

RESEARCH ARTICLE

Functional Ecology



Livestock grazing regulates ecosystem multifunctionality in semi-arid grassland

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Abstract

1. Livestock grazing has been shown to alter the structure and functions of grassland ecosystems. It is well acknowledged that grazing pressure is one of the strongest drivers of ecosystem-level effects of grazing, but few studies have assessed how grazing pressure impacts grassland biodiversity and ecosystem multifunctionality (EMF).
2. Here, we assessed how different metrics of biodiversity (i.e., plants and soil microbes) and EMF responded to seven different grazing treatments based on an 11-year field experiment in semi-arid Inner Mongolian steppe.
3. We found that soil organic carbon, plant-available nitrogen and plant functional diversity all decreased even at low grazing pressure, while above-ground primary production and bacterial abundance decreased only at high levels of grazing pressure.
4. Structural equation models revealed that EMF was driven by direct effects of grazing, rather than the effects of grazing on plant or microbial community composition. Grazing effects on plant functional diversity and soil microbial abundance did have moderate effects on EMF, while plant richness did not.
5. *Synthesis.* Our results showed ecosystem functions differ in their sensitivity to grazing pressure, requiring a low grazing threshold to achieve multiple goals in the Eurasian steppe.

KEYWORDS

functional diversity, grazing pressure, semi-arid grassland, soil microbes, species richness, threshold

1 | INTRODUCTION

Across the planet, grasslands are the most common land cover type. These ecosystems support over 2.5 billion people, most of whom

directly rely on ecosystem services for survival and livelihood (Briske, 2017; Evans, Gill, Eviner, & Bailey, 2017; MEA 2005; Reynolds et al., 2007). However, grasslands are one of the most vulnerable ecosystems, facing degradation of plant diversity, soils and ecosystem

services (MEA 2005; Teague & Barnes, 2017). Development of sustainable grazing systems that promote ecosystem resilience, enhance or maintain plant diversity, increase soil health and maintain ecosystem multifunctionality (EMF) and delivery of multiple ecosystem services is a global concern (MEA 2005; Sala, Yahdjian, Havstad, & Aguiar, 2017; Teague & Barnes, 2017). Balancing these multiple objectives can be challenging because trade-offs are common across multiple grassland management goals (Briske, Derner, Milchunas, & Tate, 2011; Jing et al., 2015; Maestre et al., 2012; MEA 2005). For example, many ecosystem services are linked with plant diversity, yet management for other ecosystem services may reduce plant diversity (e.g., maximizing productivity by promoting dominant plant species) (Bullock, Aronson, Newton, Pywell, & Rey-Benayas, 2011). Adding to this complexity, ecological impacts of grazing can be highly variable, depending on interactions between grazing management practices and environmental conditions (Briske et al., 2011). This complexity makes it difficult to set prescriptions for livestock grazing practices.

Of all aspects of grazing practices, livestock stocking density has the strongest ecosystem-level impacts (Briske et al., 2011). However, best management practices tend to focus on a subset of ecosystem characteristics. For example, moderate grazing pressure maximizes plant productivity in semi-arid Eurasian steppe grasslands (Li, Xu, Zheng, Taube, & Bai, 2017; Liu, Kan, Yang, & Zhang, 2015), and improves plant diversity in relatively productive grasslands, but reduces plant diversity in less productive grasslands (Huston, 1979; Kondoh & Williams, 2001). Understanding the effects of herbivore density, or grazing pressure, on the ability of an ecosystem to deliver multiple functions (hereafter Ecosystem Multifunctionality, EMF) is critical to determine sustainable grazing practices and the delivery of multiple ecosystem services (Schonbach et al., 2011; Stein, Harpole, & Suding, 2016).

Approximately 45% of variation in EMF is explained through combined effects of above- and below-ground biodiversity (Jing et al., 2015). Thus, the development of best management practices requires improving our understanding of the influence of herbivory on plant and microbial communities and their effects on multiple ecosystem processes (Bardgett & Wardle, 2003; Evans et al., 2017; Harrison & Bardgett, 2010; Liu et al., 2018; Sitters & Venterink, 2015). Herbivory can strongly affect plant community structure and function (Diaz et al., 2007; Stein et al., 2016), through the direct effects of herbivores on plants, and grazing-induced changes in soil nutrients and fungal communities (Chen, Christensen, Nan, & Hou, 2017). Lack of grazing can decrease species diversity because of competitive exclusion and light limitation (Borer et al., 2014). These changes in plant community composition can lead to large shifts in soil microbial communities and processes (Stein et al., 2016; Wilson, Strickland, Hutchings, Bianchi, & Flory, 2018). Grazing-induced changes in plant functional traits can be particularly important in understanding ecosystem multifunctionality. High grazing pressure has been shown to reduce functional diversity (FD) (Baert, De Laender, Sabbe, & Janssen, 2016; Gross, Suding, Lavorel, & Roumet, 2007; Gross et al., 2014; Li et al., 2017). Relatively high FD may benefit an

ecosystem by enhancing plant community complementarity in resource acquisition and utilization and promoting community resilience and resistance. Diverse plant communities and community FD are strongly related to multiple ecosystem functions (Forrestel et al., 2017; Petchey & Gaston, 2002), and high FD can maintain high EMF and ecosystem resilience (Valencia et al., 2015).

Soil biota are direct mediators of carbon, nitrogen and phosphorus cycles, and are therefore important drivers of plant diversity and ecosystem productivity (Wurzburger & Brookshire, 2017). Soil biota are strongly affected by herbivore grazing (Barto & Rillig, 2010; Chen, Zheng, Shan, Taube, & Bai, 2013; Eldridge et al., 2017; Liu et al., 2015) through multiple pathways, including changes in plant community composition, soil nutrients, moisture and compaction. In addition, carbon allocation to roots and root exudates, directly alter the abundance of arbuscular mycorrhizal (AM) fungi and other soil organisms (Van der Heyde, Bennett, Pither, & Hart, 2017).

While there is still considerable debate on the ecosystem-level effects of specific grazing practices (e.g., rotational vs. continuous grazing), it is well documented that livestock stocking density (grazing pressure) has strong impacts on all aspects of the ecosystem. However, the ideal grazing pressure for any given system is largely unresolved (Briske, 2017). Understanding the effects of grazing pressure on EMF is critical to determine sustainable grazing practices (Schonbach et al., 2011; Stein et al., 2016). Here, we examined how plant species richness, plant FD (including five functional traits: plant species height, specific leaf area, leaf dry matter content, leaf nitrogen content and stem:leaf ratio), soil microbes, grazing pressure and soil factors (soil moisture and pH) influenced EMF. In our study, we utilized EMF to summarize five key ecosystem functions and related variables: (a) above-ground biomass, (b) plant nitrogen (nitrogen pools in above-ground biomass), (c) plant-available nitrogen, (d) plant-available phosphorus and (e) soil organic carbon. Our experiment investigated the following: (a) the effects of grazing pressure on EMF (e.g., does moderate grazing pressure maintain or improve EMF, according to the intermediate disturbance hypothesis? (Hanke et al., 2014)); and (b) the extent that grazing directly alters EMF vs. indirectly affects EMF through changes in plant and microbial communities.

2 | MATERIALS AND METHODS

2.1 | Site description

Our study area is located in Inner Mongolia steppe (Bai, Han, Wu, Chen, & Li, 2004), ranging in elevation from 1,200 to 1,280 m, with a mean annual precipitation of 346.1 mm falling mainly in the growing season from May to September, and with a mean annual temperature of 0.3°C, with the lowest mean monthly temperatures ranging from −21.6°C in January to the highest 19.0°C in July. The study area has a history of long-term grazing at moderate to heavy grazing pressure, but livestock was excluded from this area 2 years prior to the start of the experiment in 2005. Each year, sheep are in the field from June to September (~95 days), in

accordance with the local summer grazing season. Soil is classified as Calcic Chernozem according to ISSS Working Group RB, 1998. Approximately 36 vascular plant species typically occur in these grasslands (eight of them are very rare), grouped by functional characteristics: perennial rhizomatous grasses, perennial bunchgrasses, perennial forbs and annual/biennial grasses (Sasaki et al., 2009; Wu et al., 2015). The dominant perennial rhizomatous grass *Leymus chinensis* and the perennial bunchgrass *Stipa grandis* together account for approximately 75% of total above-ground biomass production (Li et al., 2017).

2.2 | Grazing treatments

Our project was designed to assess the impacts of grazing at temporal and spatial scales that are both relevant to management and that can capture ecosystem- and landscape-scale effects of grazing. There has been strong support for this approach, emphasizing that small-scale plots (a) often yield different results than ecosystem-scale plots, (b) do not address heterogeneity in grazing/disturbance/management across the landscape and (c) are impossible to scale-up to inform management decisions (Carpenter, 1996; Fraterrigo & Rusak, 2008; Schindler, 1998; Schmitz, 2005). These ecosystem-scale studies require large land areas, and high levels of logistics tend to be expensive, and thus, there is limited ability to replicate large-scale experimental plots. In fact, reviews of such large-scale experiments suggest that because of the difficulty of replication, if multiple large-scale plots are feasible, it is more valuable to include additional treatments, rather than replicating the same treatment (Schindler, 1998). Strong statistical inferences can be drawn by focusing on a regression-based experimental design, in which multiple levels of a treatment are applied (with or without replication). This regression approach is more powerful statistically than replicated ANOVA-based designs, and allows for research that is more relevant to both management and predictive ecology, by assessing how the effects of the treatment vary with level of the treatment (Cottingham, Lennon, & Brown, 2005). This regression approach is particularly effective for a broad array of management-scale questions, ranging from effects of grazing to effects of precipitation change (Beier et al., 2012; Bransby, Conrad, Dicks, & Drane, 1988).

Following a regression-based design, in April 2005, a grazing experiment covering 160 ha was established and maintained for 11 years (Schonbach et al., 2011). The grazing manipulations occurred at two site types (flat or sloped), with each site type containing seven plots that were randomly assigned to seven grazing pressures (GP) (GP = 0, 1.5, 3.0, 4.5, 6.0, 7.5 or 9.0 sheep/ha). These two site types have similar response to grazing treatments (Supporting Information Figure S5a,b) and thus were pooled in the statistical analyses.

Our study utilized non-lactating female sheep with an average live weight of 35 kg. The plots were ~2 ha in size, except for the lowest grazing pressure (1.5 sheep/ha), which was ~4 ha to ensure at least six sheep per plot. There was no significant difference between plots in either plant species composition or relative abundance of

plant species before initiation of our study, but species composition and community structure did change in response to grazing treatments (see Li et al., 2017).

2.3 | Plant and soil sampling

All plant and soil measures were collected at the end of the 2015 growing season, a year with higher annual precipitation and temperature than average. Higher precipitation is likely linked with higher species diversity. Samples were collected from nine randomly placed 1-m² quadrats within each treatment plot.

2.3.1 | Plant sampling

In these plots, we assessed plant species composition (% cover) and richness (number of plant species). Table 1 contains a list of all vascular plant species identified. To measure biomass throughout the growing season, we established three exclosure cages (2 × 3 m) in each plot before sheep began grazing. From June through September, above-ground biomass was clipped in a 1-m² quadrat from both inside and outside of each exclosure. After each monthly clipping, exclosures were moved. Annual above-ground net primary productivity (ANPP) inside (i) and outside (o) exclosures in grazed plots was calculated with the formula: $ANPP = W1o + (W2i - W1o) + (W3i - W2o) + (W4i - W3o)$. Where W_i represents standing plant biomass at the start of each month (1 = June, 2 = July, 3 = August and 4 = September). The biomass is presented on a dry weight basis. We determined plant tissue N concentration using the Kjeldahl method (Kjelttec 8100 Analyser Unit, FOSS, Sweden).

2.3.2 | Soil sampling

Soil samples (diameter of 3 cm, depth of 10 cm) were collected at the end of the 2015 growing season from nine randomly placed locations in each plot. Subsamples for soil organic carbon and plant-available phosphorus and nitrogen analyses were air-dried, sieved through a 2 mm mesh and ground to a fine powder. Subsamples were also separated for soil moisture, soil pH and soil microbial analyses (AM extra-radical hyphae, saprophytic fungi and bacteria). Soil bulk density at 0–10 cm depth was measured using a cutting ring (volume of 100 cm³).

2.4 | Soil properties determination

Plant-available P was measured by the Olsen method. Soil organic C was analysed by the dry combustion method (Multi N/C 2100, Analytik Jena, Germany). Plant-available N was also measured by Multi N/C 2100, from extractions with 50 ml of 2 M K₂SO₄ from 10 g fresh field soil. To determine soil moisture content, twenty grams of fresh soil was weighed before and after oven-drying at 105°C for 24 hr. Ten grams of field soil was mixed with 25 ml of 1 M KCl solution to measure pH using a pH meter (PB-10, Sartorius, Germany). Extra-radical hyphal length densities of AM fungi were

TABLE 1 Relative abundance (RA) of all plant species at low and high grazing pressure in the Inner Mongolia steppe grassland (lowest grazing level (non-zero)/highest grazing level $\pm$ SEM). Nomenclature follows the editorial committee of Chinese plant records

Dominant species		Common species	
Latin name	RA (%)	Latin name	RA (%)
<i>Leymus chinensis</i>	(39.25/27.38 $\pm$ 3.58)*	<i>Cleistogenes squarrosa</i>	(10.51/7.32 $\pm$ 1.51)**
<i>Carex korshinskyi</i>	(38.89/36.16 $\pm$ 2.75)	<i>Agropyron cristatum</i>	(3.53/5.00 $\pm$ 1.30)
<i>Stipa grandis</i>	(27.58/12.96 $\pm$ 1.72)**	<i>Achnatherum sibiricum</i>	(2.77/0.14 $\pm$ 0.65)***
Rare species			
Latin name	RA (%)		
<i>Koeleria macrantha</i>	(0.94/0.00 $\pm$ 0.37)***	<i>Potentilla bifurca</i>	(0.08/0.00 $\pm$ 0.07)**
<i>Allium condensatum</i>	(0.04/0.00 $\pm$ 0.02)**	<i>Allium senescens</i>	(0.04/0.00 $\pm$ 0.02)*
<i>Phlomis umbrosa</i>	(0.04/0.00 $\pm$ 0.02)**	<i>Potentilla verticillaris</i>	(0.01/0.00 $\pm$ 0.02)
<i>Adenophora stenanthina</i>	(0.01/0.00 $\pm$ 0.01)	<i>Adenophora gmelinii</i>	(0.01/0.00 $\pm$ 0.01)
<i>Allium tenuissimum</i>	(0.03/0.00 $\pm$ 0.01)*	<i>Poa annua</i>	(0.04/0.00 $\pm$ 0.01)*
<i>Allium anisopodium</i>	(0.02/0.00 $\pm$ 0.01)*	<i>Kochia prostrata</i>	(0.01/0.00 $\pm$ 0.01)
<i>Allium ramosum</i>	(0.01/0.00 $\pm$ 0.01)	<i>Iris tenuifolia</i>	(0.01/0.00 $\pm$ 0.01)
<i>Thalictrum petaloideum</i>	(0.57/0.02 $\pm$ 0.26)**	<i>Potentilla acaulis</i>	(0.05/0.05 $\pm$ 0.02)
<i>Dontostemon micranthus</i>	(0.02/0.02 $\pm$ 0.01)	<i>Axyris amaranthoides</i>	(0.01/0.01 $\pm$ 0.01)
<i>Chenopodium glaucum</i>	(0.01/0.01 $\pm$ 0.01)	<i>Serratula centauroides</i>	(0.01/0.01 $\pm$ 0.01)
<i>Artemisia scoparia</i>	(0.00/0.01 $\pm$ 0.01)	<i>Salsola collina</i>	(0.01/0.04 $\pm$ 0.02)*

Note. *Means: $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $p < 0.001$.

extracted from soil using the membrane filter technique and the gridline intercept method under a microscope at 200 $\times$ magnification (Jakobsen, Abbott, & Robson, 1992). The biomass of soil bacteria and saprophytic fungi was calculated using phospholipid fatty acid (PLFA) analysis. Qualitative and quantitative fatty acid analyses were performed using an Agilent 6890 gas chromatograph (Agilent Technologies, USA) and Sherlock software (MIDI, USA). The PLFA biomarkers a15:0, i15:0, i16:0, 16:1x7, i17:0, a17:0, 17:0, cy17:0 and cy19:0 were selected to represent soil bacteria, and 18:2 ω 6c was selected to represent saprophytic fungi (Moore-Kucera & Dick, 2008).

2.5 | Quantifying functional diversity

To test grazing effects on plant functional traits, we coupled our species composition data with quantitative values for species functional traits. Functional trait data were collected from thirty plants per species, grown in non-grazed plots. We focused on five functional plant trait responses: plant species height (SH), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC) and stem:leaf ratio. These traits were chosen because they link to plant nutrient acquisition and utilization, below-ground interactions with soil microbes and fauna, and because they tend to be indicators of plant sensitivity to grazing. Plants with low SLA and high LNC are negatively affected by intense grazing pressures (Garnier et al., 2004; Li et al., 2017). To allow for comparison across traits that vary in units and magnitudes, we standardized

plant trait values by transforming them with $\log_{10}(x + 1)$. We then averaged values by species and used averages in calculations of functional diversity.

There are several ways to calculate plant functional diversity. While some, such as the community-weighted mean, focus on single traits, we opted for Mason functional diversity index, which is an integrated measure of all assessed plant functional traits at the community level (Lavorel et al., 2008; Valencia et al., 2015). The Mason functional diversity index can represent overall community-level trait values by accounting for the abundance of each species in each plot (Mason, MacGillivray, Steel, & Wilson, 2003; Mori, Osono, Cornelissen, Craine, & Uchida, 2017).

FD α represents Mason functional diversity index:

$$FD\alpha = \sum_{i=1}^S P_i(x_i - \bar{x}) \quad (1)$$

x_i represents the mean trait value of species i , and $\bar{x} = \sum_{i=1}^S P_i x_i$ represents the mean trait value of whole plant community. P_i represents the relative abundance of species i in the whole plant community, and S represents the number of species in the whole community (Mason, Mouillot, Lee, & Wilson, 2005; Mason et al., 2003).

2.6 | Quantifying ecosystem multifunctionality

EMF index is used as an integrated measure of a system's ability to sustain multiple functions simultaneously. Variables that we included in our calculation of EMF are as follows: (a) plant above-ground biomass, (b) plant tissue nitrogen content, (c) plant-available

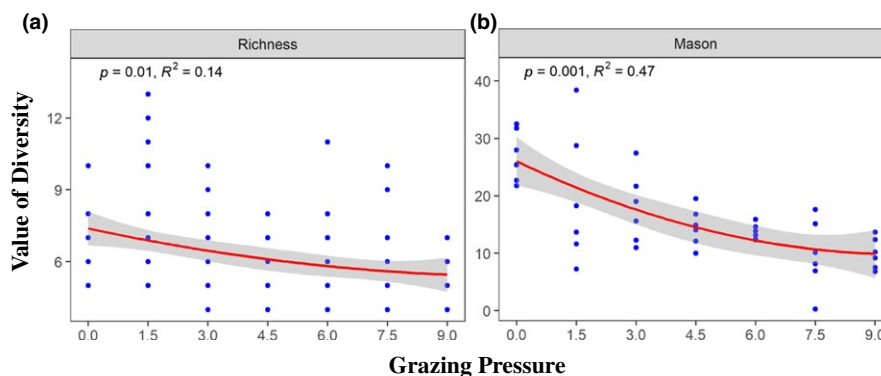


FIGURE 1 Relationship between grazing pressure (number of sheep/ha) and (a) plant species richness or (b) plant functional diversity (Mason functional diversity index). Data have been log-transformed. Red lines are fitted lines from OLS regressions. Shaded areas show 95% CI of the fit

nitrogen, (d) plant-available phosphorus and (e) soil organic carbon. All of these variables are crucial drivers of ecosystem functioning (Delgado-Baquerizo, Powell, et al., 2017; Delgado-Baquerizo, Trivedi, et al., 2017; Jing et al., 2015), as well as key factors for plant and soil health. Several methods can be used to calculate EMF, each with merits and faults. Here, we used a common method, “averaging approach (EMF index),” to calculate ecosystem multifunctionality (Hooper & Vitousek, 1998; Maestre et al., 2012). The “averaging approach (EMF index)” assesses the average effect of diversity across a suite of functions, with values of functions standardized. Because it averages, it cannot distinguish between one function being provided at a high level and another being provided at a low level vs. two functions being provided at an intermediate level (Byrnes et al., 2014). Thus, we have supplemented this averaging approach with a threshold analysis approach. Threshold analysis specifies how many functions are provided above 50% of the maximum provision. Together, these give a sense of the extent that diversity influences the average provisioning of ecosystem functions and the number of functions provided at a high level.

To calculate EMF, we standardized EMF values ranging from 0 to 1 ($f(x) = (x - \min(x)) / (\max(x) - \min(x))$), providing a unifying dimension across multiple functions (Gamfeldt & Roger, 2017).

$$EMF^{\alpha} = \left(\sum_{i=1}^F g(r_i(f_i)) \right) / F \quad (2)$$

EMF^{α} represents ecosystem multifunctionality index, f_i represents the value of function i , r_i represents mathematical function for transforming the f_i value into a positive value, g represents the standardizing of all values, and F represents the number of measured functions.

2.7 | Statistical analysis

All statistical analyses were performed using SAS Version 9.1 (SAS Institute Inc., Cary, NC, USA) and R version 3.3.1 (R Development Core Team, 2013). For all analyses, data were $\log_{10}(x + 1)$ -transformed to ensure normality and homogeneity, as confirmed by the Shapiro-Wilk test. Two replicates per grazing level (slope vs. flat areas) were

averaged and used in analyses. Ordinary least squares (OLS) regressions were used to assess how grazing pressure correlated with plant functional diversity and each ecosystem function. Adjusted R^2 and small sample size-corrected Akaike information criterion (AIC) were used to assess goodness-of-fit for different regression models.

Structural equation modelling (SEM) allows testing of multiple separate linear models together into a single causal network, evaluating complex causality between variables by translating the hypothesized causal relationships into a pattern of expected statistical relationships in the data (Jing et al., 2015). We used this SEM approach to analyse the relative importance of grazing pressure, soil microbial abundance, plant species richness and functional diversity, and their interactions on EMF. In our model, we assumed grazing pressure had effects on EMF directly or indirectly by affecting soil microbial abundance, plant species richness and functional diversity. The standardized coefficient for each path from each model component is shown (Figure 5). The inclusion of these variables in SEM requires us to first test the bivariate relationships between all variables with simple linear regressions to ensure that linear models were appropriate and then constructed a priori model based on the known effects and potential relationships. The chi-square test and its associated p -value were used to adjust the model (good fit when $0 \leq \chi^2 \leq 2$ and $0.05 < p \leq 1.00$). The RMSEA statistic (good fit when $0 \leq RMSEA \leq 0.05$ and $0.10 < p \leq 1.00$) and AIC were used to evaluate the fit of the model (Xu et al., 2015). The non-significant pathways were eliminated when significant pathways were left in the final model.

3 | RESULTS

3.1 | Relationships between grazing pressure, functional diversity and plant richness

Both plant richness (Figure 1a) and functional diversity (Figure 1b) were negatively correlated with grazing pressure. While plant richness showed a weak decline with increasing grazing pressure, FD decreased strongly across the grazing gradient (Figure 1a,b). There was no significant relationship between species richness and FD

(data not shown, $p = 0.07$, $R^2 = 0.13$). While Figure 1b shows the relationship of Mason FD index, we also calculated the community-weighted mean of all measured plant functional traits [CWM], which had similar correlations with plant richness and grazing pressure. This loss in FD is due to shifts in the relative abundance of 28 species. Most of the dominant species and common species which have major effects on ecosystem processes decreased their abundance by 30%–95% with increasing grazing pressure, with resultant increases in bare ground (Table 1). Of all dominant or common plant species, only *Agropyron cristatum* increased with increased grazing pressure, and *Carex korshinskyi* did not significantly change in relative abundance across the grazing gradient. Of rare plant species, 15 were not present at high grazing pressure, resulting in an overall loss of plant species richness. Linear correlations between edaphic factors and plant richness as well as FD were further tested. Both plant richness and FD were significantly related to plant-available nitrogen but not other factors (except pH, which correlated to plant richness) (Supporting Information Table S1).

3.2 | The effects of grazing on soil microbes

Grazing significantly reduced the abundance of AM fungi, saprophytic fungi and soil bacteria (Figure 2a–c). Grazing had its weakest effect on AM fungal abundance, which was greatest at moderate grazing pressure (3.0–4.5 sheep/ha), and only significantly declined at the highest grazing pressure (Figure 2a). Increased grazing pressure led to strong linear decreases in saprophytic fungal abundance (Figure 2b) and a curvilinear decrease in bacterial abundance (Figure 2c). To further examine relationships between soil microbes and plant richness, above-ground productivity and FD, we conducted regression analyses with soil microbial abundance as predictors (Figure 1a–i). Plant richness and plant above-ground productivity had weak ($R^2 < 0.17$) positive correlations with AM fungal, saprophytic fungal and bacterial abundances, in contrast to stronger correlations between FD and AM ($R^2 = 0.31$) and saprophytic fungal abundances ($R^2 = 0.20$) (Supporting Information Figure S1d–h).

3.3 | The effect of grazing on ecosystem multifunctionality (EMF)

As hypothesized, high grazing pressure reduced EMF (Figure 3). EMF was maximized when sheep densities were between 1.5 and 3.0 sheep/ha, and to maintain 50% of EMF, grazing pressure had to remain below 4.5 sheep/ha (Figure 4). Of the individual functions, plant-available phosphorus did not change in response to the grazing gradient (Supporting Information Figure S2d), while plant tissue nitrogen content increased along the grazing gradient (Supporting Information Figure S2b). All other functions (above-ground net primary production, soil organic carbon and plant-available nitrogen) decreased with increased grazing (Supporting Information Figure S2a–e). ANPP sharply declined at the highest grazing pressure, while soil carbon and nitrogen consistently declined with increased grazing pressure.

Plant FD had a moderate-strength positive correlation with EMF ($p = 0.01$, $R^2 = 0.20$), while plant richness and soil microbial abundance were weakly positively correlated with EMF (Supporting

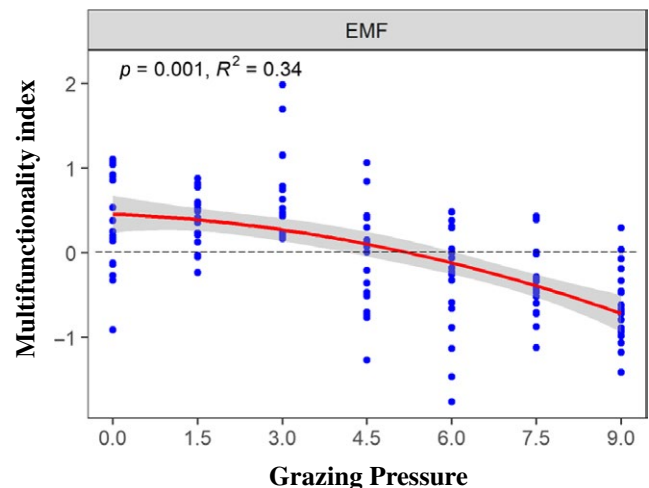


FIGURE 3 Relationship between grazing pressure (number of sheep/ha) and the multifunctionality index (EMF). Data have been log-transformed. Red lines are the fitted lines from OLS regressions. Shaded areas show the 95% CI of the fit

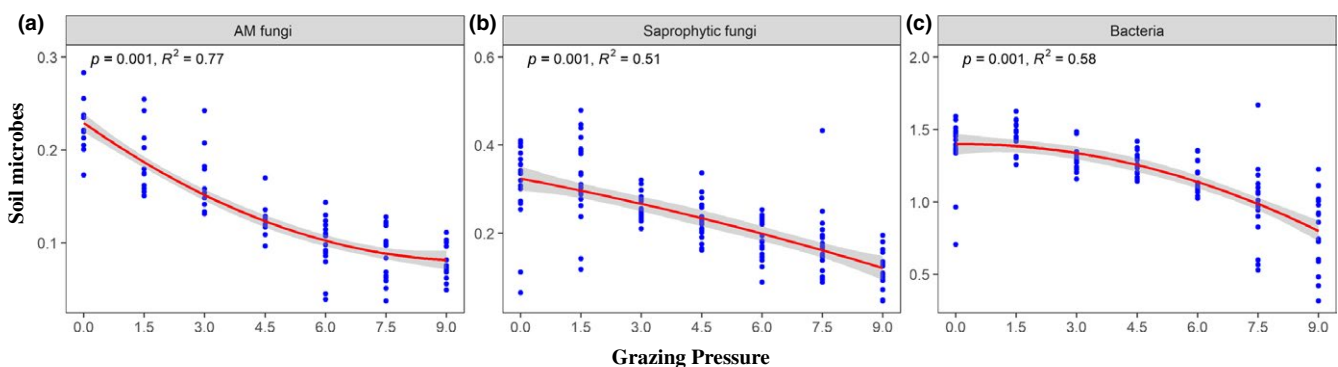


FIGURE 2 Relationship between grazing pressure (number of sheep/ha) and (a) arbuscular mycorrhizal (AM) fungal abundance, (b) saprophytic fungal abundance and (c) bacterial abundance. Red lines are fitted lines from OLS regressions. Shaded areas show 95% CI of the fit

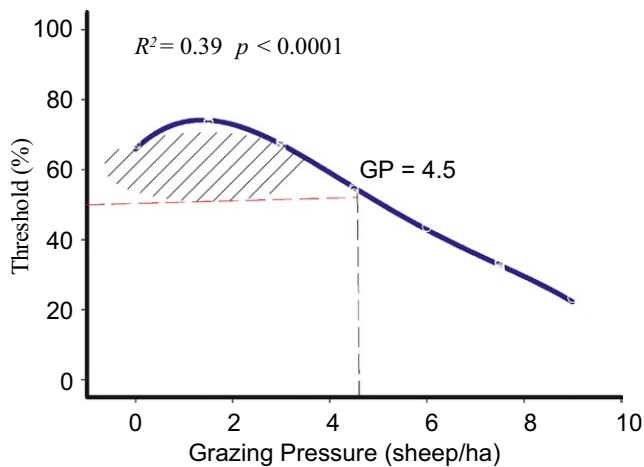


FIGURE 4 Relationship between grazing pressure (GP) and ecosystem multifunctionality (EMF) with an indication of the 50% EMF threshold level (GP = 4.5, $n = 126$). The shaded area represents the necessary grazing densities to maintain EMF above 50%

Information Figure S3a–c). Structural equation modelling (SEM) were fitted to infer direct and indirect effects of grazing pressure, soil microbes, plant richness and FD on EMF (Figure 5a,b). Two models were selected based on chi-square tests ($p > 0.05$), RMSEA

($p > 0.10$) and AIC (the least value) statistics. Our SEM indicates grazing pressure directly influenced EMF ($\beta = -0.61$, standardized path coefficients, $p < 0.001$). The indirect effects of soil microbial abundance ($\beta = -0.21$, $p > 0.05$) and plant richness ($\beta = -0.38$, $p > 0.05$) on EMF were not significant (Figure 5a). Plant richness, FD and soil microbial abundance had no interaction or significant direct effect on EMF (Figure 5b). When independently assessing the effects of soil fungi or bacteria, on EMF, only the relationship between AM fungal abundance and EMF was significant (Supporting Information Figure S4). However, the direct effect of grazing pressure on EMF was significant ($\beta_a = -0.61$, $p < 0.001$; $\beta_b = -0.48$, $p < 0.01$) and explained 22%–3% of EMF variation (Figures 3 and 5).

4 | DISCUSSION

4.1 | Multiple functions are critical to assess ecosystem impacts of grazing pressure

Moderate grazing pressures (ca. 3.0–4.5 sheep/ha) have been reported to encourage the greatest plant productivity in semi-arid Eurasian steppe (Li et al., 2017; Liu et al., 2015). However, setting grazing prescriptions based on only a few ecosystem functions may unintentionally degrade other ecosystem processes (Bennett, Peterson, & Gordon, 2009; Gordon, 1998; MEA 2005). Our study

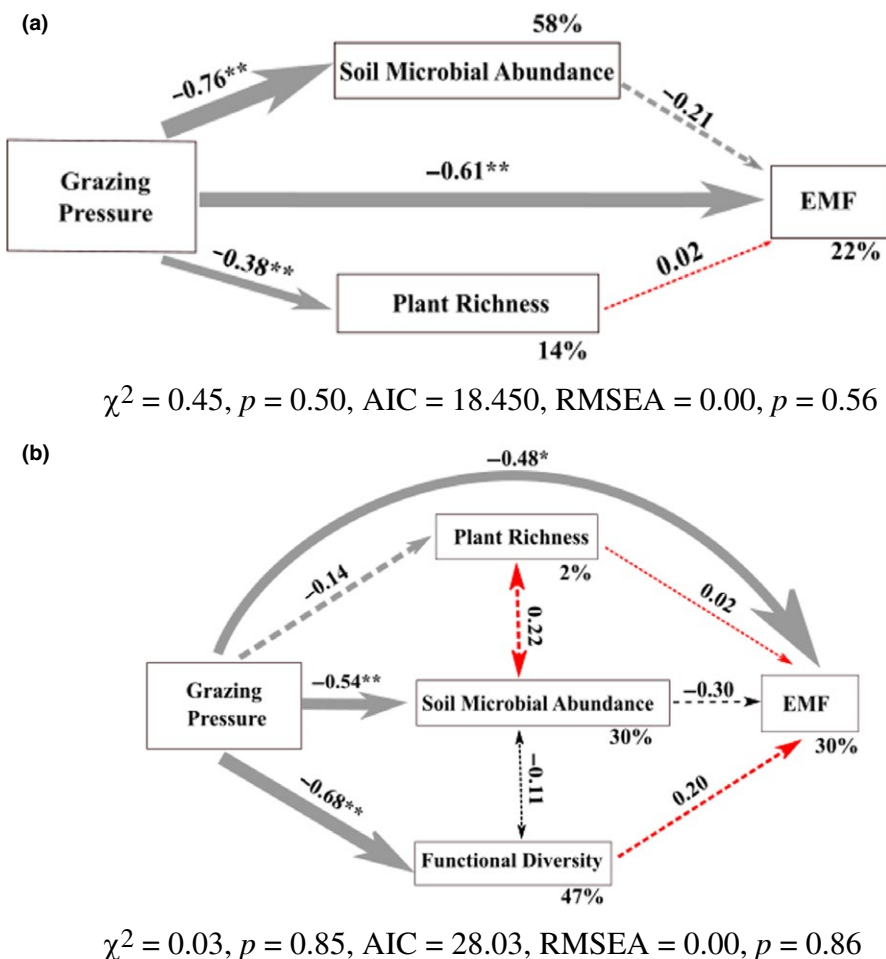


FIGURE 5 Structure equation models of grazing pressure, soil microbial abundance, plant species richness and functional diversity as predictors of ecosystem multifunctionality (EMF). Solid red lines represent positive paths ($p < 0.05$, piecewise SEM; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$), solid gray lines represent negative paths ($p < 0.05$, piecewise SEM) and dotted gray lines represent non-significant paths ($p > 0.05$, piecewise SEM). Arrow width is proportional to the strength of the relationship. We report the path coefficients as standardized effect sizes. Overall fit of piecewise SEM was evaluated using chi-square test and RMSEA statistic (if $p > 0.05$, then no paths are missing and the model is a good fit) and Akaike information criterion (AIC). The proportion of variance explained (R^2) appears alongside response variables in the model

indicates grazing assessments are more reliable when EMF is tracked, as compared to measuring a single ecosystem function such as ANPP. In our study, moderate grazing pressure (ca. 3.0–4.5 sheep/ha) did maintain ANPP, but grazing pressure above 3.0 sheep/ha directly reduced plant species richness, plant community FD and most importantly EMF (Figure 1 and Supporting Information Figure S2). Less intense grazing pressures (1.5–3.0 sheep/ha) were required to maintain EMF because soil organic carbon and plant-available nitrogen decreased linearly with grazing pressure (Supporting Information Figure S2). Similarly, fungal abundance steadily decreased along the grazing gradient (Figure 2a). In contrast, ANPP and bacterial biomass only decreased at high grazing pressures (Figure 2c and Supporting Information Figure S2a). Therefore, low-intensity grazing is a crucial biotic disturbance that can increase EMF in semi-arid grasslands; however, maintaining 4.5 sheep/ha or fewer may be a key grazing pressure tipping point (threshold) for maintaining >50% EMF in semi-arid grasslands (Figures 3 and 4).

4.2 | Plant functional diversity is the strongest indicator of grazing effects on the plant community

Functional diversity encompasses the range of traits distributed across a plant community and can be strongly linked to ecosystem properties (Cadotte, 2017; Xu et al., 2018). Plant FD was a more sensitive indicator of grazing effects on the plant community, compared with species richness (Figures 1 and 5b). Plant FD was particularly sensitive to grazing pressure and likely decreased through both the loss of rare species and decreases in abundance of dominant species (Table 1). Under relatively low grazing pressure, plant communities tend to have a wider variety of complementary traits, resulting in greater FD (Figure 1b). Conversely, functional traits of plant species tend to be more similar under increased grazing pressure, regardless of plant species richness. Diaz et al. (2007) showed grazing can strongly filter plant species by traits, benefiting annual species of short stature, with rosette or stoloniferous architecture. Li et al. (2017) demonstrated species with low specific leaf area (SLA) and high leaf nitrogen content (LNC) are negatively affected by intense grazing pressure. Functionally diverse plant communities tend to be resilient to periodic disturbances, thus maintaining ecosystem functions over time (Chapin et al., 1997; Diaz & Cabido, 2001). Managing plant functional traits in grazed grasslands could regulate species composition for both production and environmental goals, enhancing at least some ecosystem functions and services.

4.3 | Links between composition and function

Grazing significantly decreases plant FD (and to a lesser extent, richness and biomass), soil organic carbon and microbial biomass, and multiple ecosystem functions (Figures 1 and 2, Supporting Information Figure S2). While there were weak correlations between plant species richness and microbial abundance, microbial abundance and EMF, and between plant species richness and EMF (Supporting Information Figures S1 and S3), these were not

important drivers of EMF in our structural equation models. EMF was substantially and directly affected by grazing, as opposed to indirectly through the effects of grazing on plant communities or microbial abundance (Figure 5). Similarly, a recent grazing intensity study in dry lands showed that decomposition rates were strongly influenced by the direct effects of grazing, not indirectly through grazing effects on FD (Chillo, Ojeda, Capmourteres, & Anand, 2017).

In summary, grassland management strategies may be flawed when based on monitoring of individual ecosystem functions (Soliveres et al., 2016; Stein et al., 2016). Our research strongly suggests that the assessment of multiple ecosystem functions is critical to elucidate the optimal grazing thresholds or EMF relationships that ensure the delivery of a suite of ecosystem services critical for sustainable grassland management. Low grazing pressure is required to maintain delivery of multiple functions. Establishing thresholds of grazing to maintain multiple functions is critical for sustainable rangeland management and can increase prediction accuracy on grassland ecosystem responses to grazing pressure. We need more widespread assessment of grazing thresholds for multiple functions across diverse grasslands because many mesic grasslands are predicted to become more arid under a changing climate and thus are likely to decrease the intensity of grazing that can be sustained.

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AUTHORS' CONTRIBUTIONS

H.R., Y.B., S.H. and Y.Z. designed the research; H.R., W.G. and G.Y. performed the research; H.R., G.W.T.W., A.B.C. and V.T.E. analysed the data; and all co-authors contributed to the writing of the manuscript.

DATA ACCESSIBILITY

All plant and soil data for this paper are accessible at Dryad Digital Repository: <https://doi.org/10.5061/dryad.j87b5b8> (Ren et al. 2018).

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SUPPORTING INFORMATION

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