegetation cover (Cover), (b) plant height (Height), (c) species richness (SR), (d) aboveground biomass (AGB), (e) belowground biomass (BGB), (f) soil water content (SW), (g) soil organic carbon content (SOC), (h) soil total nitrogen content (STN), (i) soil microbial biomass carbon (MBC), (j) soil microbial biomass nitrogen (MBN), (k) soil ammonia nitrogen (NH_4^+-N), and (l) soil nitrate nitrogen (NO_3^--N) for the alpine steppes encroached by a leguminous shrub (*Caragana spinifera*) and by an none-leguminous shrub (*Dasiphora fruticosa*). Mean +- SD is shown in error bars. Asterisks represent the significant differences between the shrub encroached plots and non-shrub encroached plots. *$p < 0.05$; ** $p < 0.01$; *** $p< 0.001$.

Figure 3 Differences in the relative interaction intensity (RII) values of individual ecosystem functions for the alpine steppes encroached by (a) a leguminous shrub (*Caragana spinifera*) and (b) by an none-leguminous shrub (*Dasiphora fruticosa*). Cover, vegetation cover; Height, plant height; SR, species richness; AGB, aboveground biomass; BGB, belowground biomass; SW, soil water content; SOC, soil organic carbon content; STN, soil total nitrogen content; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; NH_4^+-N, soil ammonia nitrogen; NO_3^--N, soil nitrate nitrogen. Bars indicated the SD of mean value. Asterisks represent the significant differences between the shrub encroached plots and non-shrub encroached plots. * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$.

Figure 4 Differences in (a) the ecosystem multifunctionality (EMF), (b) aboveground ecosystem multifunctionality (AEMF), (c) belowground ecosystem multifunctionality (BEMF) indexes between the shrub encroached plots and non-shrub encroached plots and the relative interaction intensity (RII) values of EMF, AEMF, and BEMF for the alpine steppes encroached by (e) a leguminous shrub (*Caragana spinifera*) and (f) by an none-leguminous shrub (*Dasiphora fruticosa*). Bars indicated the SD of mean value. Asterisks represent the significant differences between the shrub encroached plots and non-shrub encroached plots. * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$.

Figure 5 Correlation coefficients among the individual ecosystem functions and multiple ecosystem functions relevant to the ecosystem multifunctionality (EMF), aboveground ecosystem multifunctionality (AEMF), belowground ecosystem multifunctionality (BEMF) in the semi-arid alpine steppes. Cover, vegetation cover; Height, plant height; SR, species richness; AGB, aboveground biomass; BGB, belowground biomass; SW, soil water content; SOC, soil organic carbon content; STN, soil total nitrogen content; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; NH_4^+-N, soil ammonia nitrogen; NO_3^--N, soil nitrate nitrogen. Bars indicated the SD of mean value. Asterisks represent the significant differences between the shrub encroached plots and non-shrub encroached plots. * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$.

Figure 6 Correlation coefficients among the relative interaction intensity (RII) values of individual ecosystem functions and multiple ecosystem functions relevant to the ecosystem multifunctionality (EMF), aboveground ecosystem multifunctionality (AEMF), belowground ecosystem multifunctionality (BEMF) in respond to shrub encroachment. Cover, vegetation cover; Height, plant height; SR, species richness; AGB, aboveground biomass; BGB, belowground biomass; SW, soil water content; SOC, soil organic carbon content; STN, soil total nitrogen content; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; NH_4^+-N, soil ammonia nitrogen; NO_3^--N, soil nitrate nitrogen. Bars indicated the SD of mean value. Asterisks represent the significant differences between the shrub encroached plots and non-shrub encroached plots. * $p < 0.05$; ** $p< 0.01$; *** $p < 0.001$.

Figure 7 A schematic diagram for understanding the potential ways of shrub encroachment on the individual ecosystem functions and multiple ecosystem functions in the semi-arid alpine steppes.

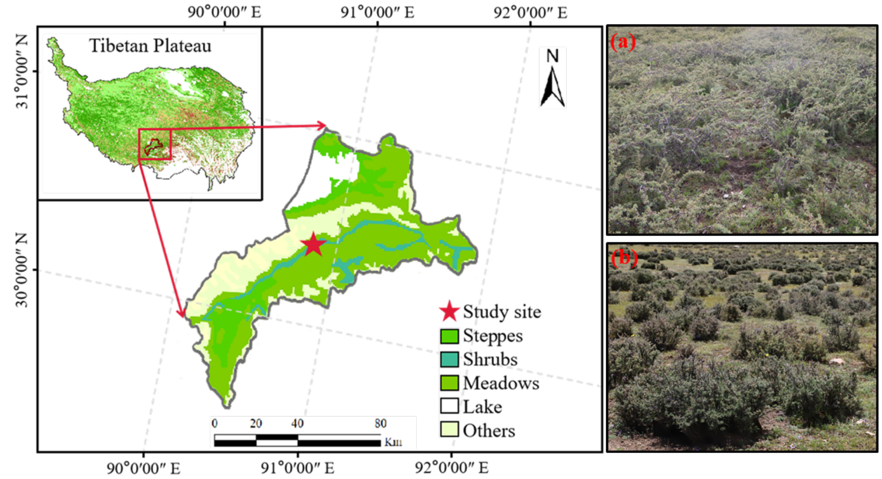


Figure 1

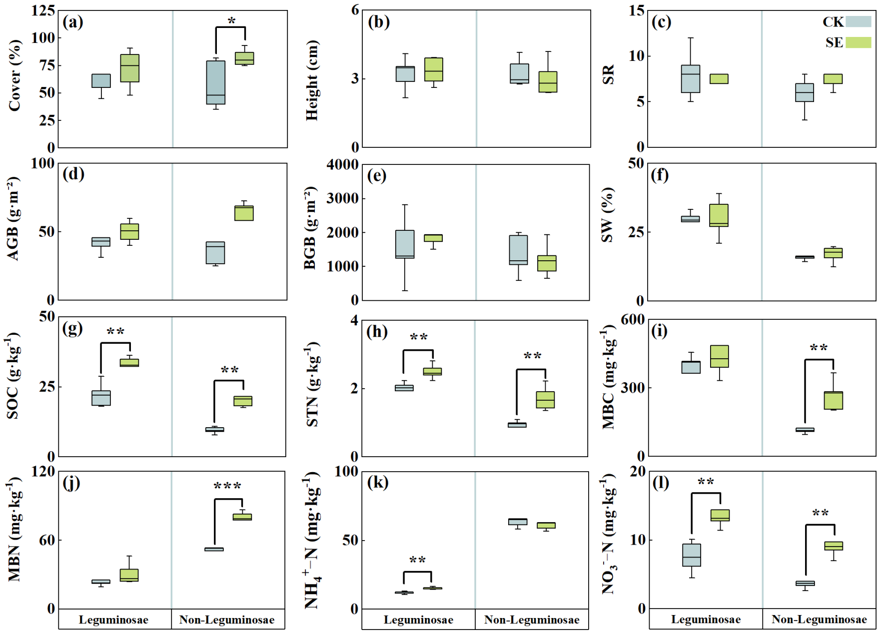
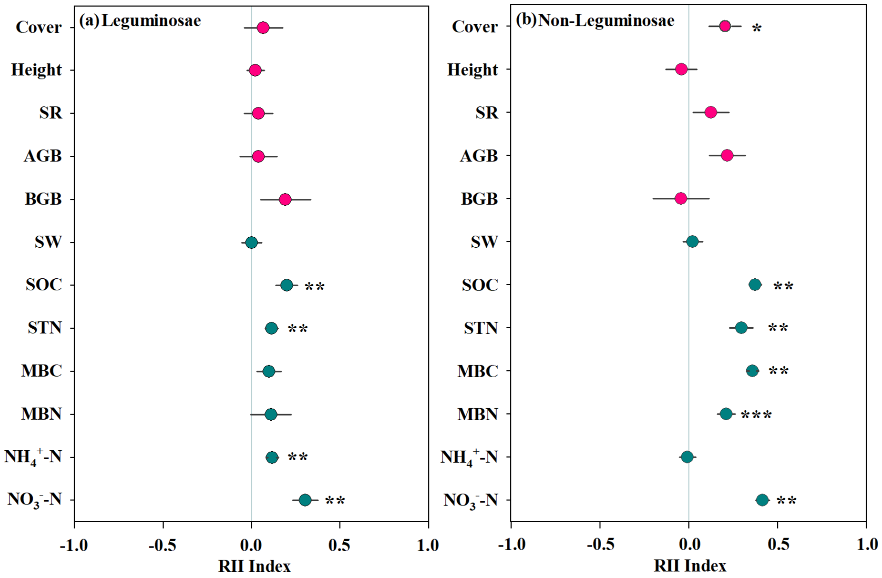


Figure 2



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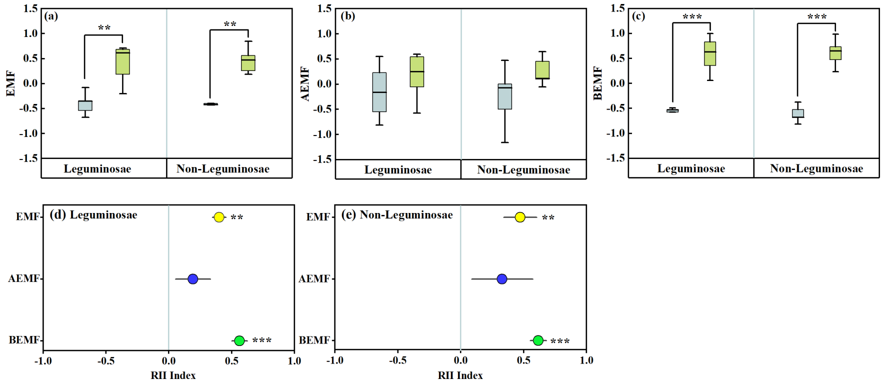

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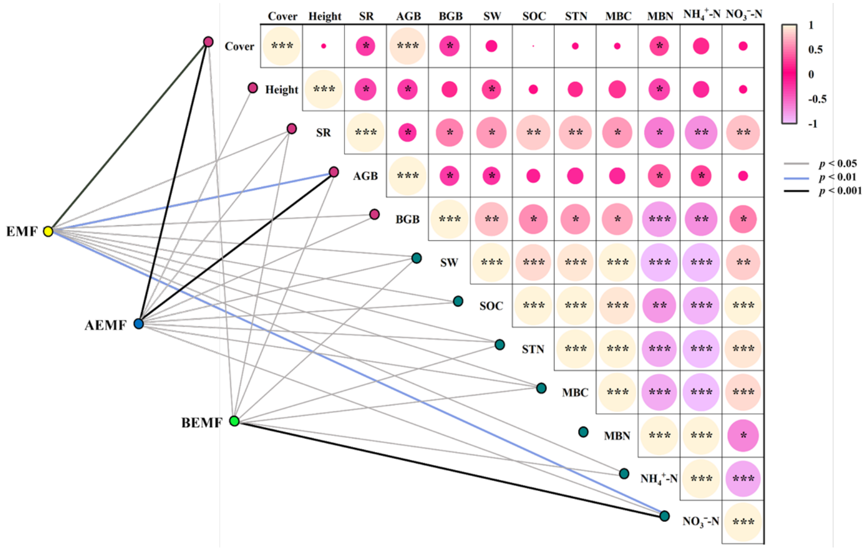

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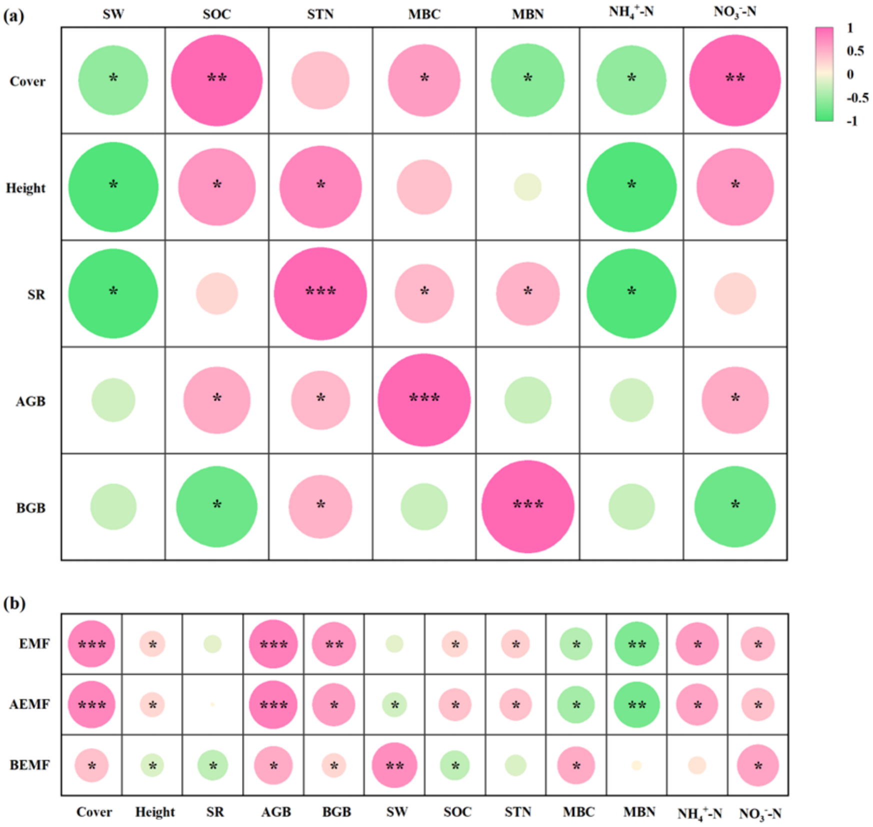

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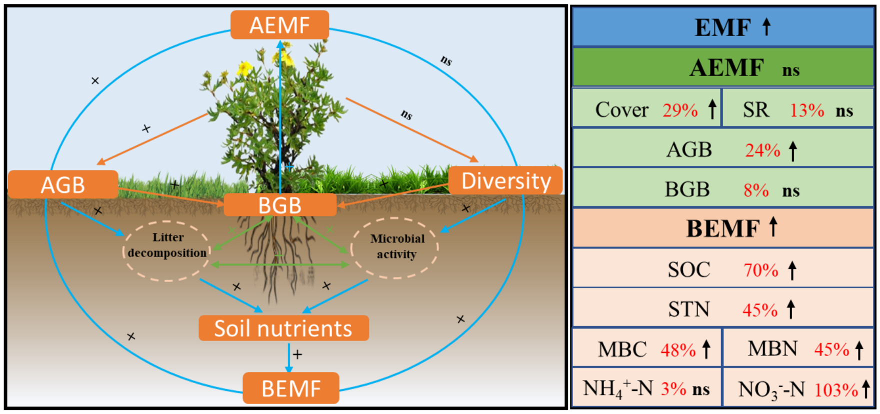

Figure 7

Table S1 Relative importance of plant species in the alpine steppes with and without Leguminosae and Non-Leguminosae shrubs encroachment.

Species	Functional groups	Leguminosae	Leguminosae	Non-Leguminosae	Non-Leguminosae
		SE	CK	SE	CK
Carex atrofusca	Sedges	0.05	0.09	0.18	0.12
Carex moorcroftii	Sedges	0.1	0.05	0.08	0.23
Carex parvula	Sedges	0.26	0.2	0.04	0.05
Stipa capillacea	Grasses	0.34	0.18	0.23	0.11
Stipa purpurea	Grasses	-	0.06	-	-
Artemisia lancea	Forbs	0.01	-	-	-
Artemisia wellbyi	Forbs	0.04	0.02	-	-
Potentilla saundersiana	Forbs	-	0.02	0.01	-
Potentilla multifida	Forbs	-	0.01	-	-
Argentina anserina	Forbs	-	0.11	0.05	-
Sibbaldianthe bifurca	Forbs	0.12	-	0.19	0.17
Tibetia himalaica	Forbs	0.03	-	-	-
Oxytropis alpina	Forbs	-	-	0.01	-
Aster boweri	Forbs	-	0.01	0.05	0.13
Rhodiola tibetica	Forbs	-	-	0.02	0.01
Leontopodium pusillum	Forbs	-	0.05	-	0.03
Oxytropis proboscidea	Forbs	0.01	-	-	-
Pleurospermum hedinii	Forbs	0.04	0.09	-	-
Artemisia frigida	Forbs	0.04	0.03	0.02	0.01
Anaphalis xylorhiza	Forbs	-	0.02	0.03	0.04
Taraxacum tibetanum	Forbs	0.02	-	-	-
Lancea tibetica	Forbs	0.02	-	-	-
Stellera chamaejasme	Forbs	-	0.03	-	-
Gentianopsis paludosa	Forbs	0.11	-	-	-
Microula sikkimensis	Forbs	0.03	0.05	0.08	0.07
Oxygraphis kamchatica	Forbs	0.02	0.03	-	-
Iris collettii Hook	Forbs	-	0.03	-	-
Eremogone capillaris	Forbs	-	-	-	0.02

Table S2 Results of the ANOVA analyses (F-values) for the effects of shrub type (ST), shrub encroachment (SE), and their interaction (ST × SE) on the individual ecosystem functions in the semi-arid alpine grasslands. Cover, vegetation cover; Height, plant height; SR, species richness; AGB, aboveground biomass; BGB, belowground biomass; SW, soil water content; SOC, soil organic carbon content; STN, soil total nitrogen content; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; NH_4^+-N, soil ammonia nitrogen; NO_3^--N, soil nitrate nitrogen. *,$p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Variables	ST	SE	ST × SE
Cover	0.081	4.967*	1.129
Height	0.210	0.052	0.333
SR	3.568	1.000	0.309
AGB	0.106	2.320	1.682
BGB	2.717	0.160	0.895
SW	50.268***	0.154	0.007
SOC	66.591***	55.367***	0.074
STN	69.632***	34.540***	1.675
MBC	27.388***	7.549*	0.234
MBN	134.713***	28.242***	10.285**
NH_4^+-N	364.502***	0.193	0.524
NO_3^--N	18.889**	40.801***	0.221

Table S3 Results of the ANOVA analyses (F-values) for the effects of shrub type (ST), shrub encroachment (SE), and their interaction (ST × SE) on the multiple ecosystem functions of semi-arid alpine steppes. EMF, ecosystem multifunctionality; AEMF, aboveground ecosystem multifunctionality; BEMF, belowground ecosystem multifunctionality. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Variables	ST	SE	ST × SE
EMF	0.000	39.789***	0.229
AEMF	0.000	3.225	0.202
BEMF	0.000	109.821***	0.125