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Livestock exclusion enhances shrub encroachment in an alpine meadow on the eastern Qinghai-Tibetan Plateau

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Abstract

The Qinghai-Tibetan Plateau alpine grassland is experiencing shrub encroachment, which threatens the livelihoods of local nomads. Livestock exclusion management policies have also been implemented in this grassland. It has been predicted that shrubs here will likely encroach after long-term yak elimination, but this inference is not supported by a manipulation experiment. To determine how shrubs respond to livestock grazing cessation, we investigated *Potentilla fruticosa* L. characteristics and properties of herbs and soil in a 'livestock exclusion-free grazing' system with enclosure experiments of 9, 17, and 23 years in the northeast region of the Plateau. We showed that each characteristic of shrub growth and reproduction was significantly greater in enclosures than in control plots, and shrub properties enhancements by livestock exclusion increased over time. We further found that this livestock exclusion induced-shrub encroachment was related not only to the exclusion of livestock's direct disturbances but also to the competitive advantage gain of shrubs through plant-plant interactions and improvement of resources in deep soil for shrubs. Given the negative influences of shrub encroachment, especially lowering rangeland quality, livestock exclusion management in alpine grasslands should be used with caution.

KEYWORDS

alpine meadow, grassland management, livestock exclusion, Qinghai-Tibetan Plateau, shrub encroachment

1 | INTRODUCTION

In the majority of herb-dominated biomes, woody plants have been advancing noticeably for decades or even more than 100 years, from tropical to temperate to frigid zones (Nackley et al., 2017; Tape et al., 2006). The enhancement in the dominance of indigenous shrubby species, which have been at lower densities for thousands of years, is called shrub encroachment (Saintilan & Rogers, 2015; Van Auken, 2000). This shift in vegetation composition may profoundly affect a myriad of ecosystem structures, functions, and services, such as improving gross primary production and soil carbon and nitrogen (Li et al., 2019; Wang, Xiao, et al., 2018), but also impairing biodiversity, grass productivity, nutrient balance, and livestock production (Anadón et al., 2014; Eldridge et al., 2011; Ratajczak et al., 2012; Zhou et al., 2018). Therefore, to regulate its impact on the grassland

ecosystem and livestock husbandry, it is necessary to ascertain the trigger of shrub encroachment for the establishment of a reasonable policy and the implementation of adaptive management.

Factors affecting shrub encroachment include air temperature (Myers-Smith & Hik, 2018), atmospheric CO₂ concentration (Morgan et al., 2007), precipitation amounts and variability (Good & Caylor, 2011), and large ungulate herbivorous mammals (Venter et al., 2018). Among various factors, the effect of herbivorous mammals on shrub encroachment is a hot topic. The earliest relative study on how large herbivores influence shrub expansion on record can be traced back to the 1920s, when overgrazing of domestic livestock was thought to be the reason for shrub dune formation in the Jornada Grassland (Buffington & Herbel, 1965). Currently, it is receiving increasing attention from scientists worldwide (Bakker et al., 2016; Dantas & Pausas, 2022). However, owing to the diverse influences of herbivore

behaviours, there is still no scientific consensus on whether the presence or absence of large herbivores enhances shrub encroachment.

The overgrazing hypothesis indicates that livestock can enrich shrub cover by scavenging on palatable herbs (Van Auken, 2000), causing shrubs to escape traps from less frequent and severe fires (Roques et al., 2001) and reallocating soil resources to shrubs through erosion intensification (Archer et al., 2017). To date, this opinion shows universality across many continents, especially North America and Africa (Archer et al., 2017; Venter et al., 2018). However, with technological advances and long-term enclosure experiments, more recent studies have shown that the loss of wild large herbivores contributes to the displacement of herbs by shrubs (Bakker et al., 2016; Guyton et al., 2020; Venter et al., 2018). Elimination of these herbivores avoids their inhibition of shrubs regeneration, growth, and survival from feeding (generally by browsers), physical damage, and fire trap to realize shrub encroachment (Augustine & McNaughton, 2004; Pringle et al., 2014; Van Langevelde et al., 2003). In addition, livestock exclusion may lead to shrub-dominated vegetation composition by blocking similar pathways of consuming (Alvarez-Martinez et al., 2016) and mechanically harming shrubs (Thomas et al., 2007) to wild ungulates, and by changing plant-plant interactions and reallocating more resources to deep soil. However, the present discussion on these mechanisms is limited. Furthermore, there are few studies on how other factors (such as herbivorous foraging behaviour, grassland type, grassland history, and soil texture) would influence the effect of large ungulates on shrubs.

Vegetative composition transition requires a long time to appear (Hopping et al., 2018), particularly with shrub species characterized by long generation and growth times (Bakker et al., 2016). Therefore, a long-term temporal scale is extremely valuable for capturing shrub dynamics after livestock exclusion. On the other hand, most studies investigating shrub change generally use indices such as density, cover, biomass, and height (Asner et al., 2009; Gherardi & Sala, 2015; Harte et al., 2015; Johansson et al., 2018; Morgan et al., 2007; Tobler et al., 2003). Reproductive output (seed number) and regeneration (seedling recruitment) are also important characteristics that can indicate species reordering direction and help predict shrub dynamics (Moreno-de las Heras et al., 2016; Woods et al., 2019). However, relatively little is known about the change in the reproductive output and regeneration of shrubs following the exclusion of livestock grazing.

The Qinghai-Tibetan Plateau (QTP) alpine grassland has witnessed obvious shrub encroachment, and livestock have been excluded in ~10% of the total area since 2003 (<http://www.gov.cn/>) to protect ecosystems and improve livelihoods (Lu et al., 2018). A recent study predicted that alpine meadows would possibly transform into shrublands after long-term yak elimination (Hopping et al., 2018); however, to the best of our knowledge, there is no experimental support for this prediction. Therefore, we employed a livestock exclusion-free grazing system including 9, 17, and 23 years of enclosure manipulation, and measured multiple characteristics of shrubs, herbs, and soil in a QTP alpine meadow. The objectives of this study were: (a) to detect the changes in shrubs following a protracted period of livestock exclusion; (b) to determine the succession of shrub encroachment over time; (c) to explore the relationships between shrub encroachment and changes in livestock browsing, species interactions, and soil resources. By

addressing these goals, this work intends to provide an improved understanding on the causes of shrub encroachment and critical suggestions for grassland livestock management.

2 | MATERIALS AND METHODS

2.1 | Study site

We implemented our study at the Qinghai Haibei National Field Research Station of Alpine Grassland Ecosystem (37°36' N, 101°19' E, 3215 m a.s.l.), located in the northeast region of the QTP, in Qinghai Province, China (Figure 1a). This region is characterized by

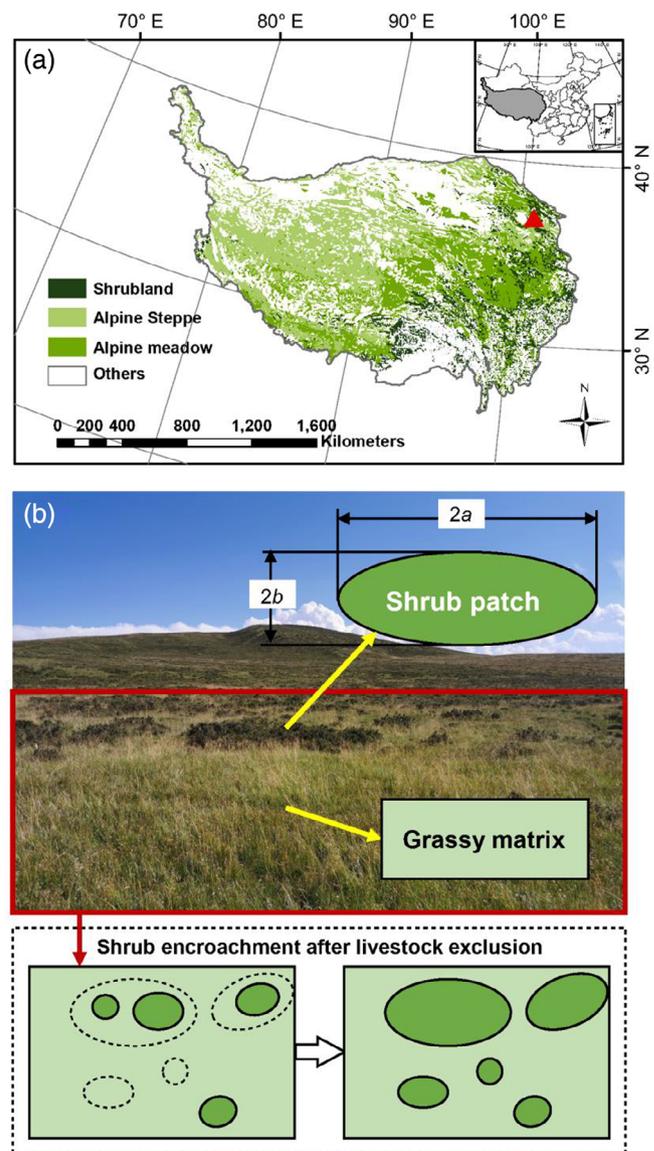


FIGURE 1 Study site and shrub encroachment. Geographical location of the study site against the vegetation map background of the Qinghai-Tibetan plateau (a). Illustrations of shrub patches, grassy matrix, and shrub encroachment after livestock exclusion (b). Wiley acknowledges that the borders within the figure are subject to multiple territorial claims [Colour figure can be viewed at wileyonlinelibrary.com]

a continental monsoon climate, with a short, cool summer and a long, cold winter. The average annual air temperature here is -1.1°C , with the highest at 28°C in July and the lowest at -37°C in January (Ma et al., 2017). The average annual precipitation is 488 mm, with 84% falling between May and September (Wang et al., 2020). The soil type is Mat-Gryic Cambisol, with a mean soil bulk density, organic carbon content, and pH in the top layer of 0.8 g cm^{-3} , 63.1 g kg^{-1} , and 7.8 respectively (Wang et al., 2020). As for the soil texture in the top layer, the contents of clay and sand are $>60\%$ and $<30\%$ respectively (Yang et al., 2017).

This mesic meadow is dominated by grasses including *Stipa aliena*, *Elymus nutans*, and *Helictotrichon tibeticum*. In addition to herbs, there are also shrub species, which are generally regarded as forbs if they exist only in the field layer. The most common shrub is the deciduous *Potentilla fruticosa* L. (*P. fruticosa*). This shrub has a strong reproductive ability and is tolerant to drought and infertility, with a well-developed root system mainly spreading over 0–50 cm of the soil layer (He, 2017). This plateau has a long history of livestock grazing for thousands of years (Hopping et al., 2018). This area has been used as a winter pasture since the 1980s, with the domestic herbivores sheep and yak grazing lightly and freely from October to May of the following year. During the non-growing season, these ungulates can browse *P. fruticosa* by chance (personal observation from Huijin Shi). In the early growing season, sheep can browse the fresh leaves and stems of *P. fruticosa* (Klein et al., 2007).

2.2 | Experimental design and measurements

Using space for time substitution, we established a paired livestock exclusion-free grazing (control) system to evaluate the effects of livestock exclusion on shrubs at Haibei Research Station. Enclosure manipulation experiments were conducted in 1997, 2003, and 2011. Small mammals cannot be eliminated using these fences. There were two 9-year enclosures, six 17-year enclosures, and one 23-year enclosure, all $30\text{ m} \times 30\text{ m}$ in size. The enclosures were adjacent to an open pasture. Control plots were delineated temporarily near the enclosures by outlining the boundary with plastic wires and wood posts in the open pasture. There were four, four, and one control plots for the 9-, 17-, and 23-year enclosures respectively. Notably, the topography, vegetation, and soil types were similar between the enclosures and corresponding control plots before fencing. From August to September 2020, we conducted the sampling and investigation.

2.2.1 | Herb sampling

In each plot, we chose five *P. fruticosa* shrub patches according to the canopy area frequency distribution of shrub patches (from the investigation in Section 2.2.3) and randomly chose five herb patches as far away from the shrub patches as possible in the grassy matrix (Figure 1b). One quadrat of $50\text{ cm} \times 50\text{ cm}$ was set in each shrub and herb patch. We harvested all aboveground biomass (AGB) at ground

level from the quadrats. Live aboveground biomass was divided into four functional groups (grass, sedge, legume, and non-legume forb), and dead aboveground biomass was separated into standing and soil surface litter. The classified biomass was dried in an oven to a constant weight at 65°C and weighed.

2.2.2 | Soil sampling and laboratory analyses

Soil was sampled at the above-mentioned chosen five shrub patches and five herb patches in each plot. For each patch, we used soil bulk density drilling (with a cutting ring volume of 100 cm^3) to extract 100 cm^3 soil at 0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm. The soil samples were rapidly brought back to the laboratory and weighed. After oven-drying at 105°C to a constant weight, soil samples were weighed again. Soil water content was calculated as the percentage of water weight in the fresh soil.

At each shrub and herb patch, we also randomly selected 3–7 sampling points and collected samples at 0–5, 5–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm using a soil auger of 5 cm diameter and completely mixed soils from the same depth. Soil samples were air-dried indoors immediately after returning to the laboratory and sieved to pass a 2 mm screen with debris eliminated. After sieving, the roots were carefully removed using tweezers. Soil-water mixtures at a 1:5 ratio (w:v) were prepared to determine pH using a pH meter. Representative sub-samples were passed through a 0.25 mm sieve for soil element measurements. Soil total carbon (STC) and total nitrogen (TN) contents were measured using an elemental analyzer (Vario EL cube; Elementar, Langensfeld, Germany) at the College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, China. The soil inorganic carbon (SIC) and total phosphorus (TP) contents were determined using a SKALAR carbon element analyzer (2SN100903#; Skalar Analytical B.V., Breda, The Netherlands) and an automated discrete analyzer (Smarchem450; AMS, Italy), respectively, at the State Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems, College of Pastoral Agriculture Science and Technology, Lanzhou University. Soil organic carbon (SOC) content was calculated as the difference between the STC and SIC content.

2.2.3 | Shrub investigation

The shrub investigation included two parts: shrub patch investigation and shrub investigation of herb patches. For *P. fruticosa* shrub patches, it is difficult to count individuals, as *P. fruticosa* mainly carries out vegetative propagation by creeping stems belowground. We measured each *P. fruticosa* patch's (1) canopy longest axis $2a$ and perpendicular $2b$, which we used for the ellipse area formula (πab) as the patch canopy area (shrub patch is regarded as an ellipse); (2) largest height; (3) number of branches from previous years; and (4) number of twigs, which are young hairy red brown stems coming out in the current year. For reproductive output, we counted the number of ovaries

surrounded by the calyx for each patch, selected 20–30 of the ovaries in each plot to measure the internal achene (containing one seed) number, and acquired the patch's seed number by multiplying its ovary number by the corresponding average number of achenes in the ovary. We also estimated the number of seedlings under the patch-projected area. For the larger patches that had especially high numbers of branches, twigs, seeds, or seedlings, we selected a representative part to measure and multiplied by an estimated multiple. *Potentilla fruticosa* patches close to each other in the 23-year enclosure were separated by the height and color of the patches. For *P. fruticosa* shrubs in the herb patch, we investigated in five 50 cm × 50 cm quadrats set in the same herb patch as in Section 2.2.1. The shrub properties were measured in a similar manner to the shrub patch.

The aboveground biomass of *P. fruticosa* was nondestructively estimated by the following estimation formula (Liang et al., 2013):

$$AB = 113.02P^2H + 29.77$$

where AB, P , and H are the aboveground biomass (g), canopy perimeter (m), and height (m), respectively, of the shrub patch. The perimeter of an ellipse cannot be estimated accurately; however, there are approximation formulas, of which one of the Ramanujan formulas is famous for its brevity:

$$P \approx \pi \left[3(a+b) - \sqrt{[(3a+b)(a+3b)]} \right].$$

We obtained climatic data from the meteorological station installed in 1980 at the Haibei Research Station.

2.3 | Property calculations

2.3.1 | Herb and soil properties

We used richness, Shannon diversity, Simpson diversity, and Pielou's evenness to evaluate herb diversity in the quadrats of shrub or herb patches.

To understand the properties of herbs and soil at the plot level, we summed the properties obtained from the shrub and herb patches after being weighted by cover. As the calculations for these properties are similar, the equations for determining herb aboveground live biomass at the plot level as an example are as follows:

$$AGB = AGB_S + AGB_H$$

$$AGB_S = \sum_k^5 AGB_{Sk} \frac{C_S}{1.25}$$

$$AGB_H = \sum_j^5 AGB_{Hj} \frac{1-C_S}{1.25}$$

where AGB, AGB_S , AGB_H , AGB_{Sk} , C_S , and AGB_{Hj} are the herb live AGB at the plot level ($g\ m^{-2}$), herb live AGB in the field layer under all shrub

patches ($g\ m^{-2}$), herb live AGB in the field layer of all herb patches ($g\ m^{-2}$), herb live AGB in the quadrat of shrub patch k (g), cover of all shrub patches (%), and herb live AGB in the quadrat of herb patch j (g) respectively.

2.3.2 | Shrub characteristics

For analyses of shrub characteristics at the plot level, we summed the characteristics of shrub patch and shrub in the herb patch. The formulae for the cover are as follows:

$$C = C_S + C_H$$

$$C_S = \frac{\sum_i^n CA_i}{900}$$

$$C_H = \sum_j^5 C_{Hj} \frac{1-C_S}{5}$$

where C , C_S , C_H , CA_i , n , and C_{Hj} are the shrub cover at the plot level (%), cover of all shrub patches (%), shrub cover in all herb patches (%), canopy area of shrub patch i (m^2), shrub patch number, and shrub cover in the quadrat of herb patch j (%), respectively.

For height, we summed the weighted heights to determine the height at the plot level:

$$H_{CW} = H_{SCW} + H_{HCW}$$

$$H_{SCW} = \sum_i^n H_{Si} \frac{CA_i}{900C_S}$$

$$H_{HCW} = H_H(1 - C_S)$$

where H_{CW} , H_{SCW} , H_{HCW} , H_{Si} , and H_H are the shrub community weighted height at the plot level (cm), community weighted height of all shrub patches (cm), shrub community weighted height in all herb patches (cm), largest height of shrub patch i (cm), and largest height in the quadrats of the five herb patches (cm) respectively.

We standardized the densities of branches, twigs, seeds, seedlings, and aboveground biomass to the square meter level. As the calculations of these shrub characteristics at the plot level are similar, we showed an example of functions of branch density at the plot level as follows here:

$$B = B_S + B_H$$

$$B_S = \frac{\sum_i^n B_{Si}}{900C_S}$$

$$B_H = \sum_j^5 B_{Hj} \frac{1-C_S}{1.25}$$

where B , B_S , B_H , B_{Si} , and B_{Hj} are the shrub branch density at the plot level (branches m^{-2}), branch density of all shrub patches (branches

m^{-2}), shrub branch density in all herb patches (branches m^{-2}), branch number in shrub patch i , and branch number in the quadrat of herb patch j respectively. We calculated the changes in the properties caused by livestock exclusion as differences between the mean values of the livestock exclusion plot and the corresponding control plot, which was the nearest one to the enclosure.

2.4 | Statistical analysis

We used t -tests to evaluate the differences in shrub, herb, and soil properties at the plot level and shrub patch characteristics between livestock exclusion and control treatments for all and/or respective exclusion periods. For paired sample t -tests, we chose the grazing plot nearest the enclosure plot as its corresponding control plot. Furthermore, we tested for the differences in the properties of shrub and herb using one-way analysis of variance (ANOVA) as functions of livestock exclusion years under the control and livestock exclusion treatment respectively. When significant differences were detected, Tukey's honestly significant difference (HSD) post-hoc tests were used to investigate the differences among the livestock exclusion years. The differences of changes in shrub properties among the fencing years were also analyzed using ANOVA and Tukey's HSD tests. The relationships between shrub characteristics and herb and soil properties were tested using simple linear regression. Pearson correlation analyses were applied to examine the temporal dynamic trends of air temperature and precipitation from 1997–2020.

Before the t -tests, ANOVA, regression, and correlation analyses, we tested the normality and homoscedasticity of the data. Square root, logarithmic, or Box–Cox transformations were used for response variables if the transformations allowed residuals to be normally distributed and variance to be homogenous. However, if it failed to meet the conditions, we used corresponding non-parametric tests, including the paired two-sample Wilcoxon rank test, two-sample Wilcoxon rank test, Kruskal–Wallis rank sum test, and Spearman correlation replacing the paired sample t -test, two-sample t -test, one-way ANOVA, and Pearson correlation respectively. We used the 'nparcomp' package in R to conduct a non-parametric multiple comparison after the Kruskal–Wallis rank sum test, replacing Tukey's HSD test (Konietschke et al., 2015). All statistical analyses and figure productions were conducted in R version 4.1.3 (R Foundation for Statistical Computing, Vienna, Austria).

3 | RESULTS

3.1 | Herb and soil properties

Overall, livestock exclusion significantly increased the total AGB, including the live AGB of shrubs and herbs and dead AGB of standing and soil surface litter (Table S1, $p < 0.01$). However, the herbs' live AGB, Shannon diversity, and Pielou's evenness all decreased after livestock removal (all $p < 0.05$), and these patterns were similar for

plant functional groups, except for non-legume forb live AGB (Table S2, all $p < 0.1$). Furthermore, the disparities between enclosures and control plots varied among different years of livestock elimination, with the largest differences observed after 23 years of livestock absence (Figure 2, most of $p < 0.1$ from t -tests). For soil properties, livestock exclusion significantly improved soil resources (Table S3, most of $p < 0.1$), especially in soil depths below 20 cm. For example, after nine years of livestock removal, SOC, TN, and TP in the 0–100 cm layer increased by 7%, 4%, and 10%, respectively (all $p < 0.05$), but the increases were larger in the subsoil (20–100 cm; Figure S1).

3.2 | Shrub characteristics

At the plot level, shrub characteristics of growth (cover, community weighted height, branch density, twig density, and aboveground live biomass) and reproduction (seed density and seedling density) in enclosures were approximately three to eight-fold larger than those in control plots (Table 1, all $p < 0.001$). Specifically, shrubs, on average, expanded 12% of cover, rose 10 cm for community weighted height, and increased 175 g of aboveground live biomass and 59 branches, 894 twigs, 2987 seeds, and 33 seedlings per square meter at the plot level after livestock exclusion. Not only were shrub properties at the plot level enhanced after fencing but the growth (canopy area, height, number of branches and twigs, and aboveground live biomass) and reproduction (seed number) of shrub patches were also improved following livestock exclusion (Table S4, all $p < 0.001$).

Furthermore, shrub characteristics increased after different periods of livestock exclusion. After 9 years of livestock grazing cessation, *P. fruticosa* growth characteristics increased by 15–144-fold from those in corresponding control plots, while reproduction characteristics increased by 7–11-fold (Figure 3). These properties in the 17-year enclosures were significantly promoted (all $p < 0.01$ from t -tests), and were 18–391 times of those in corresponding grazing plots. The noticeable increases in the 9- and 17-year enclosures were relative to low values in the control plots. After 23 years of livestock elimination, the improvements in *P. fruticosa* characteristics were 3–11 times greater than those in the control plots. In addition, the tendencies of shrub encroachment were similar: the extent of each *P. fruticosa* characteristic's enhancement increased over the period of livestock exclusion, and the largest increase occurred following 23 years of livestock absence (Figure 4; all $p < 0.05$).

3.3 | Relationships of shrub characteristics and herb and soil properties

In general, all shrub characteristics at the plot level had similar correlations with the herb and soil properties (Tables 2, S5, and S6). Shrub growth and reproduction were positively correlated with total AGB (all $p < 0.001$), but negatively correlated with herb AGB (all $p < 0.001$).

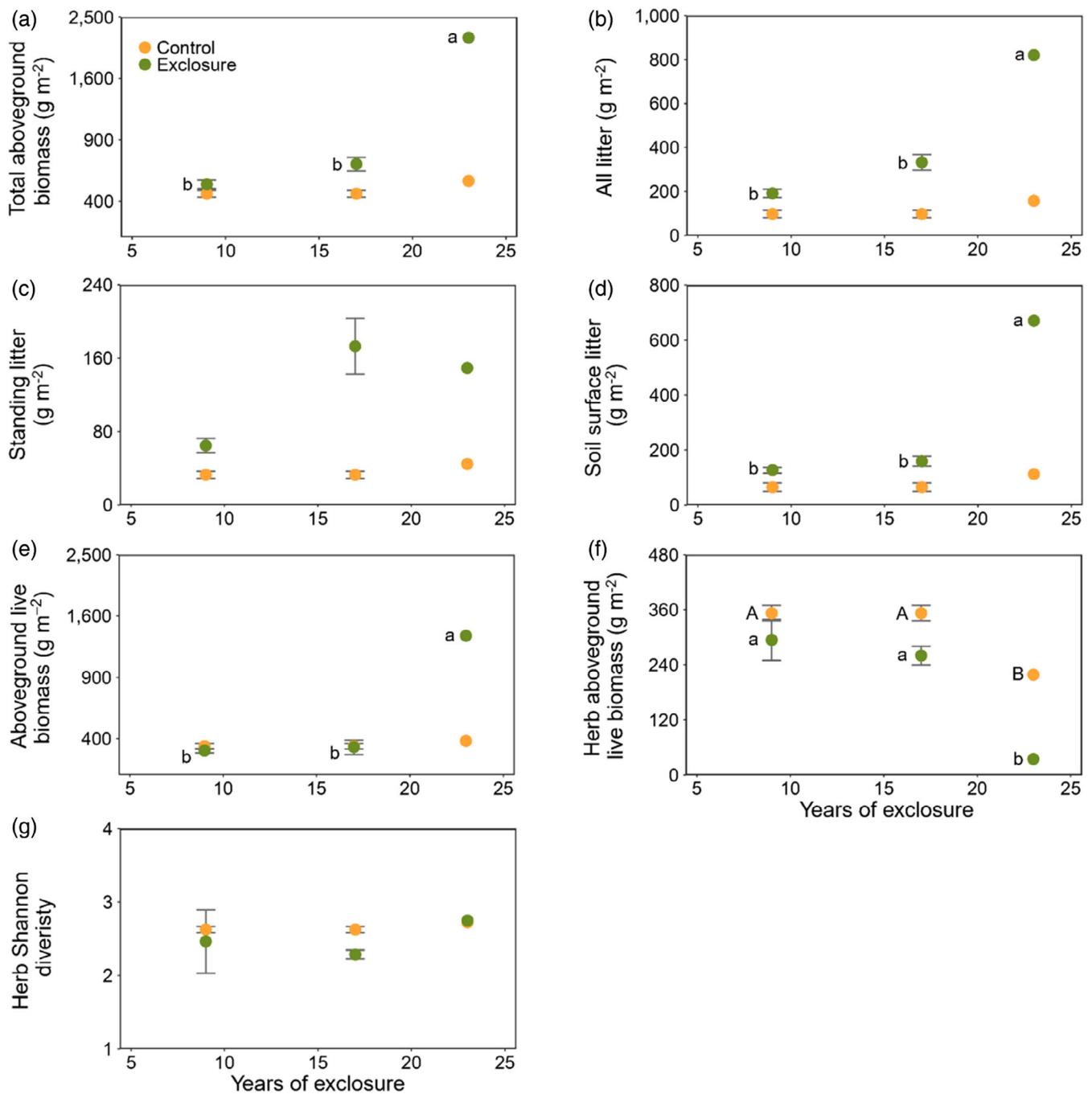


FIGURE 2 Biotic factors at the plot level. Total aboveground biomass including live and dead biomass (a), all litter (b), standing litter (c), soil surface litter (d), aboveground live biomass for all plants (e), herb aboveground live biomass (f), and herb Shannon diversity (g) for groups of livestock exclusion for 9, 17, and 23 years and corresponding control groups. Error bars indicate standard errors. Different upper-case and lower-case letters represent significant differences among different years of livestock exclusion under control and livestock exclusion treatment at the 0.05 confidence level respectively [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

For different functional groups, shrub properties were negatively related to the AGB of grass, legume, and non-legume forbs, and the Shannon diversity of grass (most of $p < 0.1$). The relationships between shrub characteristics and soil properties (including soil water, SOC, and TN) were positive (all $p < 0.05$). For the soil properties at different soil depths, the relationships were all significant, except for some soil properties at 70–100 cm (all $p < 0.1$). Based on the above results, the enhancement of shrub characteristics after livestock

exclusion may be related to the decrease in herb biomass and diversity and the increase in soil resources.

4 | DISCUSSION

Scientists have put many efforts into exploring the driving factors of shrub encroachment in grasslands; however, whether livestock

TABLE 1 *Potentilla fruticosa* L. characteristics at the plot level in livestock exclusion and control plots for all exclusion periods (mean \pm standard error)

	Control	Exclusion
Cover (%)	3.76 \pm 3.64	15.40 \pm 9.04***
Community weighted height (cm)	1.36 \pm 1.34	11.77 \pm 7.84***
Branch density (branches m ⁻²)	7.25 \pm 6.67	66.62 \pm 43.16***
Twig density (twigs m ⁻²)	155.86 \pm 145.93	1049.79 \pm 734.26***
Aboveground live biomass (g m ⁻²)	31.75 \pm 31.53	206.42 \pm 137.06***
Seed density (seeds m ⁻²)	932.62 \pm 905.04	3919.39 \pm 3196.61***
Seedling density (seedlings m ⁻²)	11.42 \pm 10.05	44.89 \pm 24.08***

***Indicates significant difference at the 0.001 confidence level.

exclusion enhances or suppresses shrub expansion remains controversial. Our study testified experimentally that livestock exclusion facilitated shrub encroachment and the encroachment had an increasing trend over a long time. To the best of our knowledge, this is the first long-term evidence of livestock exclusion-induced shrub encroachment in the Qinghai-Tibetan Plateau alpine meadow. Our study further found that not only was livestock exclusion-induced shrub encroachment related to exclusion of browsing but it was also associated with competitive advantage gain of shrubs through plant-plant interactions and improvement in deep soil resources. Our findings will help expand the theory on the reason for shrub encroachment and its mechanisms and provide a reference for grassland management.

4.1 | Mechanisms of livestock exclusion-induced shrub encroachment

4.1.1 | Exclusion of direct browsing by livestock

Our study found that shrubs encroached after 9–23 years of livestock exclusion (Table 1, Figure 3), which is consistent with previous finding on the QTP (Wang et al., 2022). However, grazing cessation for 3 and 6 years did not impact shrub cover or biomass in other regions of the QTP (Hopping et al., 2018; Zhou et al., 2006). We suppose that the results may have been limited by duration. Generally, species reordering takes a long time to emerge (Hopping et al., 2018), particularly with woody species characterized by long regeneration and growth times (Bakker et al., 2016). Hence, long-term fencing is more successful in promoting shrub encroachment, as supported by other studies (Hejčmanová et al., 2010; Li et al., 2013; Olofsson et al., 2009). Our study also provided a qualitative perspective on the rising tendency of shrub encroachment over livestock exclusion years (Figure 4). In addition, release from livestock led to increases in seed and seedling

density, which means that shrubs will possibly continue to encroach in the future (Browning et al., 2008; Moreno-de las Heras et al., 2016). This trend may be caused by positive feedbacks between shrubs and the influencing variables (He et al., 2015). Unfortunately, our study was limited by a lack of sufficient number of repeats. Therefore, additional long-term observations and experiments on the QTP need to be conducted to obtain a more robust generalization of the dynamics of shrub encroachment over livestock exclusion years.

Similar to our results, a few studies worldwide have shown that livestock elimination causes woody encroachment. Domestic animals, such as goats, prefer browsing to grazing; thus, their exclusion can promote woody expansion (Aharon et al., 2007; Elias et al., 2018; Gomez & Gonzalez-Megias, 2002). However, in our study, sheep and yaks browse shrubs occasionally (observed by Huijin Shi; Klein et al., 2007), which is similar to the observations in several humid and sub-humid grasslands (Altesor et al., 2006; Costello et al., 2000; Lunt et al., 2010). Under relatively humid conditions, herbs can possess a high resilience against negative disturbances (such as livestock) with high plant diversity (Isbell et al., 2015). Moreover, the probability of shrubs (particularly seedlings) near palatable neighbors being unintentionally eaten or damaged physically can be increased with high plant density (Bisigato et al., 2005; Palmer et al., 2003; Thomas et al., 2007), and shrubs may be sensitive to browsing and other disturbances, which may inhibit the regeneration and growth of shrubs or even increase their mortality (Altesor et al., 2006; Strauss & Agrawal, 1999).

4.1.2 | Competitive advantage transformation through plant-plant interactions

It has been widely accepted that in grasslands with long-term grazing history, vegetation composition has already formed a strong tolerance to livestock and is stable, with compensatory growth of herbs at high density (Manier & Hobbs, 2006; McNaughton, 1983). In the meadow of this study, which has thousands of years of grazing history, herbs were found to produce more AGB, seeds, and sexual seedlings in areas with livestock than those without livestock (Chu et al., 2019; Li et al., 2020; Wu et al., 2011). The effects of the livestock solidify the competitive advantage possessed by herbs to outweigh any benefit conveyed to shrubs by domestic animals, which can be explained by the 73% occupation of total live AGB by herbs in free grazing plots (Table S1). In contrast, livestock exclusion is the disturbance that breaks the balance among species (Dorji et al., 2018), causing shrub competitive superiority to appear, followed by shrub encroachment (Table 1). Our results are also supported by studies on European grasslands with a long history of pastoralism (Listopad et al., 2018; Tonelli et al., 2019).

Furthermore, livestock exclusion enhanced the total AGB (Table S1, Figure 2a), which aggravated light limitation (Borer et al., 2014). In this case, shrubs that more effectively vertically distribute the leaf area may grow more successfully than herbs (Altesor

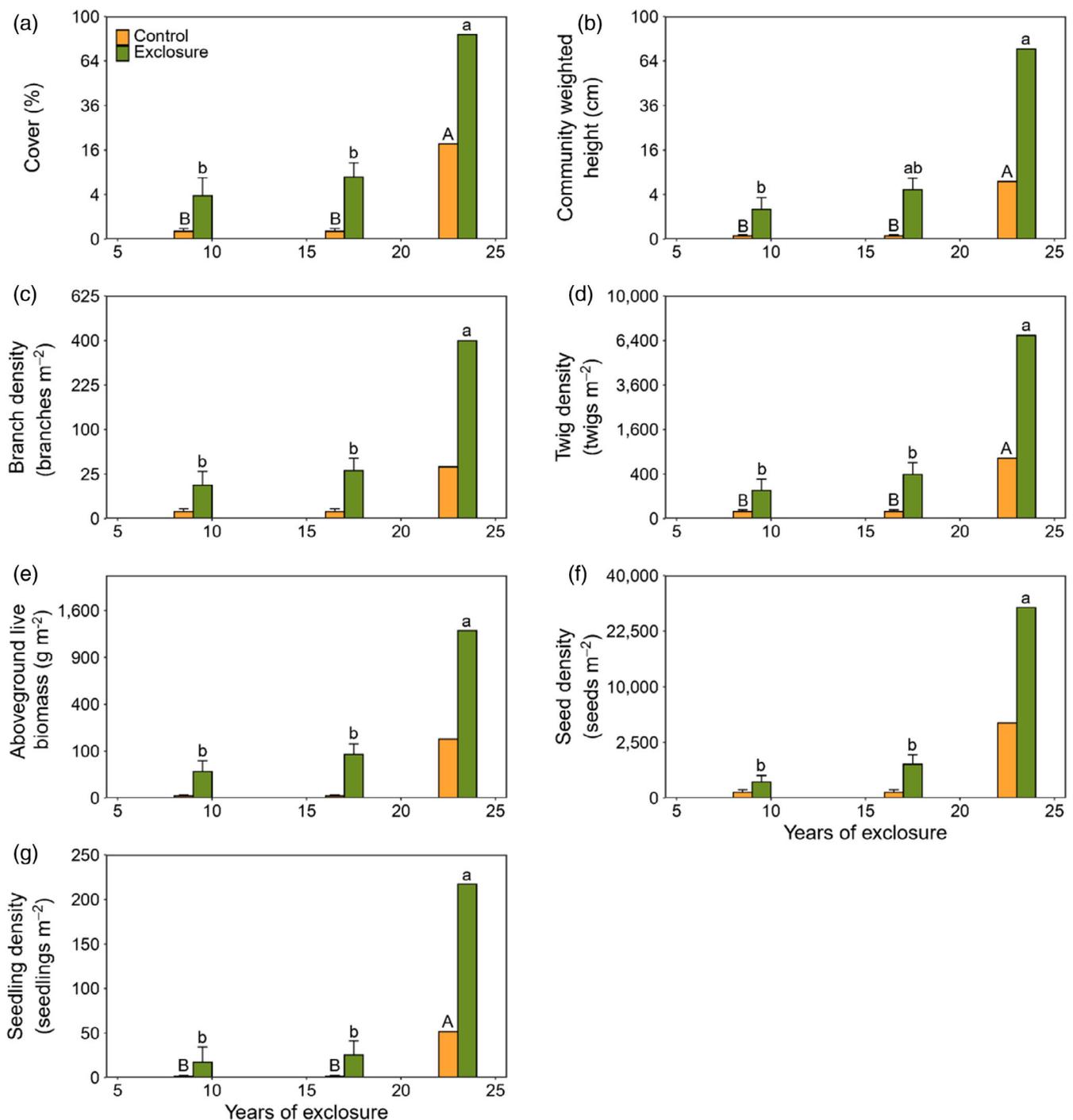


FIGURE 3 Characteristics of *Potentilla fruticosa* L. growth and reproduction at the plot level. Cover (a), community weighted height (b), branch density (c), twig density (d), aboveground live biomass (e), seed density (f), seedling density (g) for groups of livestock exclusion for 9, 17, and 23 years and corresponding control groups. Error bars indicate standard errors. Different upper-case and lower-case letters represent significant differences among different years of livestock exclusion under control and livestock exclusion treatment at the 0.05 confidence level respectively [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

et al., 2006; Perkins & Owens, 2003). In our study, herb AGB and Shannon diversity significantly reduced after livestock exclusion (Tables S1 and S2, Figure 2f-g), which may result in more vacant niches for shrubs (Dong et al., 2020). Simple linear regression analyses showed that the AGB of functional groups (except sedge) and Shannon diversity of grass were negatively correlated with shrub

characteristics (Tables 2 and S5), indicating that shrub encroachment after livestock exclusion was related to the interactions of herbs and shrubs. Other than plant species competition, shrub encroachment may also be impacted by livestock exclusion through other biotic factors (including small herbivores, insects, and microorganisms; Gomez & Gonzalez-Megias, 2002; Maclean et al., 2011); however, further

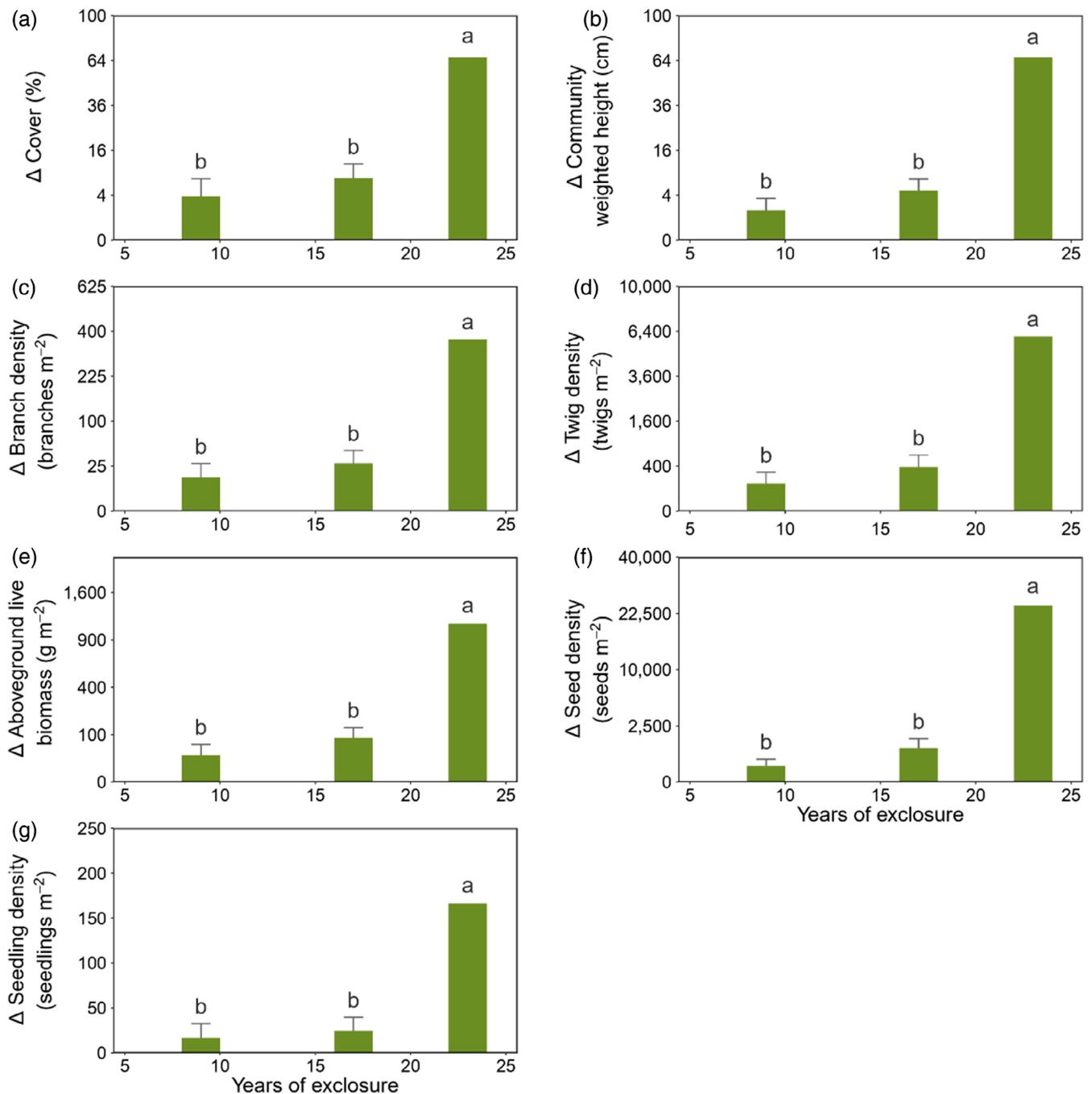


FIGURE 4 Changes in *Potentilla fruticosa* L. growth and reproduction at the plot level. Differences of cover (a), community weighted height (b), branch density (c), twig density (d), aboveground biomass (e), seed density (f), and seedling density (g) between plots of livestock exclusion for 9, 17, and 23 years and corresponding control plots. Error bars indicate standard errors. Different lower-case letters represent significant differences among different years of livestock exclusion at the 0.05 confidence level [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

research is required to clarify the impacts of these other biotic factors on shrub encroachment.

4.1.3 | Improvement in deep soil resources

Our study demonstrated that as the soil in the meadow is fine-textured, after livestock trampling a certain amount of resources were retained in the topsoil, and shallower-rooted herbs dominated the

vegetation (Tables S1 and S3). Once livestock were eliminated, litter accumulation (Table S1, Figure 2b-d) and improvement in soil texture (Veldhuis et al., 2014) would lead to evaporation alleviation and higher contents of soil water and nutrients in the deep soil layers (Table S3, Figure S1; Sun et al., 2021; Wang, Gan, et al., 2018). Our regression analysis of shrubs with soil resources (Table S6) showed that improved resources in the deep soil were beneficial to deeper-rooted *P. fruticosa* (He, 2017), which was supported by the “two-layer hypothesis” and previous studies conducted on the QTP (Dorji

TABLE 2 Results of simple linear regression analyses for shrub cover (%) with biotic and abiotic factors, including the regression coefficient, standard error (SE), R^2 , and p

	Regression coefficient	SE	R^2	p value
Total aboveground biomass (g m^{-2})	0.048	0.004	0.923	<0.001
Herb live aboveground biomass (g m^{-2})	-0.212	0.037	0.731	<0.001
Grass aboveground live biomass (g m^{-2})	-0.295	0.066	0.622	<0.001
Sedge aboveground live biomass (g m^{-2})	-0.053	0.072	0.043	0.475
Legume aboveground live biomass (g m^{-2})	-0.083	0.032	0.365	0.022
No-legume forb aboveground live biomass (g m^{-2})	-0.044	0.022	0.255	0.065
Herb Shannon diversity	1.412	2.339	0.029	0.557
Grass Shannon diversity	-4.969	1.839	0.378	0.019
Sedge Shannon diversity	2.280	2.439	0.068	0.368
Legume Shannon diversity	-2.061	1.646	0.116	0.234
No-legume forb Shannon diversity	1.017	1.703	0.029	0.562
Soil water mean content (%)	6.691	1.594	0.638	0.002
Soil organic carbon mean content (g kg^{-1})	2.396	0.483	0.711	<0.001
Soil total nitrogen mean content (g kg^{-1})	37.846	10.470	0.567	0.005
Soil total phosphorus mean content (g kg^{-1})	-5.007	9.746	0.026	0.619

et al., 2018; Ward et al., 2013). Therefore, shrub encroachment after livestock exclusion may be related to improvement in deep soil resources. A similar mechanism (shrubs expanded with deep soil resources increased) with an opposite result (shrubs expansion was driven by grazing) was observed in an Inner Mongolian typical grassland (Zhang et al., 2017), which may have been due to different soil textures. In the Inner Mongolian grassland with sandy loam soil, heavy grazing further increased sand content, allowing more resources to enter the deep soil and shrubs to subsequently expand (Liu et al., 2021; Su et al., 2005).

Climate is also an important abiotic factor in shrub expansion. Many model simulations, experiments, and paleo-data on the QTP indicate that warming and wetting both generate shrub expansion (Khan et al., 2018; Lu et al., 2019; Wang et al., 2021; Zhao et al., 2021). However, the air temperature and precipitation did not change during our enclosure experiments from 1997 to 2020 at the Haibei Research Station (Figure S2), which would not favor shrubs. Thus, we believe that shrub encroachment in our study was caused only by livestock exclusion. However, our study is still insufficient to appropriately describe the mechanisms behind livestock exclusion-induced shrub encroachment, and the current related researches have mainly inferred those mechanisms without thorough experimental evidence supporting these inferences (Altesor et al., 2006; Alvarez-Martinez et al., 2016). Therefore, further exploration of the mechanisms is needed in the future studies.

4.2 | Implications

This study has several important implications. First, the theory of shrub encroachment causes was supplemented with valuable relative

data. Second, we emphasized that besides exclusion of browsing, livestock exclusion-induced shrub encroachment was related to changes in interspecies interactions and deep soil resources, which should be included in the analyses of the future enclosure experiments. Finally, based on the negative ecological, economic, and cultural consequences of shrub expansion, in particular rangeland quality (Hopping et al., 2018; Stanton Jr et al., 2018; Zhou et al., 2018), and common utilization of livestock exclusion as grassland management in large, degraded areas on the QTP (Lu et al., 2018), alternative methods (such as reseeding) are needed to restore grassland degradation, and livestock exclusion should be used with more caution in the future grassland management.

5 | CONCLUSIONS

In the current study, we examined the shrub features and associated herb and soil qualities in 9, 17, and 23 years of enclosure manipulation trials in the QTP alpine meadow. The results showed that: (1) Livestock exclusion drove shrub encroachment, as evidenced by the three to eight-fold increases in shrub characteristics of growth and reproduction following livestock grazing cessation; (2) There was an increasing trend of shrub encroachment (i.e. an increase in each shrub characteristic) over long time of livestock exclusion; (3) Removal of browsing, shrubs' competitive advantage due to species interactions, and improvements in deep soil resources were all factors that contributed to shrub encroachment. Therefore, livestock exclusion is not usually the best advice for managing grasslands sustainably. More long-term field observations and experiments of shrubs dynamic change and its mechanisms after livestock exclusion in the QTP should be strengthened in the future studies.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding authors upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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