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RESEARCH ARTICLE

The effects of grazing on shrub expansion depend on species' palatability and long-term alterations in propagule banks in an alpine meadow

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Abstract

1. Shrub expansion is commonly observed in grassland ecosystems under climate change. In these systems, palatability is considered an important factor shaping plant community dynamics, particularly under grazing management. However, direct evidence remains limited regarding the effects of grazing and shrub palatability on shrub expansion in alpine meadows, particularly from the perspective of propagule bank dynamics.
2. We conducted a field experiment on the Qinghai–Tibetan Plateau to quantify the direct and indirect impacts of grazing and shrub palatability on the shrub expansion of six dominant shrubs from 2013 to 2021. We quantified shrub palatability and characterized species composition and density of the community's soil seed bank and bud bank.
3. Grazing reduced the shrub expansion rate from 12% to 3% compared to non-grazed plots, largely due to decreased expansion of high-palatable shrub species in grazed plots. Specifically, the annual expansion rates of highly palatable shrubs *Salix rehderiana* and *Dasiphora fruticosa* were −0.99% and −0.33%, respectively, in the grazed plots, but 1.8% and 0.3% in the nongrazed plots. Compared to the highly palatable shrubs, grazing was less effective in controlling the annual expansion rates of medium-palatability shrubs (*Spiraea alpina and Caragana jubata*) and did not affect low-palatability shrubs (*Rhododendron capitatum* and *R. thymifolium*). Grazing significantly increased the soil seed bank densities under the canopy of high-palatable shrubs, but significantly decreased their shrub bud bank densities. The piecewise structural equation models showed that the main factors regulating the shrub expansion rate were shrub palatability and bud bank in grazed plots.

4. *Synthesis and applications*: Effects of grazing on shrub expansion varied with shrub species' palatability and were jointly controlled by long-term alterations in propagule banks in alpine meadows. Grazing intensity at 6.0 Tibetan sheep/ha, which is the current rotational grazing system in the Qinghai–Tibetan Plateau, could not reverse the trend of shrub expansion, but could reduce the rate of shrub expansion. Therefore, it may be beneficial for grassland managers and policymakers to take shrub palatability into account when developing grazing strategies to manage shrub expansion in grassland.

KEYWORDS
alpine meadow, bud bank, grazing management, Qinghai–Tibet Plateau, shrub expansion, shrub palatability, soil seed bank

1 | INTRODUCTION

Shrub expansion is a widespread phenomenon, which is defined as a rapid increase in the height, coverage and biomass of shrubs in grassland ecosystems (Criado et al., 2020; Ding & Eldridge, 2023; Jackson et al., 2002). Many factors contribute to shrub expansion, such as global climate warming, alterations in precipitation patterns, fire management, overgrazing and land use changes (Leipe & Carey, 2021; Nunes et al., 2019). Shrub expansion results in the fragmentation of grassland habitats, increases spatial heterogeneity in vegetation and soil, decreases the proportion of high-quality forage (Abella et al., 2020; Cannone et al., 2022). There has been a gradual increase in the number of studies of shrub expansion in alpine meadows in recent years and the expansion mechanisms and ecological consequences of shrub expansion (Dang et al., 2025; Lara-Romero et al., 2016). However, direct evidence for the effects of grazing on propagule banks and shrub expansion differing in palatability remains limited.

Grazing is the primary method of realizing the economic value of grasslands. Experimental fencing studies have confirmed that mammalian herbivores regulate shrub expansion. Populations of the shrub *Mimosa pigra* increased between 1972 and 2015, coinciding with a period of massive decline and even near extinction of large herbivores, and then declined from 2015 to 2019 as ungulate biomass recovered (Guyton et al., 2020). Browsing behaviour of large herbivores induced the death of mature shrubs, reducing shrub cover and converting these areas to grasslands; heavy grazing might also contribute to this process (Cornelissen et al., 2014). In contrast, some previous studies have shown that grazing does not induce decreases in the height and coverage of most shrub species (e.g. *Artemisia tridentata*and *Eriogonum fasciculatum*) but reduces the coverage and height of herbaceous plants (Grupenhoff & Molinari, 2021). Shrub palatability might explain the inconsistent conclusions among the aforementioned studies. For instance, M*imosa pigra* and *Leucaena leucocephala* are leguminous shrubs with high nutritional value, and *Artemisia tridentata*, *Eriogonum fasciculatum* and *Quercus berberidifolia* are usually unpalatable (very low palatability) to herbivores. Nevertheless, most studies have only examined one or two shrub species and have not compared shrubs varying in palatability, especially under long-term grazing management.

Propagule banks, which include the bud bank and soil seed bank, are potential plant communities, and they provide direct indicators of the direction of vegetation succession (Polo-Avila et al., 2019). Livestock can directly influence shrub population changes through selective eating and indirectly influence shrub expansion rates through the propagule banks. For example, grazing can alter the canopy structure of shrubs and lead to spatial heterogeneity in seed rainfall drop locations and the soil seed bank distribution. Shrubs can intercept wind-borne seeds and store them in the topsoil, which makes seed densities higher (seed islands) in the soil under the shrub canopy than outside the shrub canopy (Leder et al., 2022; Maciel-Najera et al., 2020; Rehm et al., 2023). However, grassland plants are mostly clone species, and they undergo population expansion and community renewal mainly through buds (He et al., 2015; Qian et al., 2023). There is thus a need to measure changes in whole propagule banks to explore the direction of succession of shrub-encroached grassland communities under grazing.

The distribution of propagule banks influences the directional succession of the community and indicates the dynamics of shrub expansion. However, how the expansion rate of shrubs with different palatability responds to long-term grazing, and the relationship between shrub expansion rates and propagule bank dynamics, remains unclear. Thus, we conducted a field experiment in a shrub–grass ecotone on the Qinghai–Tibet Plateau, which is an important area for local herders, with grazing and non-grazing treatments. Here, the palatability and propagule banks of six dominant shrubs (*Salix rehderiana*, *Dasiphora fruticosa*, *Spiraea alpina*, *Caragana jubata*, *Rhododendron capitatum* and *R. thymifolium*), and their changes in coverage from 2013 to 2021, were measured. We aimed to (1) evaluate the palatability of dominant shrubs and describe changes in the propagule bank under 8-year grazing management, (2) compare the expansion rate of shrubs with different palatability in grazed and nongrazed plots and (3) clarify how grazing and shrub palatability interactively regulate shrub expansion rates and the contribution of propagule bank dynamics to shrub expansion rates. We hypothesized that (1) grazing management

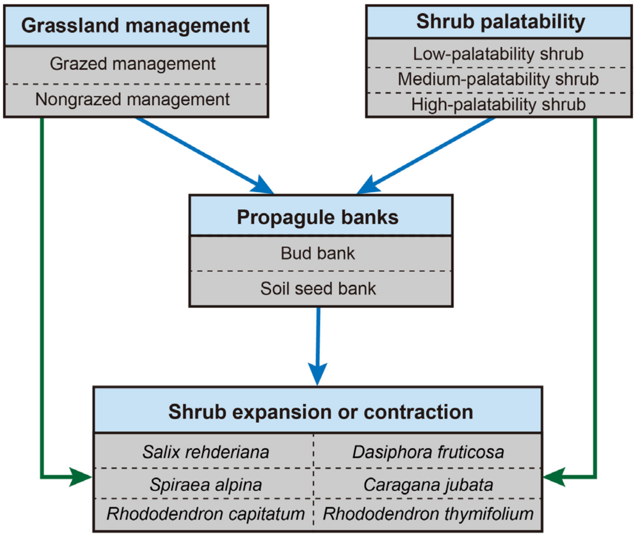

FIGURE 1 Direct effects of grassland management and shrub palatability and indirect effects of propagule banks (soil seed bank and bud bank) on shrub expansion in alpine meadows. Green arrows indicate direct impacts and blue arrows indicate indirect impacts.

and shrub palatability conjointly affect shrub expansion rates; and (2) propagule banks under shrub canopy and in the open areas would be differentially altered by grazing management, which could explain the expansion rates of six shrubs with different shrub palatability (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The experimental site is located in Qilian Mountain National Park on the eastern Qinghai–Tibet Plateau (37°10′12″ N, 102°47′12″ E, 3040.5 m asl), nearing the Tianzhu Alpine Grassland Ecosystem Experimental Station, Gansu Agricultural University. No permission was required for fieldwork. The climate is cold and humid; the annual average temperature is 1.6°C, and the annual average precipitation is 1006.6 mm (Figure S1). Approximately 76% of the precipitation occurs from June to September. The annual plant growth period is approximately 120 days. The main vegetation types in the area are alpine shrubland and alpine grassland. The dominant shrub species include *S. rehderiana*, *D. fruticosa*, *S. alpina*, *C. jubata*, *R. capitatum* and *R. thymifolium*; other shrubs include *S. oritrepha*, *R. anthopogonoides*, *R. przewalskii*, *D. glabra* and *C. stenophylla*. The dominant grasses include *Carex pseuduncinoides*, *C. atrofusca*, *Bistorta vivipara*, *Equisetum arvense* and *Rheum pumilum*; other companion grasses include *Anemone cathayensis*, *Ranunculus tanguticus*, *Argentina anserina*, *Geranium pylzowianum* and *B. macrophylla*.

The experiment was conducted in a uniformly shrubby meadow. Grazed plots and nongrazed plots were established in a randomized design before plants turned green in 2014; there were three replications of each plot type. The area of each plot was 50 m × 100 m, and the total area of the experimental site was approximately 5.0 ha. Each plot is blocked off with a wire fence. Our experiment referred to the main local grassland management (rotational grazing system), that is, grazing was conducted from March to May and from September to November each year. As the principal local grazing livestock in the alpine meadows, three adult Tibetan sheep (6.0 Tibetan sheep/ha) were put in each grazed plot. Given that the livestock-carrying capacity of shrub–grassland is lower than that of purely herbaceous grassland, a grazing intensity of 6.0 Tibetan sheep/ha represents a high level. This is consistent with the local grazing practices and effectively illustrates the impact of grazing on the shrub–grassland community. Therefore, the findings of this study can inform the development of sustainable grazing management strategies.

2.2 | Vegetation survey and shrub palatability analysis

Vegetation surveys were conducted in August from 2013 to 2021. Three 10 m × 10 m squares were randomly set up in each plot, and the density of shrubs was calculated by counting the number of shrub species and individuals in the sample squares. Shrub coverage was determined by a 100-m measuring rope (Method S1, Figure S2). According to the base data of experiment plots, six shrubs, *S. rehderiana*, *D. fruticosa*, *S. alpina*, *C. jubata*, *R. capitatum* and *R. thymifolium*, comprised 92.6% of the total shrub percentage and were present in all the sampling plots. They were thus the dominant shrubs in the study area. Grass species and coverage were determined using 0.5 m × 0.5 m quadrats placed in inter-shrub spaces, mowed flush with the ground and brought grass samples back to the laboratory. The grass samples were dried at 105°C for half an hour and then dried at 60°C until a constant weight was achieved, and the weight was then used to calculate the above-ground biomass of grass.

The palatability of these six shrubs was determined in August 2021 using the standard shrub method (Wang et al., 2021). Specifically, a total of 30 intact, disease-free shrubs (five each of *S. rehderiana*, *D. fruticosa*, *S. alpina*, *C. jubata*, *R. capitatum* and *R. thymifolium*) were selected from each sample plot as standard individuals in the grazed plots and nongrazed plots. Well-grown branches of the same diameter were sampled from standard shrubs and used as standard branches, with five standard branches from each shrub species per plot. A total of 15 standard branches were collected for each shrub species, and the leaves on the standard branches were counted and collected. Shrub leaves and grass samples from the same plot were mixed into one sample each, then biomass and nutrient composition and content within dry matter, crude protein, ether extract, crude fibre, crude ash, nitrogen-free extract, acid detergent fibre and neutral detergent fibre were measured. Shrub leaves' biomass is conducted in the same way as the grass above-ground biomass. Nutrient indexes of plant samples were determined following the method of Bao et al. (2000). Finally, the grazing residual index (GRI) was used to determine the palatability of shrubs and grass.

2.3 | Community propagule bank

2.3.1 | Soil seed bank sampling and seed tray maintenance

Soil samples were collected in April 2021, before seed germination to capture transient and persistent seed banks; soil samples were collected in July 2021 to characterize persistent seed banks. The 0–10 cm cylindrical soil cores (5 cm diameter) were collected in four directions under the canopy of standard shrubs and mixed into one soil sample; five 0–10 cm cylindrical soil cores (5 cm diameter) were collected in open areas of each sample plot. Stone, roots, and other debris were removed from all soil seed bank samples, air-dried, and then sieved through 0.5, 1.0 and 2.0 mm sieves to measure the proportion of seed banks with different sizes in soil. The heterogeneous fall of mature plant seeds to the ground is called seed rain (Garcia-Rodriguez et al., 2022; Rehm et al., 2023). Seed rain constitutes the primary input for the soil seed bank, with its temporal patterns and spatial distribution being key factors influencing the bank's composition and density. To capture this seed rain, we deployed a total of 240 seed traps across the study plots. The sampling design consisted of placing 30 traps under standard shrub canopies and 10 traps in adjacent open areas within each plot. Comprehensive details regarding the seed rain collection, along with the seed composition and density, are provided in the Supporting Information (Methods S2).

To examine the species density and composition of the soil seed bank, seed germination experiments were conducted in the plant growth room. We identified and counted seedlings of the sampled species from the soil seed bank. Each tray (15 cm diameter) was uniformly covered with a layer of sand that was 15 cm thick, which had been sterilized at 140°C for 24 h (An et al., 2020; Ma et al., 2020). Each soil sample was then spread evenly on the sand to a thickness of approximately 1 cm and watered twice a day to maintain soil moisture; the temperature was maintained at 20°C (Li, 2015). Germination was recorded daily, and seedling species were identified and counted. Seedlings were removed from the tray after they were identified to avoid seedling competition (An et al., 2022; Ma et al., 2023). If no seedlings emerged over 1 month, the germination experiment ceased. The soil in the trays was carefully examined and washed, and no seeds were detected.

2.3.2 | Shrub bud bank and grass bud bank

For shrub buds, shrub bud-bank densities were calculated based on the number of buds on standard shrubs and shrub densities in the grazed plots and nongrazed plots. For grass bud measurements, 25 cm (length) × 25 cm (width) × 10 cm (depth) of soil in its original state was collected under shrubs and in the inter-shrub space, and the soil was completely excavated along with the above-ground plant (Ferraro et al., 2022; Liu et al., 2022). First, the plants were separated from the soil and washed with water. Next, each plant in the samples was carefully examined and identified to species. Subterranean buds on each plant were identified using a magnifying glass, and the numbers of buds were recorded. Finally, the bud density of each plant was determined, and the bud composition (including tiller buds, rhizome buds, crown buds and root-sprouting buds) was determined based on the location of the buds.

2.4 | Statistical analysis

Before the analyses, all data were tested for normality and homogeneity of variances using SPSS version 20 software. Results showed that our data met the normality and homoscedasticity requirements of analysis of variance (ANOVA). Then, one-way ANOVA, followed by the Turkey test, was conducted to show the effects of grazing on shrub leaf properties (e.g. crude ash, nitrogen free extract), shrub expansion indexes (e.g. shrub coverage) and propagule banks. The formulas for the shrub annual expansion rate, relative feeding value and species similarity between the vegetation, seed rain, soil seed bank and bud bank were included in the Supporting Information (Method S3). To further explore the underlying mechanisms of the shrub expansion rate in the response of shrub palatability and propagule banks, piecewise structural equation modelling (piecewiseSEM) was employed to evaluate the direct and indirect effects and its relative importance (Lefcheck, 2016). A priori model was constructed, in which shrub palatability, bud bank, seed rain, soil seed bank and shrub expansion rate were simultaneously accounted. We need to acknowledge that our models in this study do not incorporate certain important environmental factors, such as global climate warming and alterations in precipitation patterns, which may also influence shrub expansion dynamics under grazing. This simplification was necessary to reduce complexity and to provide a focused investigation into the direct and indirect effects of the main factors under study—namely, palatability, bud bank, seed rain and soil seed bank. Consequently, this approach enables a clearer examination of the core mechanisms behind shrub expansion. Furthermore, no significant trends in warming or precipitation regimes were observed over the 8-year duration of the experiment (Figure S1), a period likely insufficient to capture long-term climatic shifts. First, composite variables for bud banks, seeds and soil seed banks were constructed based on species diversity and density, respectively, and then incorporated into a structural equation model (SEM). We used a piecewiseSEM to account for sampling point random effects, providing 'marginal' and 'conditional' contributions of variables. We constructed composite variables for bud banks, seed rain, and soil seed banks based on species richness and density, respectively, and then included in SEM. We used piecewiseSEM model to account for random effects of sampling point, providing 'conditional' and 'marginal' contributions (R_m^2 and R_c^2) of variables (Tian et al., 2021). These analyses were conducted using 'nlme', 'lme4' and 'piecewiseSEM' packages in R. In the SEMs, palatability was represented by the inverse of the residuals of foliage. Akaike information criterion (AIC), Fisher *C* and *p*-values were used to determine whether the model fits the data adequately. If the model did not fit the data adequately, further correction of the model path was required (Lefcheck, 2016).

3 | RESULTS

3.1 | Shrub palatability and shrub annual expansion rate

Grazing significantly reduced the quantity of residue in standardized branches of *S. rehderiana*, *D. fruticosa*, *S. alpina* and *C. jubata* by 11.1%, 16.5%, 18.4% and 38.5%, respectively, in nongrazed plots, with corresponding biomass of residue decreasing by 6.3%, 15.8%, 42.1% and 44.9% (Table 1). Palatability of six shrubs was defined according to calculated grazing residual index (GRI values), which is the mean value of the quantity of residue and biomass of residue. The calculated grazing residual index demonstrated distinct palatability gradients: *S. rehderiana* (grazing residual index) and *D. fruticosa* were classified as high-palatability shrubs, while *S. alpina* and *C. jubata* were classified as medium-palatability shrubs. Shrubs of *R. capitatum* and *R. thymifolium* were classified as low-palatability shrubs (Table 1). Nutrient composition also showed that higher palatability shrubs generally contained higher crude protein contents and relative feeding values, or vice versa for lower palatability shrubs (Tables S1 and S2).

While both grazed and nongrazed systems exhibited progressive increases in total shrub coverage based on data spanning eight annual growth cycles, the cumulative increasing effect of grazing was lower than that of the nongrazed treatment. Specifically, shrub coverage in grazed plots in 2021 only increased 3.0% as compared with that in 2013, while shrub coverage in nongrazed plots in 2021 increased by 12.3% (Figure 2a). The annual expansion rates of the high-palatable shrubs *S. rehderiana* and *D. fruticose* in grazed plots

TABLE 1 Palatability of dominant shrubs and grasses in alpine meadows.

	Leaf numbers		Leaf biomass (g)					
Parameter	Grazed plots	Nongrazed plots	Grazed plots	Nongrazed plots	QR (%)	BR (%)	GRI (%)	Palatability
S. rehderiana	28.0 ± 19.8b	253.3 ± 54.4a	0.2 ± 0.1b	3.8 ± 0.6a	11.1	6.3	8.7	High
D. fruticosa	34.5 ± 9.1b	209.1 ± 53.7a	0.3 ± 0.1b	1.8 ± 0.4a	16.5	15.8	16.2	High
S. alpina	406.2 ± 158.8b	2185.5 ± 546.9a	2.5 ± 0.7b	5.9 ± 2.2a	18.4	42.1	30.2	Medium
C. jubata	77.2 ± 28.1b	200.8 ± 51.3a	4.5 ± 1.5b	10.0 ± 2.5a	38.5	44.9	41.7	Medium
R. capitatum	477.0 ± 81.9a	462.5 ± 54.1a	6.7 ± 1.3a	7.1 ± 1.0a	103.1	93.8	98.5	Low
R. thymifolium	1597.4 ± 239.8a	1589.9 ± 273.7a	5.5 ± 0.6a	5.7 ± 0.6a	100.5	96.8	98.6	Low
Grass	—	—	24.7 ± 10.2a	145.8 ± 38.2b	—	16.9	16.9	High

Note: Quantity of residue (QR) and biomass of residue (BR) indicate the quantity and biomass of leaf residue after grazing, respectively. Palatability was quantified using the grazing residual index (GRI) with formulas being included in the Supporting Information (mean value of QR and BR). Lowercase letters indicate significant differences ($p < 0.05$) between grazed plots and nongrazed plots.

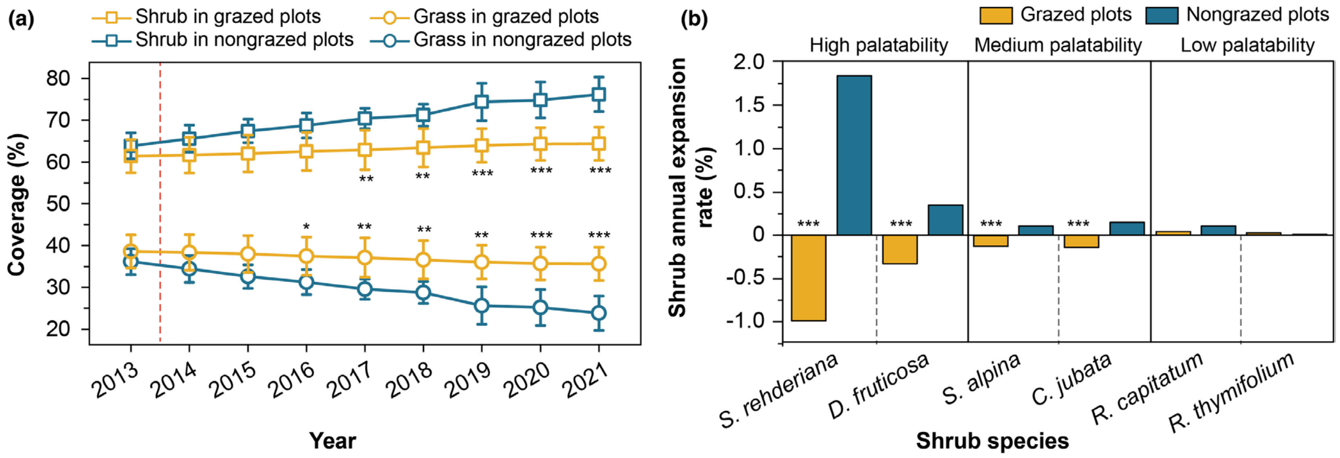

FIGURE 2 Shrub and grass coverage (a) and the shrub annual expansion rate (b) in grazed and nongrazed plots from 2013 to 2021. The red dotted line in panel A indicates when the fence was established. One-way ANOVA was conducted between grazed and nongrazed plots, and asterisks indicate significant differences at $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

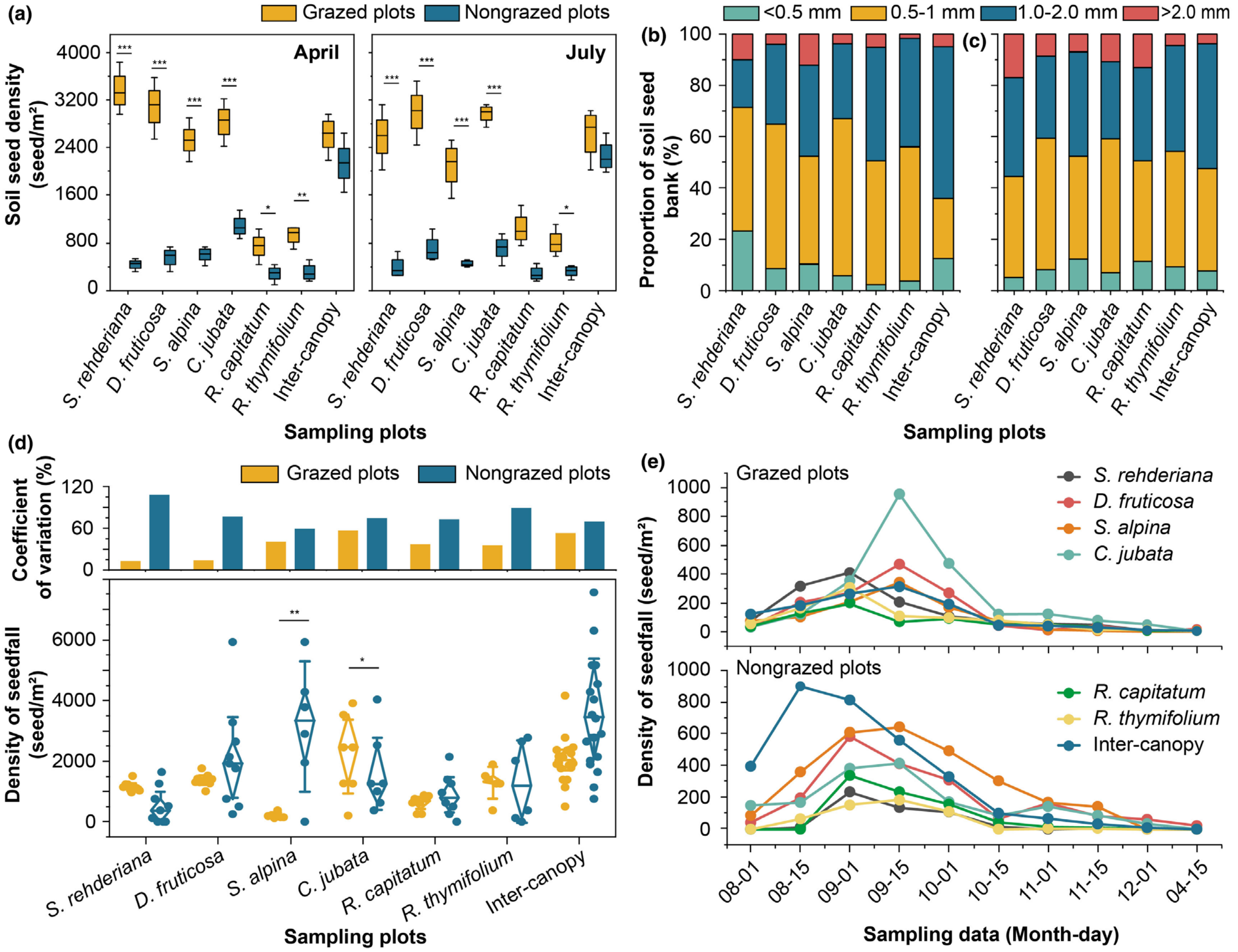

FIGURE 3 Distributions and densities of seed rain and soil seed bank under different shrub canopies. Seeds derive from both shrub and grass species. Panel (a) shows soil seed density in April (transient and persistent seed bank) and July (persistent seed bank) under the canopy of plants varying in palatability. Panels (b and c) show the proportion of plant seeds of different grain sizes in the soil of the grazed and nongrazed plots, respectively. Panel (d) shows the seedfall density of different palatable plants and the coefficients of variation for the inter-canopy and sub-canopy areas in 2021. Panel (e) shows the time of plant seedfall, and the dates on the horizontal axis are the times when traps were harvested. Asterisks indicate significant differences, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

were −0.99% and −0.33%, respectively, while those were 1.84% and 0.35% in nongrazed plots, respectively. Grazing significantly reduced the annual expansion rate of *S. rehderiana*, *D. fruticosa*, *S. alpina* and *C. jubata*, but had no significant effect on the low-palatable shrub *R. capitatum* and *R. thymifolium* (Figure 2b).

3.2 | Effects of grazing on the propagule bank

Grazed and nongrazed management resulted in differences in densities of soil seedfall and seed bank under shrub canopies and open areas (Figure 3). A total of 63 species belonging to 18 families were identified in the soil seed bank samples, with high species richness observed in the Gramineae and Fabaceae families (Figure S3). In April, under the canopies of *S. rehderiana*, *D. fruticosa*, *S. alpina* and *C. jubata*, soil seed bank densities were significantly higher in grazed samples compared to nongrazed plots, whereas the opposite pattern was observed for the two rhododendron shrubs. Furthermore, the densities of soil seed banks were 28.63% (*S. rehderiana*), 18.03% (*D. fruticosa*) and 8.67% (*C. jubata*) significantly higher in the under-canopy region than in open areas, and the soil seed valley effect was observed in soil samples in the under-canopy region of low-palatability shrubs. Changes in soil seed banks in July were characterized similarly to April. Approximately 84.6% (grazed plots) and 82.3% (nongrazed plots) of the soil seeds were found in the 0.5–2.0 mm size range. Grazing decreased the proportion of large seeds (>2.0 mm) in the soil under the canopy of highly palatable plants (Figure 3b,c). The seedfall density was significantly higher under *C. jubata* canopies and significantly lower under *S. alpina* canopies in grazed plots than in nongrazed plots (Figure 3d). Seedfall density in the shrub inter-canopy region in nongrazed plots peaked from August 1 to 15; seedfall density

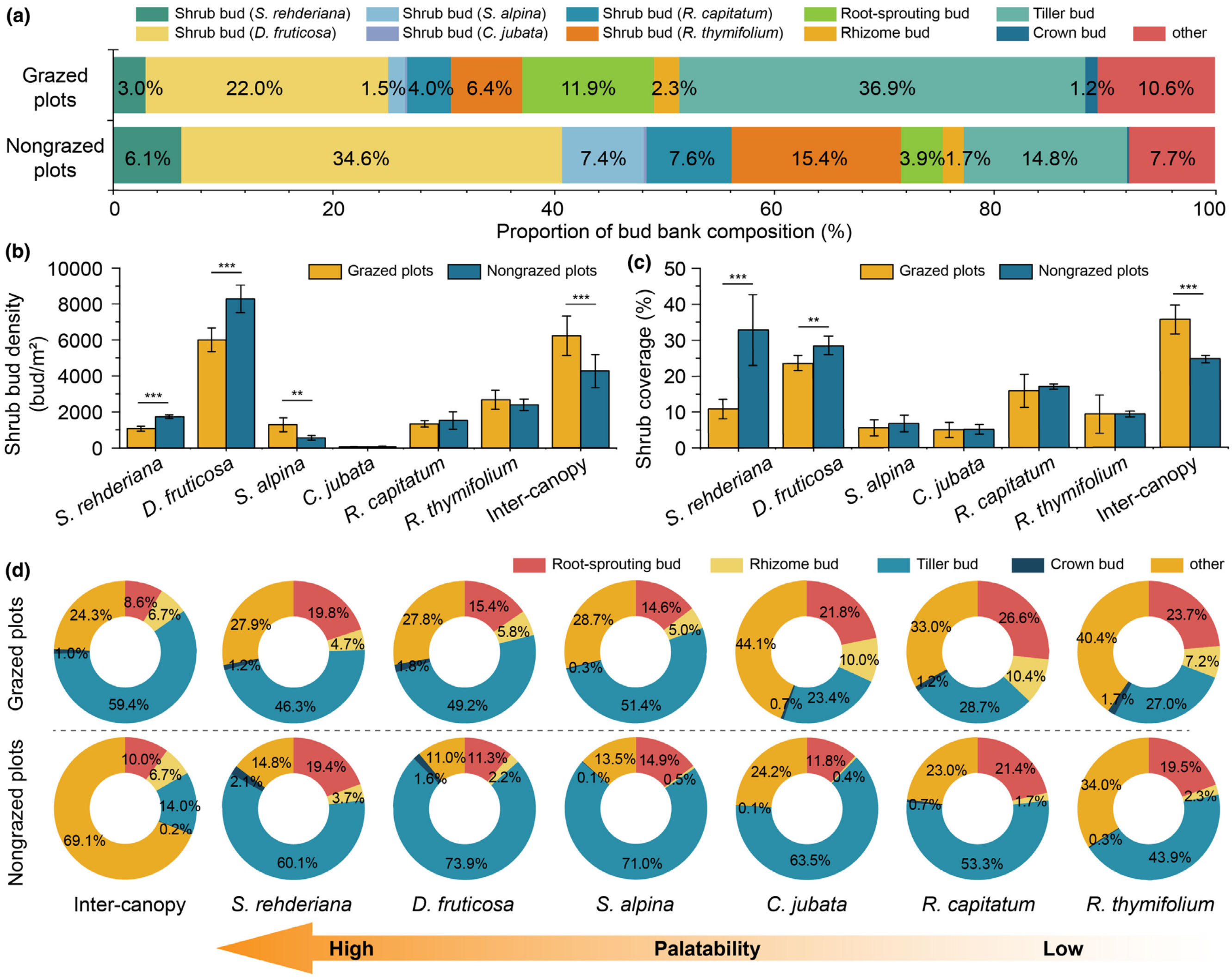

FIGURE 4 The composition (shrub buds and grass buds) and density of the bud bank in grazed plots (GPs) and nongrazed plots (NPs). Panel (a) shows the compositional ratio of the community bud bank, disaggregated into shrub species (*S. rehderiana*, *D. fruticosa*, *S. alpina*, *C. jubata*, *R. capitatum* and *R. thymifolium*) and grass bud types (root-sprouting, rhizome, tiller, crown, and others). The numerical labels indicate each category's proportion of the total bud count. Panel (b) shows the density of the bud bank from different shrub species. Panel (c) describes the coverage of different shrub species in GPs and NPs. Panel (d) demonstrates how grazing management influences bud bank composition beneath shrubs of different palatability. The numerical labels on the rings show the proportional contribution of each bud category to the total under-shrub bud bank. Asterisks indicate significant differences between grazed and nongrazed plots, *$p<0.05$, **$p<0.01$, ***$p<0.001$.

under the canopy in nongrazed plots peaked from September 1 to 15 (Figure 3e). Species with high seed-drop density were *B. vivipara*, *B. macrophylla* and *C. alatauensis* (Figure S4). 20.5% of the seeds dropped before August 15 in the grazed plots compared with 12.6% in the nongrazed plots, suggesting that the timing of seed drop was advanced by grazing.

Shrub bud banks accounted for 37.1% of the total bud bank in grazed plots and 71.5% of the total bud bank in nongrazed plots. The size of the shrub bud bank was greatest for *D. fruticosa*, followed by *R. thymifolium*, *R. capitatum*, *S. alpina*, *S. rehderiana* and *C. jubata* (Figure 4a). Shrub bud densities of *S. rehderiana* and *D. fruticosa* were 5.7% and 27.5% significantly lower in grazed plots than in nongrazed plots, respectively (Figure 4b). Shrub bud density varied with shrub coverage, and the density of highly palatable shrubs was significantly lower in grazed plots than in nongrazed plots (Figure 4c). The amount of grass bud banks was significantly higher in the grazed plots than in the nongrazed plot. Grazing increased the proportion of herbaceous tiller buds, rhizome buds, and other types of buds (mainly propagules of *B. vivipara*) under the canopies of palatable shrubs (Figure 4d). Grazing significantly increased the complexity of the shrub branching, where 8th-level branches were the highest observed in grazed plots, compared to 6th-level branches in nongrazed plots (Figure S5). Buds mainly grow on the 3rd- and 4th-level branches of shrubs (Figure S6). The Sørensen similarity index (SSI) between the vegetation and bud bank was high in both grazed plots and nongrazed plots, and the SSI between the vegetation and soil seed bank was low (Table S3). The SSI between vegetation and the soil seed bank was high under high-palatability shrubs and low

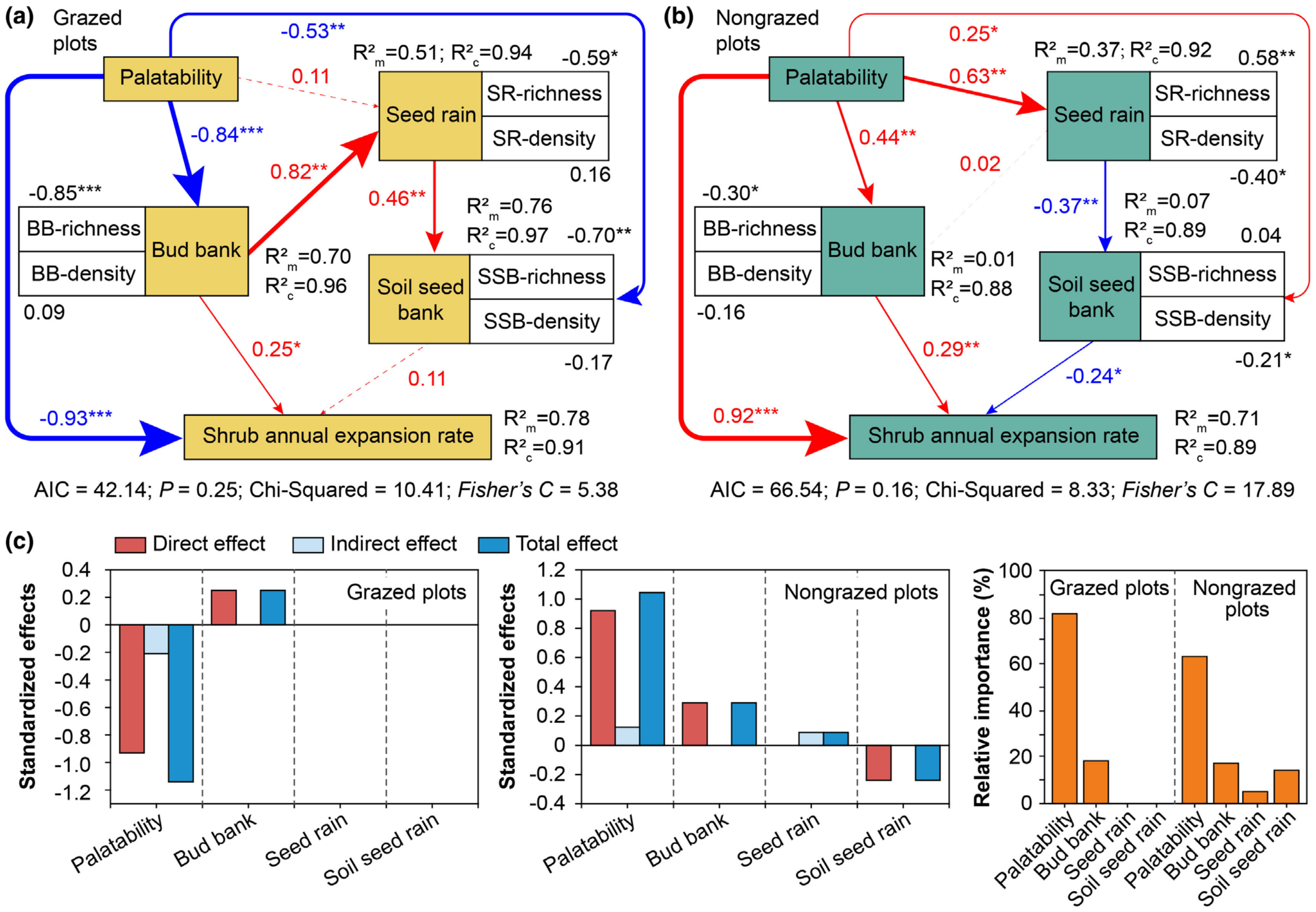

FIGURE 5 Pathways through which palatability and propagule banks influence shrub expansion rate. Piecewise structural equation modelling (piecewiseSEM) was used to quantify the direct and indirect effects of palatability, bud bank (BB), seed rain (SR) and soil seed bank (SSB) on shrub expansion rates in both grazed (a) and nongrazed (b) plots. The bud bank, seed rain and soil seed bank were incorporated as composite variables. Numerical values adjacent to observed variables represent their loadings onto the corresponding composite variables. Path diagrams use red lines to indicate positive effects and blue lines to indicate negative effects. Solid lines denote significant pathways, while dashed lines represent nonsignificant relationships; the thickness of each line corresponds to the magnitude of the effect. Numbers alongside arrows are standardized path coefficients, reflecting the direct effect size of each relationship. Panel (c) presents the standardized direct, indirect and total effects of palatability and propagule banks on shrub expansion rates, along with their relative importance in grazed and nongrazed plots. Nonsignificant paths have been omitted. The total standardized effects of composite variables are shown, and R^2_m and R^2_c indicate the marginal and conditional coefficients of determination, representing the proportion of variance explained by fixed effects alone and by both fixed and random effects (i.e. sampling point), respectively. Relationships among residual terms of measured predictors are not displayed. Significance levels are indicated as follows: $*p<0.05$, $**p<0.01$, $***p<0.001$.

under low-palatability shrubs. The SSI of vegetation, seed rain, and the soil seed bank was significantly reduced by grazing exclusion under palatable shrubs, and the effect was small under unpalatable shrubs (Table S3).

3.3 | Relationships between shrub palatability, the propagule bank and shrub annual expansion rate

The piecewiseSEM was employed to further elucidate the direct and indirect pathways through which regulatory factors mediate the effects of grazing on shrub expansion rates. As shown in Figure 5, after accounting for the random effects of 'sampling point', shrub palatability, bud bank, seed rain and soil seed bank collectively explained a large proportion of the variance in shrub expansion rates in both grazed (0.91) and nongrazed (0.89) plots. The results demonstrate that palatability consistently played a significant role in regulating shrub expansion, both directly and indirectly—by modifying the bud bank, seed rain and soil seed bank. Grazing altered the direct effect of palatability on shrub expansion, with standardized path estimates of −0.93 in grazed plots and 0.92 in nongrazed plots (Figure 5a,b). Compared to nongrazed plots, grazing significantly increased the relative importance of palatability (62.86% in grazed plots vs. 82.01% in nongrazed plots) and the bud bank (17.47% in grazed plots vs. 17.99% in nongrazed plots) in driving shrub expansion, while substantially reducing the contributions of seed rain and soil seed bank (Figure 5c). Therefore, the main factors regulating shrub expansion rates in grazed plots were shrub palatability and the bud bank, whereas in nongrazed plots, expansion was co-driven by palatability, bud bank, soil seed bank and seed rain.

4 | DISCUSSION

4.1 | Shrub palatability and its conjoint effects with grazing on shrub expansion

Consistent with our first hypothesis, we found that the effects of grazing on shrub expansion vary with shrub palatability. The shrub expansion rates decrease with increasing shrub palatability under grazing management. The overall average yearly expansion rates were 1.5% in nongrazed plots and 0.4% in grazed plots, and the average yearly expansion rates of the highly palatable shrub species were below zero in grazed plots. These results indicated that shrub palatability is important in controlling shrub expansion. The plant palatability index is generally based on observations of herbivore feeding, which is a direct method for assessing selective plant feeding by livestock (Freeland & Janzen, 1974). In this study, we identified the shrub palatability mainly using the grazing residual index (GRI) of standardized branches, and further combined the nutrient composition of shrub leaves. In grazing systems, shrubs with different palatability generally contain different nutrient contents and have different defensive strategies (Smit et al., 2010). For instance, the slower growth rates of *R. capitatum* and *R. thymifolium* might put them at a disadvantage compared with deciduous shrubs (e.g. *D. fruticosa*, *S. alpina*, *C. jubata* and *R. capitatum*), but they have a high concentration of secondary compounds to combat herbivores (Christie et al., 2015). The shrub *C. jubata* belongs to Leguminosae and is rich in nutrients, but individual plants are covered with long, hard spines that prevent herbivory.

It is easy to understand that the effects of grazing management and shrub palatability on shrub expansion rates were conjoint because the effects of shrub palatability work on livestock. In contrast to our results, Gomez-Garcia et al. (2023) found that grazing is not effective in reversing the progress of shrub expansion in Mediterranean mountain grasslands. They reported that the average yearly expansion rates of the dominant shrubs *Cytisus oromediterraneus*, *Erinacea anthyllis*, *Juniperus alpina* and *Juniperus sabina* were 0.69%, −0.25%, 0.35% and 0.52% in grazed areas, respectively. These inconsistencies might stem from differences in the locations of these studies and the shrub species. Shrub expansion rates are lower in alpine regions than in arid and semi-arid regions. Rates of shrub cover change were 1.8 times lower in tundra than in savanna (Criado et al., 2020), and rates of shrub cover increase were 1.7 times lower in tundra compared with savanna; shrubs in the north can expand at an annual rate of up to 5.8% (Leipe & Carey, 2021). The direct effect was associated with the foraging activities of livestock, which led to direct decreases in high-palatability shrub species. However, the expansion rate remained high regardless of the grazing treatment for low-palatability shrub species. The results support the findings of Ding and Eldridge (2023), showing that there is a strong relationship between shrub expansion and plant traits, such as plant height, root type, deciduous versus evergreen habit, allelopathic properties and palatability. Although shrubs tended to encroach after grazing by Tibetan sheep, the rate of expansion was significantly reduced, especially the expansion of high-palatability shrubs, and low-palatability shrubs continued to expand. The timely removal of low-palatability shrubs could provide an effective solution. However, how the grazing strategy (including livestock species, grazing intensity and grazing time) should be modified to control the expansion of shrubs varying in palatability requires further study.

4.2 | Alterations in the propagule bank could explain shrub expansion under grazing in the long run

In support of our second hypothesis, we found that grazing tends to alter the size of the propagule bank, and the effects differed between the under-canopy and inter-canopy regions. The effects of grazing varied among shrub species and were related to shrub palatability. Specifically, the decrease in propagule banks in grazed plots might be related to the duration of seedfall. We found that the seedfall time was more concentrated in grazed plots than in nongrazed plots, and the seedfall period was longer in nongrazed plots. In addition, grazing decreased the proportion of small seeds (size <0.5 mm) under *D. fruticose* canopy, which indicates that less time and energy were available for the production of seeds for plants in grazed plots compared with nongrazed plots. This pattern was consistent with observations of seed development in short-lived plants (Aguirrebengoa et al., 2021). Second, the density of the soil persistent seed bank was significantly lower under canopies of *R. capitatum* and *R. thymifolium* than in the inter-canopy region in grazed plots. This stems from their low palatability. Tibetan sheep seldom forage or avoid feeding on rhododendron shrubs, and the shading effect results in small soil seed-bank densities where herbaceous plants cannot survive; this explains why rhododendron shrubs have been able to expand steadily (Atkins et al., 2018; Malfasi & Cannone, 2020). Finally, the distributions of transient and persistent seed banks differed under shrub canopies regardless of grazing management. This resulted in earlier seed drop in nongrazed plots than in grazed plots in this study. In July, the soil seed bank primarily comprised persistent seeds, and the density of the soil seed bank of *D. fruticosa* and *C. jubata* was higher than that in the inter-canopy region; in April, the soil seed bank was the sum of the transient and persistent seed bank (An et al., 2022; Thompson & Grime, 1979) and the soil seed bank was greater under canopies of *S. rehderiana*, *D. fruticosa*, *S. alpina* and *C. jubata* than outside the canopies of these shrubs. This stemmed from the fact that *S. rehderiana* and *S. alpina* had greater nurse effects, and more seeds formed in under-canopy grass; alternatively, seeds were intercepted at a greater rate in under-canopy grass (An et al., 2022).

Our results suggest that shrub expansion in alpine meadows is affected more strongly by the bud bank than by the soil seed bank in grazed plots. Previous studies have shown that the foraging activities of livestock promote the sprouting of shrub buds, which directly leads to an increase in the density of the bud bank (Dalgleish et al., 2012; Fidelis et al., 2014). However, grazing reduced the proportion of all shrub bud banks in community bud banks. This might stem from the high grazing intensity; 6 Tibetan sheep/ha is a high grazing intensity in shrub grassland ecosystems. The fast-expanding shrubs *S. rehderiana* and *D. fruticosa* continue to expand mainly via buds; *S. rehderiana* grows mainly through above-ground buds, and goldenrod has above-ground buds and underground rhizome buds, which occur in fertile soil over long distances and are not consumed by Tibetan sheep. Grazing also alters the relationships among seed rain, the bud bank, and the soil seed bank, and the effect of the bud bank on the shrub expansion rate is greater than that of seed rain and the soil seed bank; this is supported by the high values of the relative importance of bud richness and the SSI between vegetation and the bud bank. The soil seed distribution is mainly related to seed dispersal (Erfanzadah et al., 2022). Seedfall density was higher in the inter-canopy region in nongrazed plots, and the presence of shrubs increased the heterogeneity of seed rain dispersal. The low similarity index in this study indicates that the soil seed bank contributes little to the recovery of vegetation in the shrub–grass ecotone in nongrazed plots (Malfasi & Cannone, 2020). Short-term grazing exclusion did not affect alpine grassland vegetation succession and soil seed bank species composition (Huang et al., 2022). In contrast to nongrazed plots, the lower proportion of shrub buds than that of herbaceous plants in grazed plots was the main reason for the rapid expansion of shrubs in nongrazed plots. This pattern differs from the results of previous studies of arid habitats (Erfanzadah et al., 2022; Shi et al., 2022).

5 | CONCLUSION

We investigated the effects of grazing and shrub palatability on shrub expansion based on an eight-year field experiment on the Qinghai–Tibet Plateau and explained these changes through the propagule bank. We concluded that the effects of grazing on shrub expansion depended on shrub palatability and long-term alterations in propagule banks by characterizing the palatability of six dominant shrubs and investigating the dynamics of seed rain, buds and soil seed banks. We found that the current rotational grazing system (a grazing intensity of 6.0 Tibetan sheep/ha) can control the rate of expansion of high- and medium-palatable shrubs (*S. rehderiana*, *D. fruticosa*, *S. alpina* and *C. jubata*), but not that of low-palatable shrubs (*R. capitatum* and *R. thymifolium*). The piecewiseSEM results revealed that the main factors regulating the shrub annual expansion rate were shrub palatability and bud bank under Tibetan sheep grazing, rather than soil seed bank. Therefore, clarifying changes in shrub palatability and the propagule bank under grazing conditions is key to characterizing the expansion rate of different shrub species and addressing whether grazing can effectively control shrub expansion in alpine meadow ecosystems.

AUTHOR CONTRIBUTIONS

Shilin Wang, Wenxia Cao and Guoxiang Niu designed the study. Shilin Wang, Jinlan Wang and Wen Li performed the field measurements, while Jinlan Wang and Shilin Wang performed the laboratory measurements. Shilin Wang performed statistical analysis and made the figures. Shilin Wang and Guoxiang Niu drafted the manuscript; Guoxiang Niu, Ruzhen Wang and Jianhui Huang revised the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.30330058 (Wang et al., 2025).

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REFERENCES

Abella, S. R., Menard, K. S., Schetter, T. A., Sprow, L. A., & Jaeger, J. F. (2020). Rapid and transient changes during 20 years of restoration management in savanna-woodland-prairie habitats threatened by woody plant encroachment. *Plant Ecology*, *221*, 1201–1217. https://doi.org/10.1007/s11258-020-01075-4

Aguirrebengoa, M., Müller, C., & González-Megías, A. (2021). Pre-dispersal seed predators boost seed production in a short-lived plant. *Oecologia*, *195*, 971–982. https://doi.org/10.1007/s00442-021-04885-z

An, H., Baskin, C. C., & Ma, M. J. (2022). Nonlinear response of the soil seed bank and its role in plant community regeneration with increased grazing disturbance. *Journal of Applied Ecology*, *59*, 2593–2603. https://doi.org/10.1111/1365-2664.14259

An, H., Zhao, Y. P., & Ma, M. J. (2020). Precipitation controls seed bank size and its role in alpine meadow community regeneration with increasing altitude. *Global Change Biology*, *26*, 5767–5777. https://doi.org/10.1111/gcb.15260

Atkins, J. W., Epstein, H. E., & Welsch, D. L. (2018). Using Landsat imagery to map understory shrub expansion relative to landscape position in a mid-Appalachian watershed. *Ecosphere*, *9*, e02404. https://doi.org/10.1002/ecs2.2404

Bao, S., Jiang, R., Yang, C., Xu, G., & Han, X. (2000). *Soil chemical analysis of agriculture* (3rd ed.). Chinese Agriculture Press.

Cannone, N., Guglielmin, M., Casiraghi, C., & Malfasi, F. (2022). Salix shrub encroachment along a 1000 m elevation gradient triggers a major ecosystem change in the European Alps. *Ecography*, *2022*, e06007. https://doi.org/10.1111/ecog.06007

Christie, K. S., Bryant, J. P., Gough, L., Ravolainen, V. T., Ruess, R. W., & Tape, K. D. (2015). The role of vertebrate herbivores in regulating shrub expansion in the arctic: A synthesis. *Bioscience*, *65*, 1123–1133. https://doi.org/10.1093/biosci/biv137

Cornelissen, P., Gresnigt, M. C., Vermeulen, R. A., Bokdam, J., & Smit, R. (2014). Transition of a *Sambucus nigra* L. dominated woody vegetation into grassland by a multi-species herbivore assemblage. *Journal for Nature Conservation*, *22*, 84–92. https://doi.org/10.1016/j.jnc.2013.09.004

Criado, M. G., Myers-Smith, I. H., Bjorkman, A. D., Lehmann, C. E. R., & Stevens, N. (2020). Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Global Ecology and Biogeography*, *29*, 925–943. https://doi.org/10.1111/geb.13072

Dalgleish, H. J., Ott, J. P., Setshogo, M. P., & Hartnett, D. C. (2012). Interspecific variation in bud banks and flowering effort among semi-arid African savanna grasses. *South African Journal of Botany*, *83*, 127–133. https://doi.org/10.1016/j.sajb.2012.08.010

Dang, Y., Zhang, P., Jiang, P., Ke, J., Xiao, Y., Zhu, Y., Liu, M., Li, M., Wu, J., Liu, J., Tian, B., & Liu, X. (2025). Temperature-dependent variations in under-canopy herbaceous foliar diseases following shrub encroachment in grasslands. *Nature Communications*, *16*, 1131. https://doi.org/10.1038/s41467-025-56439-z

Ding, J., & Eldridge, D. (2023). The success of woody plant removal depends on encroachment stage and plant traits. *Nature Plants*, *9*, 58–67. https://doi.org/10.1038/s41477-022-01307-7

Erfanzadah, R., Barzegaran, F., Amoli, S. S., & Petillon, J. (2022). The effect of shrub community on understory soil seed bank with and without livestock grazing. *Community Ecology*, *23*, 75–85. https://doi.org/10.1007/s42974-021-00074-3

Ferraro, A., Silva, G. S., Martins, A. R., Piedade, S. M. D., Fidelis, A., & Appezzato-da-Gloria, B. (2022). Seasonality affects the below-ground bud bank dynamics of the Cerrado. *Journal of Vegetation Science*, *33*, e13165. https://doi.org/10.1111/jvs.13165

Fidelis, A., Appezzato-da-Glória, B., Pillar, V. D., & Pfadenhauer, J. (2014). Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands? *Flora*, *209*, 110–116. https://doi.org/10.1016/j.flora.2013.12.003

Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals: The role of plant secondary compounds. *American Naturalist*, *108*, 269–289. https://doi.org/10.1086/282907

Garcia-Rodriguez, A., Albrecht, J., Farwig, N., Frydryszak, D., Parres, A., Schabo, D. G., & Selva, N. (2022). Functional complementarity of seed dispersal services provided by birds and mammals in an alpine ecosystem. *Journal of Ecology*, *110*, 232–247. https://doi.org/10.1111/1365-2745.13799

Gomez-Garcia, D., de Juana, A. J. A., Sanchez, R. J., & Magallon, C. M. (2023). Shrub encroachment in Mediterranean mountain grasslands: Rate and consequences on plant diversity and forage availability. *Journal of Vegetation Science*, *34*, e13174. https://doi.org/10.1111/jvs.13174

Grupenhoff, A., & Molinari, N. (2021). Plant community response to fuel break construction and goat grazing in a southern California shrubland. *Fire Ecology*, *17*, 28. https://doi.org/10.1186/s42408-021-00114-3

Guyton, J. A., Pansu, J., Hutchinson, M. C., Kartzinel, T. R., Potter, A. B., Coverdale, T. C., Daskin, J. H., da Conceição, A. G., Peel, M. J. S., Stalmans, M. E., & Pringle, R. M. (2020). Trophic rewilding revives biotic resistance to shrub invasion. *Nature Ecology & Evolution*, *4*, 712–724. https://doi.org/10.1038/s41559-019-1068-y

He, Y., D'Odorico, P., & De Wekker, S. F. J. (2015). The role of vegetation–microclimate feedback in promoting shrub encroachment in the northern Chihuahuan desert. *Global Change Biology*, *21*, 2141–2154. https://doi.org/10.1111/gcb.12856

Huang, M., Sang, C., Zhao, J. X., Degen, A. A., Chen, X. P., Zhang, T., Zhao, J., Chen, X., Bai, Y., Li, S., Wang, W., Shrestha, N., & Shang, Z. (2022). Grazing exclusion altered the pattern of the soil seed bank but not the aboveground vegetation along an altitudinal gradient in alpine grassland. *Land Degradation & Development*, *33*, 3901–3913. https://doi.org/10.1002/ldr.4432

Jackson, R. B., Banner, J. L., Jobbágy, E. G., Pockman, W. T., & Wall, D. H. (2002). Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, *418*, 623–626. https://doi.org/10.1038/nature00910

Lara-Romero, C., García, C., Morente-López, J., & Iriondo, J. M. (2016). Direct and indirect effects of shrub encroachment on alpine grasslands mediated by plant–flower visitor interactions. *Functional Ecology*, *30*, 1521–1530.

Leder, C. V., Calvo, D. A., & Peter, G. (2022). Seed rain and soil seed bank compensatory roles on *Nassella tenuis* (Phil.) Barkworth seedling recruitment in ungrazed and grazed sites. *Journal of Arid Land*, *14*, 550–560. https://doi.org/10.1007/s40333-022-0015-y

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. https://doi.org/10.1111/2041-210x.12512

Leipe, S. C., & Carey, S. K. (2021). Rapid shrub expansion in a subarctic mountain basin revealed by repeat airborne LiDAR. *Environmental Research Communications*, *3*, 071001. https://doi.org/10.1088/2515-7620/ac0e0c

Li, C. M. (2015). *Study on soil seed bank and seed rain of alpine meadow in eastern Qilian Mountains*. Science Press.

Liu, W., Cao, W., Wang, W., Wang, X., Wang, S., Deng, X., Li, W., & Shi, S. (2022). Characteristics of underground bud bank and community persistence in alpine degraded gramineous mixed sowing grassland. *Acta Agrestia Sinica*, *30*, 1773–1780. https://doi.org/10.11733/j.issn.1007-0435.2022.07.019

Ma, M. J., Baskin, C. C., Zhao, Y. P., & An, H. (2023). Light controls alpine meadow community assembly during succession by affecting species recruitment from the seed bank. *Ecological Applications*, *33*, e2782. https://doi.org/10.1002/eap.2782

Ma, M. J., Collins, S. L., & Du, G. Z. (2020). Direct and indirect effects of temperature and precipitation on alpine seed banks in the Tibetan Plateau. *Ecological Applications*, *30*, e02096. https://doi.org/10.1002/eap.2096

Maciel-Najera, J. F., Hernandez-Velasco, J., Gonzalez-Elizondo, M. S., Hernandez-Diaz, J. C., Lopez-Sanchez, C. A., Antunez, P., Bailón-Soto, C. E., & Wehenkel, C. (2020). Unexpected spatial patterns of natural regeneration in typical uneven-aged mixed pine-oak forests in the Sierra Madre Occidental, Mexico. *Global Ecology and Conservation*, *23*, e01074. https://doi.org/10.1016/j.gecco.2020.e01074

Malfasi, F., & Cannone, N. (2020). Climate warming persistence triggered tree ingression after shrub encroachment in a high alpine tundra. *Ecosystems*, *23*, 1657–1675. https://doi.org/10.1007/s10021-020-00495-7

Nunes, A., Kobel, M., Pinho, P., Matos, P., Costantini, E. A. C., Soares, C., de Bello, F., Correia, O., & Branquinho, C. (2019). Local topographic and edaphic factors largely predict shrub encroachment in Mediterranean drylands. *Science of the Total Environment*, *657*, 310–318. https://doi.org/10.1016/j.scitotenv.2018.11.475

Polo-Avila, A., Infante-Izquierdo, M. D., Soto, J. M., Hermoso-López, V., Nieva, F. J. J., Castillo, J. M., & Muñoz-Rodríguez, A. F. (2019). Contrasting propagule dispersal and halophyte seed banks along the intertidal gradient. *Marine Ecology Progress Series*, *616*, 51–65. https://doi.org/10.3354/meps12943

Qian, J. Q., Zhang, Z. M., Dong, Y. W., Ma, Q., Yu, Q., Zhu, J. L., Zuo, X. A., Broderick, C. M., Collins, S. L., Han, X. G., & Luo, W. T. (2023). Responses of bud banks and shoot density to experimental drought along an aridity gradient in temperate grasslands. *Functional Ecology*, *37*, 1211–1220. https://doi.org/10.1111/1365-2435.14301

Rehm, E. M., D'Antonio, C., & Yelenik, S. (2023). Crossing the threshold: Invasive grasses inhibit forest restoration on Hawaiian islands. *Ecological Applications*, *33*, e2841. https://doi.org/10.1002/eap.2841

Shi, Y. F., Shi, S. H., Huang, X. M., Jiang, Y. S., Liu, J., Zhao, Y., & Zhang, Z. S. (2022). A global meta-analysis of grazing effects on soil seed banks. *Land Degradation & Development*, *33*, 1892–1900. https://doi.org/10.1002/ldr.4271

Smit, C., Bakker, E. S., Apol, M. E. F., & Olff, H. (2010). Effects of cattle and rabbit grazing on clonal expansion of spiny shrubs in wood-pastures. *Basic and Applied Ecology*, *11*, 685–692. https://doi.org/10.1016/j.baae.2010.08.010

Thompson, K., & Grime, J. P. (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, *67*, 893–921. https://doi.org/10.2307/2259220

Tian, P., Liu, S., Zhao, X., Sun, Z., Yao, X., Niu, S., Crowther, T. W., & Wang, Q. (2021). Past climate conditions predict the influence of nitrogen enrichment on the temperature sensitivity of soil respiration. *Communications Earth & Environment*, *2*, 251. https://doi.org/10.1038/s43247-021-00324-2

Wang, J. L., Li, W., Cao, W. X., Abalori, T. A., Liu, Y. Z., Xin, Y. Q., Wang, S. L., & Zhang, D. G. (2021). Soil bacterial community responses to short-term grazing exclusion in a degraded alpine shrubland-grassland ecotone. *Ecological Indicators*, *130*, 108043. https://doi.org/10.1016/j.ecolind.2021.108043

Wang, S., Cao, W., Wang, R., Wang, J., Li, W., Huang, J., & Niu, G. (2025). Data from: The effects of grazing on shrub expansion depend on species palatability and long-term alterations in propagule banks in an alpine meadow. *Figshare Digital Repository*. https://doi.org/10.6084/m9.figshare.30330058

SUPPORTING INFORMATION

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

Method S1 Shrub coverage measurements using a 100-m rope.

Method S2. Seed rain measurements using traps.

Method S3. Formulas.

Table S1. Nutrient composition and relative feeding value (RFV) of the shrub leaves. DM, dry matter; CP, crude protein; EE, ether extract; CF, crude fibre; CA, crude ash; NFE, nitrogen-free extract; ADF, acid detergent fibre; NDF, neutral detergent fibre. A one-way ANOVA was conducted among the different species, and different lowercase letters indicate significant differences between shrubs.

Table S2. Nutrient composition and relative feeding value (RFV) of grasses with different functional groups in grazed and nongrazed plots. DM, dry matter; CP, crude protein; EE, ether extract; CF, crude fibre; CA, crude ash; NFE, nitrogen free extract; ADF, acid detergent fibre; NDF, neutral detergent fibre. A one-way ANOVA was conducted among the different species, and different lowercase letters indicate significant differences between shrubs.

Table S3. The Sørensen similarity index of vegetation and the propagule bank. A one-way ANOVA was conducted between grazed and nongrazed plots, and bolded numbers indicate significant differences.

Figure S1. The annual mean precipitation and temperature from 2013 to 2021; The cyan bar represents the annual average precipitation, and the red line indicates the annual average temperature. The red dash line indicates the annual mean temperature (1.6°C) from 2013 to 2021, and the cyan dash line indicates the annual mean precipitation (1006.6 mm) from 2013 to 2021. Climate data were sourced from the meteorological station in the experimental site.

Figure S2. Measurements of shrub coverage. The diagram shows a top view of the sample plot, with different coloured circles indicating canopies of different shrubs and white circles indicating bare patches. Scaled line segments indicate 100 meters of measuring rope.

Figure S3. Species richness of soil seed samples in grazed plots and nongrazed plots.

Figure S4. Density and species richness of seed rain samples in grazed plots and nongrazed plots. Different coloured bars indicate plant functional groups (Gramineae, Cyperaceae, Fabaceae and forbs).

Figure S5. Number of branches of standard shrubs in nongrazed plots (A) and grazed plots (B).

Figure S6. Number of buds on branches in different levels in nongrazed plots (A) and grazed plots (B).

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