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Livestock grazing regulates ecosystem multifunctionality in semiarid grassland

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Running headline: What drives grassland ecosystem multifunctionality?

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 aboveground 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.

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

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 (MEA 2005; Reynolds *et al.* 2007; Briske 2017; Evans *et al.* 2017). 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 *et al.* 2017; Teague & Barnes 2017). Balancing these multiple objectives can be challenging because tradeoffs are common across multiple grassland management goals (MEA 2005; Briske *et al.* 2011; Maestre *et al.* 2012; Jing *et al.* 2015). 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 *et al.* 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 (Liu *et al.* 2015; Li *et al.* 2017), 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 *et al.* 2016).

Approximately 45% of variation in EMF is explained through combined effects of above-and belowground 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; Harrison & Bardgett 2010; Sitters & Venterink 2015; Evans *et al.* 2017; Liu *et al.* 2018). Herbivory can strongly affect plant community structure and function (Diaz *et al.* 2007b; Stein *et al.* 2016), through the direct effects of herbivores on plants, and grazing-induced changes in soil nutrients and fungal communities (Chen *et al.* 2017; Ren *et al*. 2018). 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 *et al.* 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) (Gross *et al.* 2007; Gross *et al.* 2014; Baert *et al.* 2016; 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 (Petchey & Gaston 2002; Forrestel *et al.* 2017), 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 (van der Heijden, 2008; Wurzburger & Brookshire 2017). Soil biota are strongly affected by herbivore grazing (Barto & Rillig 2010; Chen *et al.* 2013; Liu *et al.* 2015; Eldridge *et al.* 2017) 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 *et al.* 2017; Chen *et al*. 2017; Ren *et al*. 2018; Wilson *et al.* 2018).

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: (1) aboveground biomass, (2) plant nitrogen (nitrogen pools in aboveground biomass), (3) plant-available nitrogen, (4) plant-available phosphorus, and (5) soil organic carbon. Our experiment investigated the following: (i) 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 (ii) the extent that grazing directly alters EMF, versus indirectly affects EMF through changes in plant and microbial communities

Methods

Site description

Our study area is located in Inner Mongolia steppe (Bai *et al.* 2004), ranging in elevation from 1200 to 1280m, with a mean annual precipitation of 346.1mm 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 were excluded from this area two 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 (IUSS Working Group WRB 2006). Approximately 36 vascular plant species typically occur in these grasslands (8 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 aboveground biomass production (Li *et al.* 2017).

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: (1) often yield different results than ecosystem-scale plots, (2) do not address heterogeneity in grazing/disturbance/management across the landscape, and (3) are impossible to scale-up to inform management decisions (Carpenter 1996, Schindler 1998, Schmitz 2005, Osenberg et al. 2006, Fraterrigo and Rusak 2008). 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 et al. 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 (Brandsby et al 1998, Beier et al. 2012).

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 7 plots that were randomly assigned to 7 grazing pressures (GP) (GP = 0, 1.5, 3.0, 4.5, 6.0, 7.5, or 9.0 sheep ha^{-1}). These two site types have similar response to grazing treatments (Supplementary Fig. 5 a, 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^{-1}), 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).

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 1m^2 quadrats within each treatment plot.

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 × 3m) in each plot before sheep began grazing. From June through September, aboveground biomass was clipped in a 1m^2 quadrat from both inside and outside of each exclosure. After each monthly clipping, exclosures were moved. Annual aboveground net primary productivity

(ANPP) inside (i) and outside (o) exclusures in grazed plots was calculated with the formula: ANPP = W1o + (W2i -W1o) + (W3i -W2o) + (W4i -W3o). Where Wi 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 (Kjeltec 8100 Analyser Unit, FOSS, Sweden).

Soil sampling

Soil samples (diameter 3 cm, depth 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 2mm 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 cm^3).

Soil properties determination

Plant-available P was measured by the Olsen method. Soil organic C was analyzed 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 mol L^{-1} K_2SO_4 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 h. Ten grams of field soil was mixed with 25 mL of 1 mol L^{-1} KCl solution to measure pH using a pH meter (PB-10, Sartorius, Germany). Extra-radical hyphal length densities of AM fungi were extracted from soil using the membrane filter technique and the gridline intercept method under a microscope at 200X magnification (Jakobsen *et al.* 1992). The biomass of soil bacteria and saprophytic fungi were 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, cy19:0 were selected to represent soil bacteria, and 18:2ω6c was selected to represent saprophytic fungi (Moore-Kucera & Dick 2008).

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), stem:leaf ratio. These traits were chosen because they link to plant nutrient acquisition and utilization, belowground 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 log10 (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 *et al.* 2003; Mori *et al.* 2017).

FDα represents Mason functional diversity index:

$$\mathbf{FD\alpha} = \sum_{i=1}^{S} P\mathbf{i}\,(\mathbf{xi} - \bar{\mathbf{x}}) \qquad (1)$$

xi represents the mean trait value of species i,, $\bar{\mathbf{x}} = \sum_{i=1}^{S} P\mathbf{ixi}$ represents the mean trait value of whole plant community. Pi represents the relative abundance of species i in the whole plant community, and S represents the number of species in the whole community (Mason *et al.* 2003, 2011, 2013; Mason *et al.* 2005).

Quantifying Ecosystem Multifunctionality (EMF)

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: (1) plant aboveground biomass, (2) plant-tissue nitrogen content, (3) plant-available nitrogen, (4) plant-available phosphorus, and (5) soil organic carbon. All of these variables are crucial drivers of ecosystem functioning (Jing *et al.* 2015) (Delgado-Baquerizo *et al*. 2017a, b), 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).

$$\mathrm{EMF}^{\alpha} = \left(\sum_{i=1}^{F} g(r_i(f_i))\right)/F \qquad (3)$$

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.

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 Foundation for Statistical Computing, Vienna, Austria, 2013). For all analyses, data were log10 (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 Modeling (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 analyze 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). 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 $0 \leq \text{RMSEA} \leq 0.05$ 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.

Results

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 (Fig. 1. a, 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 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) (Supplementary Table S1).

The effects of grazing on soil microbes. Grazing significantly reduced the abundance of AM fungi, saprophytic fungi, and soil bacteria (Fig. 2 a-c). Grazing had its weakest effect on AM fungal abundance, which was greatest at moderate grazing pressure (3.0-4.5 sheep ha^{-1}), and only significantly declined at the highest grazing pressure (Fig. 2 a). Increased grazing pressure led to strong linear decreases in saprophytic fungal abundance (Figure 2b), and a curvilinear decrease in bacterial abundance (Fig. 2 c). To further examine relationships between soil microbes and plant richness, aboveground productivity, and FD, we conducted regression analyses with soil microbial abundance as predictors (Supplementary Figs.1, a-i). Plant richness and plant aboveground 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 ($R^2 = 0.20$) (Supplementary Figs.1, d-h).

The effect of grazing on Ecosystem multifunctionality (EMF). As hypothesized, high grazing pressure reduced EMF (Fig. 3). EMF was maximized when sheep densities were between 1.5 and 3.0 sheep ha^{-1}, and to maintain 50% of EMF, grazing pressure had to remain below 4.5 sheep ha^{-1} (Fig. 4). Of the individual functions, plant-available phosphorus did not change in response to the grazing gradient (Supplementary Figure 2d), while plant tissue nitrogen content increased along the grazing gradient (Supplementary figure 2b). All other functions (aboveground net primary production, soil organic carbon, and plant-available nitrogen) decreased with increased grazing (Supplementary Figs. 2, a-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 (Supplementary Figs. 3 a-c). Structural equation models (SEM) were fitted to infer direct and indirect effects of grazing pressure, soil microbes, plant richness, and FD on EMF (Fig. 5. a, 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 (Fig. 5. a). Plant richness, FD, and soil microbial abundance had no interaction or significant direct effect on EMF (Fig. 5. b). When independently assessing the effects of soil fungi or bacteria, on EMF, only the relationship between AM fungal abundance and EMF was significant (Supplementary Figs. 4). 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 (Fig. 3 and Fig. 5).

Discussion

Multiple functions are critical to assess ecosystem impacts of grazing pressure. Moderate grazing pressures (ca. 3.0-4.5 sheep ha^{-1}) have been reported to encourage the greatest plant productivity in semi-arid Eurasian steppe (Liu *et al.* 2015; Li *et al.* 2017). However, setting grazing prescriptions based on only a few ecosystem functions may unintentionally degrade other ecosystem processes (Gordon 1998; MEA 2005; Bennett *et al.* 2009). Our study 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^{-1}) did maintain ANPP, but grazing pressure above 3.0 sheep ha^{-1} directly reduced plant species richness, plant community FD, and most importantly EMF (Figure 1 and supplementary Figure 2). Less intense grazing pressures (1.5-3.0 sheep ha^{-1}) were required to maintain EMF because soil organic carbon and plant-available nitrogen decreased linearly with grazing pressure (Supplementary Figure 2). 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 supplementary Figure 2a). Therefore, low-intensity grazing is a crucial biotic disturbance that can increase EMF in semi-arid grasslands; however, maintaining 4.5 sheep ha^{-1} or fewer may be a key grazing pressure tipping point (threshold) for maintaining > 50% EMF in semi-arid grasslands (Figure 3 and Figure 4).

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 (Figure 1 and Figure 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.* (2007a) 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.

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 (Figure 1, 2 and supplementary figure 2). While there were weak correlations between plant species richness and microbial abundance, microbial abundance and EMF, and between plant species richness and EMF (Supplementary Figure 1 and 3), 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 drylands showed that decomposition rates were strongly influenced by the direct effects of grazing, not indirectly through grazing effects on FD (Chillo et al. 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 wide-spread 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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Author contributions

Haiyan Ren, Yongfei Bai, Shuijin Hu, and Yingjun Zhang designed the research; Haiyan Ren, Weiyang Gui, and Gaowen Yang performed the research; Haiyan Ren, Gail W. T. Wilson, Adam B. Cobb, and Valerie Eviner analyzed the data; and all coauthors contributed to the writing of the manuscript.

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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 ± s.e.m.). Nomenclature follows the editorial committee of Chinese plant records.

Dominant species		Common species	
Latin name	RA (%)	Latin name	RA (%)
Leymus chinensis	(39.25/27.38±3.58)*	*Cleistogenes squarrosa*	(10.51/7.32±1.51)**
Carex korshinskyi	(38.89/36.16±2.75)	*Agropyron cristatum*	(3.53/5.00±1.30)
Stipa grandis	(27.58/12.96±1.72)**	*Achnatherum sibiricum*	(2.77/0.14±0.65)***

Rare species			
Latin name	RA (%)		
Koeleria macrantha	(0.94/0.00±0.37)***	*Potentilla bifurca*	(0.08/0.00±0.07)**
Allium condensatum	(0.04/0.00±0.02)**	*Allium senescens*	(0.04/0.00±0.02)*
Phlomis umbrosa	(0.04/0.00±0.02)**	*Potentilla verticillaris*	(0.01/0.00±0.02)
Adenophora stenanthina	(0.01/0.00±0.01)	*Adenophora gmelinii*	(0.01/0.00±0.01)
Allium tenuissimum	(0.03/0.00±0.01)*	*Poa annua*	(0.04/0.00±0.01)*
Allium anisopodium	(0.02/0.00±0.01)*	*Kochia prostrata*	(0.01/0.00±0.01)
Allium ramosum	(0.01/0.00±0.01)	*Iris tenuifolia*	(0.01/0.00±0.01)
Thalictrum petaloideum	(0.57/0.02±0.26)**	*Potentilla acaulis*	(0.05/0.05±0.02)
Dontostemon micranthus	(0.02/0.02±0.01)	*Axyris amaranthoides*	(0.01/0.01±0.01)
Chenopodium glaucum	(0.01/0.01±0.01)	*Serratula centauroides*	(0.01/0.01±0.01)
Artemisia scoparia	(0.00/0.01±0.01)	*Salsola collina*	(0.01/0.04±0.02)*

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

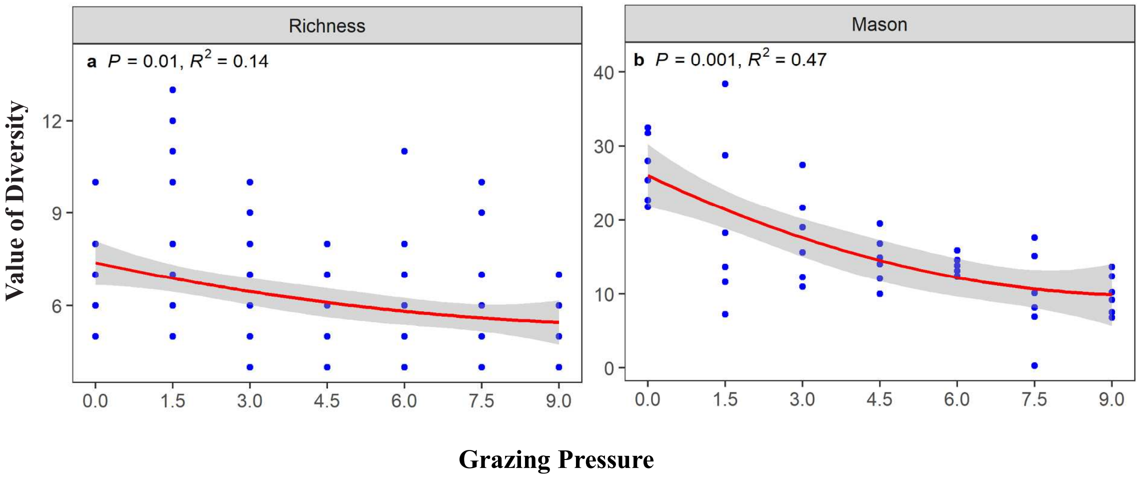
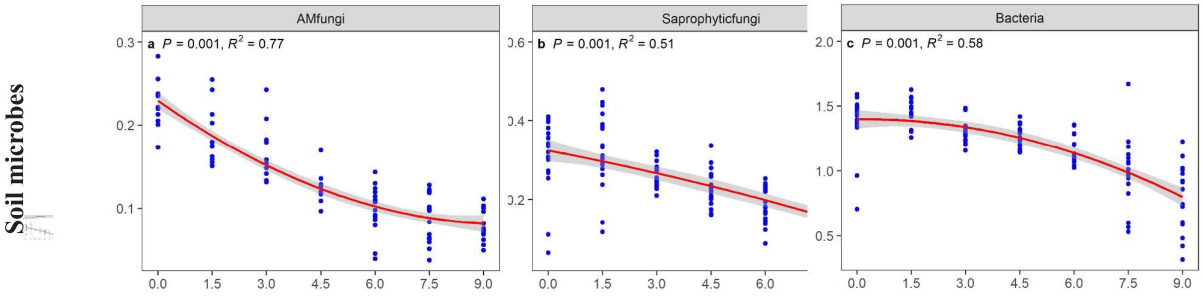


Figure 1. Relationship between grazing pressure (number of sheep ha^{-1}) and a) plant species richness or b) plant functional diversity (Mason functional diversity index). Data have been log-transformed. Red lines are fitted lines from OLS regressions. Shaded areas show 95% CI of the fit.



Grazing PressureFigure 2. Relationship between grazing pressure (number of sheep ha^{-1}) 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.

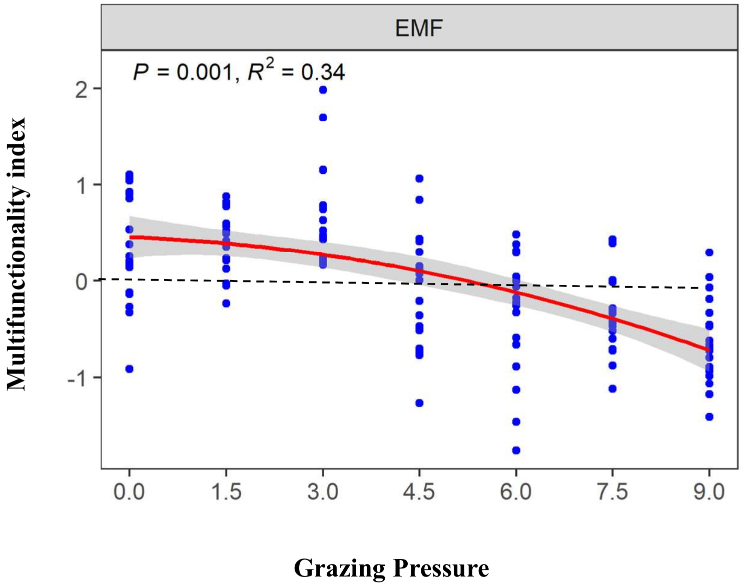


Figure 3. Relationship between grazing pressure (number of sheep ha^{-1}) and the multifunctionality index (EMF). Data have been log-transformed. Red lines are the fitted lines from OLS regressions. Shaded areas show the 95% CI of the fit.

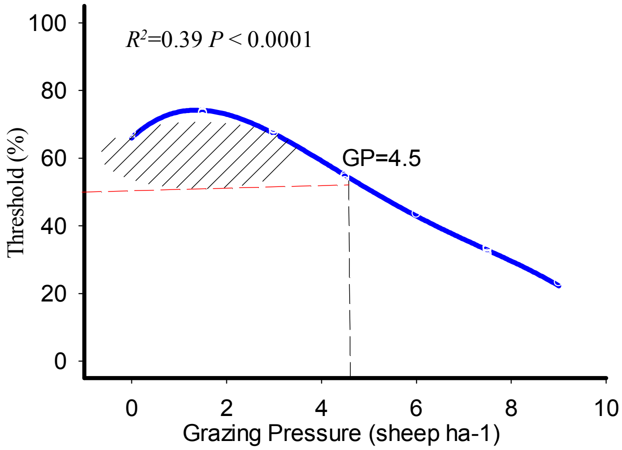
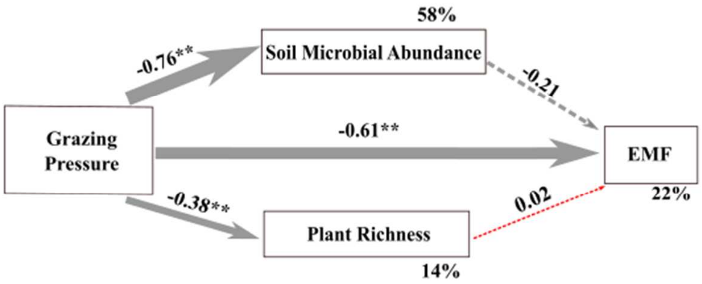
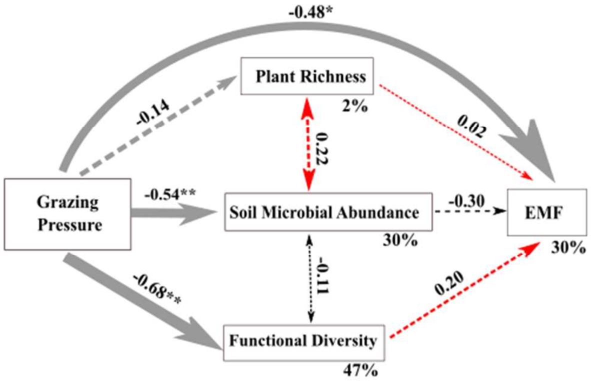


Figure 4. Relationship between grazing pressure (GP) and ecosystem multifuntionality (EMF) with an indication of the 50% EMF threshold level (GP = 4.5, n = 126). The shaded area represents the necessary grazing densities to maintain EMF above 50%.



a. $\chi^2 = 0.45$, $p = 0.50$, AIC =18.450, RMSEA = 0.00, $p = 0.56$



b. $\chi^2 = 0.03$, $p = 0.85$, AIC = 28.03, RMSEA = 0.00, $p = 0.86$

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 s.e.m.; ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$), solid gray lines represent negative paths ($p < 0.05$, piecewise s.e.m.) and dotted gray lines represent non-significant paths ($p > 0.05$, piecewise s.e.m.). Arrow width is proportional to the strength of the relationship. We report the path coefficients as standardized effect sizes. Overall fit of piecewise s.e.m. was evaluated using Chi-square test and RMSEA statistic (if $p > 0.05$, then no paths are missing and the model is a goodfit) and

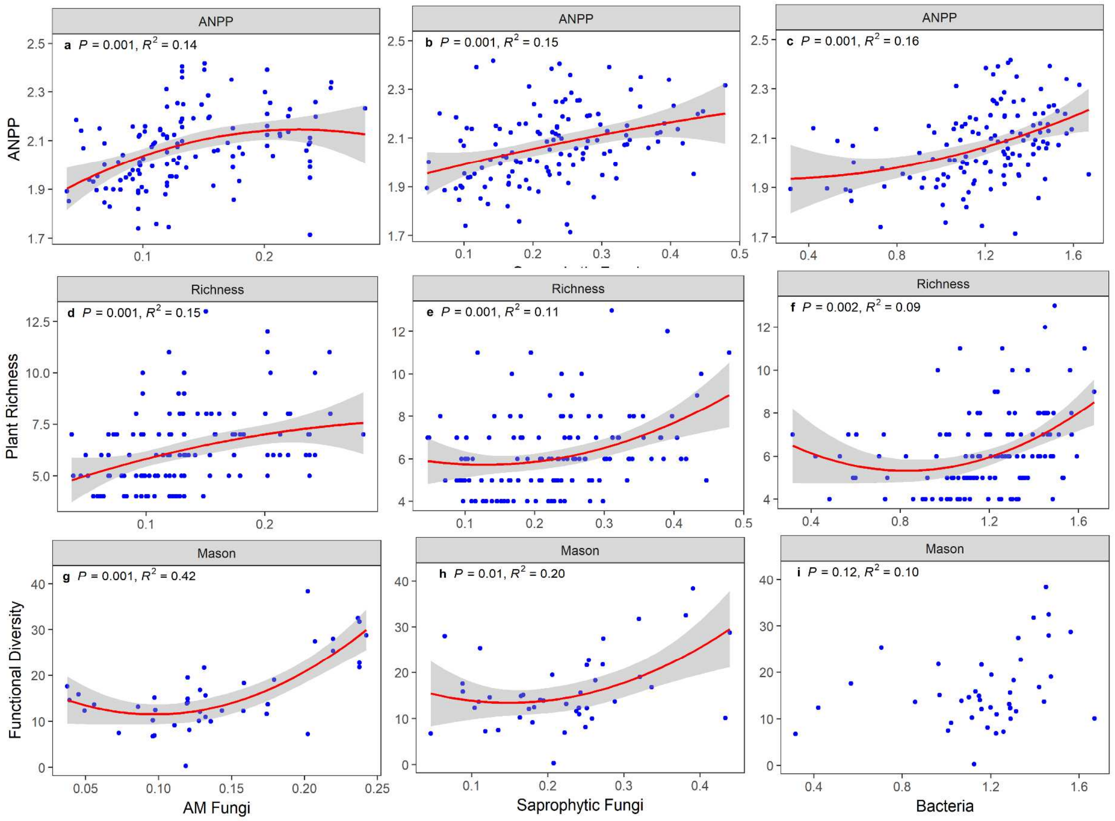
Akaike information criterion (AIC). The proportion of variance explained (R^2) appears alongside response variables in the model.

Table. S1 R^2-values statistics from generalized linear models (GLM) between plant richness, functional diversity (FD) and edaphic factors.

Edaphic factors	Plant richness	Edaphic factors	FD
SAN	0.22**	SAN	0.18*
SAP	0.14ns	SAP	0.00ns
SOC	0.07ns	SOC	0.05ns
SM	0.08ns	SM	0.12ns
PH	0.18*	PH	0.03ns

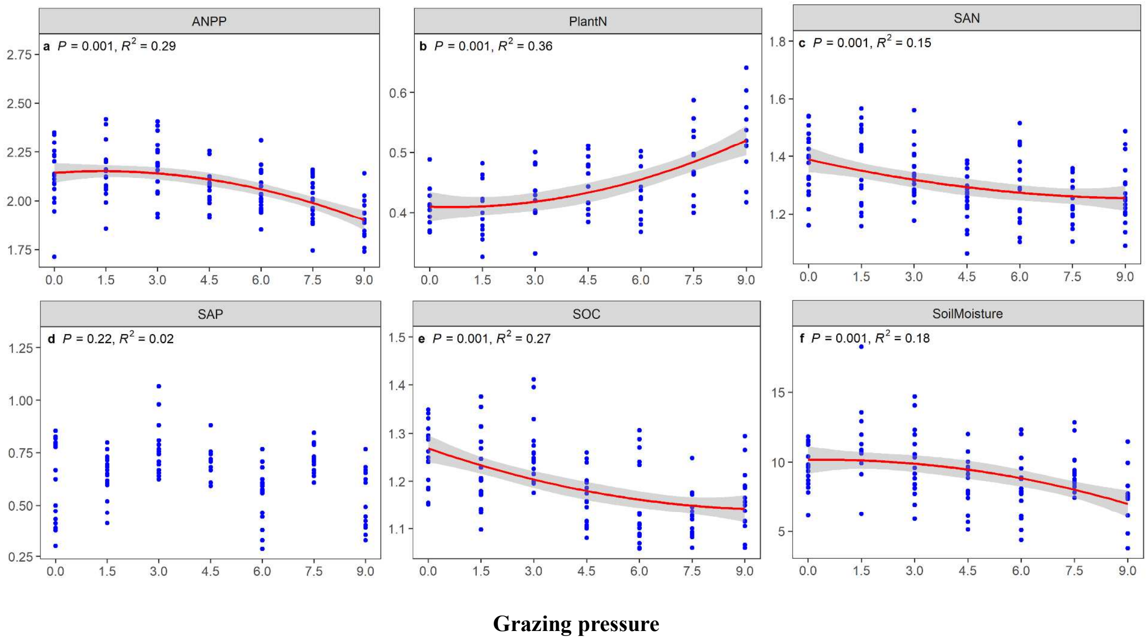
Abbreviations: soil plant-available nitrogen (SAN), soil plant-available phosphorus (SAP), soil organic carbon (SOC), soil moisture (SM).

Stars denote for significance at $p < 0.05$, $p < 0.01$ and $p < 0.001$ probability levels (*, ** and ***, respectively).

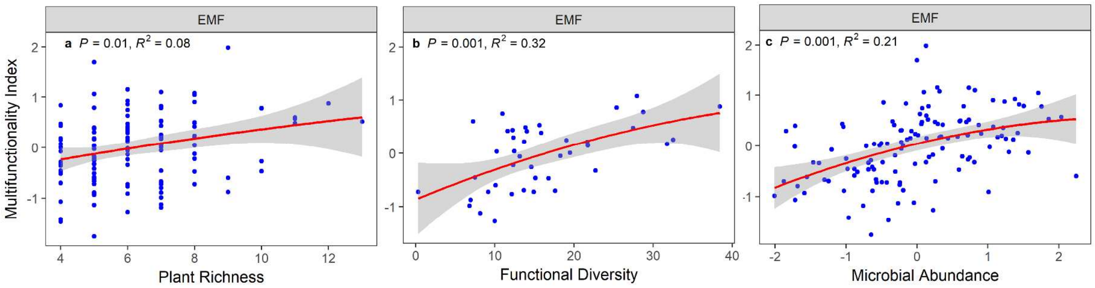


Soil Microbial Abundance

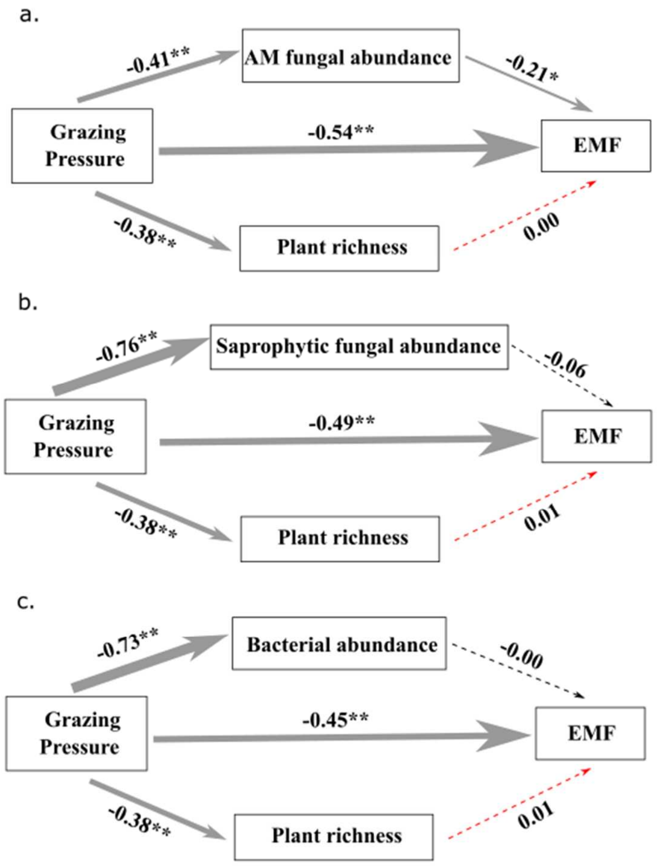
Supplementary Figure 1. Relationships between ANPP (log-transformed) and a) AM fungal abundance, b) saprophytic fungal abundance, and c) bacterial abundance. Relationships between plant species richness and d) AM fungal abundance, e) saprophytic fungal abundance, and f) bacterial abundance. Relationships between functional diversity, and g) AM fungal abundance, h) saprophytic fungal abundance, and i) bacterial abundance. Red lines are the fitted lines from OLS regressions. Shaded areas show the 95% CI of the fit.



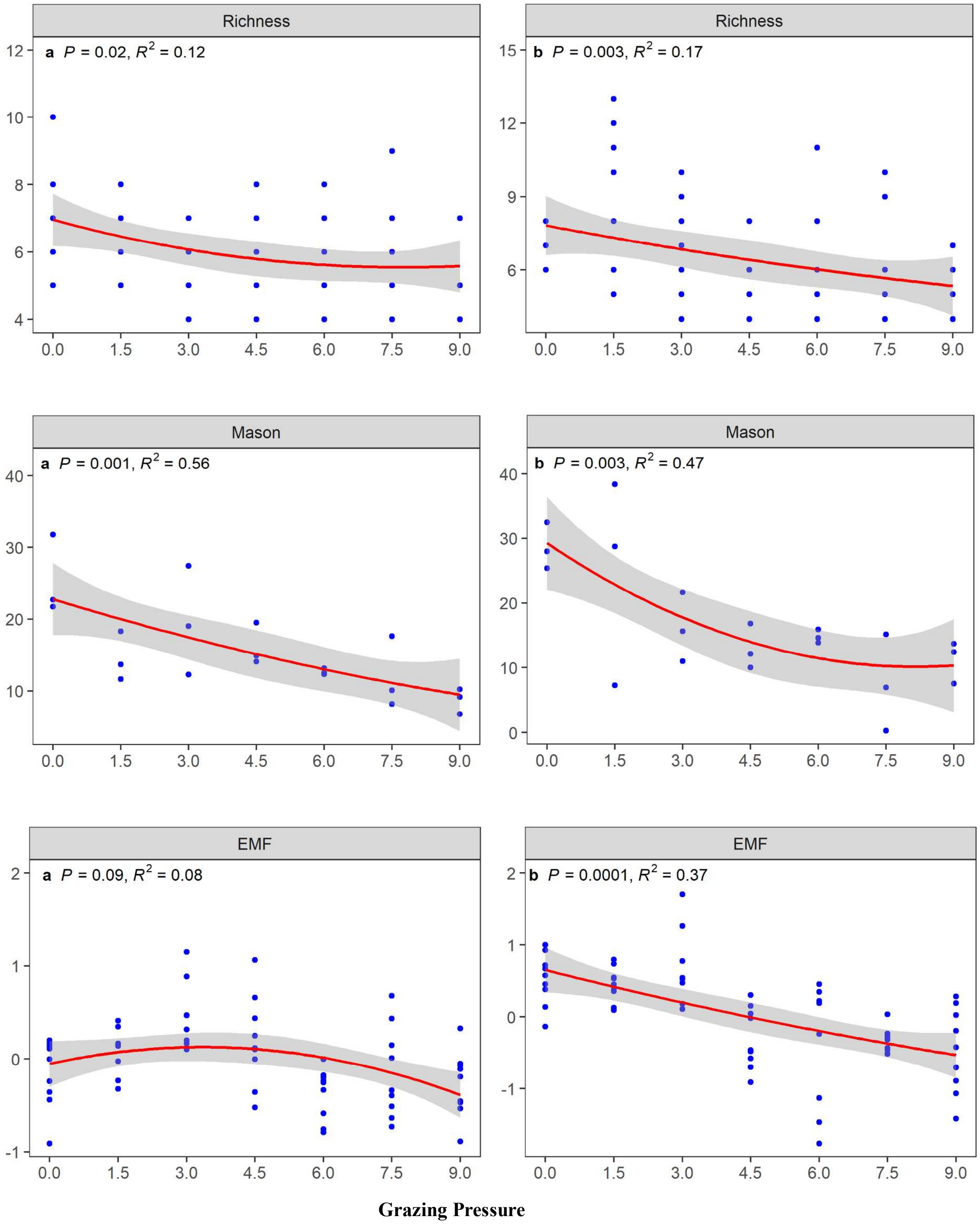
Supplementary Figure 2. Relationship between each component of ecosystem multifunctionality: a) aboveground net primary productivity (ANPP), b) plant-tissue nitrogen content, c) soil plant-available nitrogen, d) soil plant-available phosphorus, e) soil organic carbon, f) soil moisture across grazing densities. Red lines are the fitted lines from OLS regressions. Shaded areas show the 95% CI of the fit.



Supplementary Figure 3. Relationship between ecosystem multifunctionality and a) plant species richness or b) functional diversity (Mason functional diversity index) or c) soil microbial abundance. Red lines are fitted lines from OLS regressions. Shaded areas show 95% CI of the fit.



Supplementary Figure 4. Structure equation models of grazing pressure, soil microbial abundance, and plant species richness as predictors of ecosystem multifunctionality (EMF). Solid red lines represent positive paths ($p < 0.05$, piecewise s.e.m.; ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$), solid gray lines represent negative paths ($p < 0.05$, piecewise s.e.m.) and dotted gray lines represent non-significant paths ($p > 0.05$, piecewise s.e.m.). Arrow width is proportional to the strength of the relationship. We report the path coefficients as standardized effect sizes. a) AM fungal abundance: $\chi^2 = 0.03$, $p = 0.87$, AIC = 18.020, RMSEA = 0.00, $p = 0.89$, b) saprophytic fungal abundance: $\chi^2 = 1.56$, $p = 0.21$, AIC = 19.560, RMSEA = 0.07, $p = 0.28$, c) bacterial abundance: $\chi^2 = 0.23$, $p = 0.63$, AIC = 18.230, RMSEA = 0.00, $p = 0.68$.



Supplementary Figure 5. Relationship between grazing pressure and plant species richness, functional diversity (Mason functional diversity index) and ecosystem multifunctionality (EMF) in (a) sloped system and (b) flat system. Red lines are fitted lines from OLS regressions. Shaded areas show 95% CI of the fit.

GI	System	SAN	SAP	SOC	ANPP	AMF	Bacteria	Fungi
0	1	1.395274	0.498841	1.186269	1.713491	0.23764598	1.33613	0.253892
0	1	1.302205	0.411101	1.286599	2.014605	0.23764598	0.963069	0.272238
0	1	1.27782	0.471517	1.293862	1.991817	0.23764598	1.394619	0.3199
0	1	1.216641	0.388939	1.202915	2.228466	0.22118957	1.488416	0.355654
0	1	1.328253	0.432188	1.249564	2.232878	0.28296075	1.511516	0.40431
0	1	1.26674	0.30103	1.155459	2.254435	0.20482143	1.371767	0.267411
0	1	1.266965	0.388939	1.295623	2.11133	0.23764598	1.39349	0.335231
0	1	1.321619	0.377418	1.249181	2.092791	0.23764598	1.427161	0.340405
0	1	1.15982	0.388939	1.183571	1.94714	0.23764598	1.353139	0.300542
1.5	1	1.204478	0.667692	1.172209	2.058173	0.1585502	1.302944	0.262421
1.5	1	1.418252	0.681335	1.134568	1.991034	0.17419461	1.314365	0.237619
1.5	1	1.289428	0.694563	1.246538	1.856497	0.17484853	1.441217	0.288196
1.5	1	1.237916	0.731988	1.246705	2.060534	0.16180362	1.44322	0.277507
1.5	1	1.318414	0.798362	1.201866	2.119278	0.21289192	1.568569	0.380231
1.5	1	1.230071	0.766442	1.174417	2.198034	0.15501805	1.424963	0.294583
1.5	1	1.156961	0.731988	1.179222	2.072875	0.17937668	1.532394	0.33288
1.5	1	1.191915	0.766442	1.097872	2.036489	0.17419461	1.418438	0.30339
1.5	1	1.298604	0.719867	1.139714	2.151584	0.17419461	1.418438	0.336434
3	1	1.365993	0.766442	1.175775	1.914132	0.15813967	1.287477	0.251201
3	1	1.265285	0.707399	1.241529	2.037692	0.20717053	1.324642	0.272854
3	1	1.281065	0.694563	1.225552	1.933521	0.17928542	1.471846	0.320842
3	1	1.363608	0.694563	1.239594	2.046349	0.18220157	1.282458	0.311924
3	1	1.273635	0.623986	1.244685	2.191339	0.14149476	1.28833	0.210234
3	1	1.31716	0.667692	1.274154	2.285257	0.15386744	1.286806	0.255651
3	1	1.319064	0.667692	1.28393	2.258685	0.2421724	1.271301	0.247016
3	1	1.24032	0.639048	1.198649	2.247949	0.14830983	1.330169	0.242809
3	1	1.175547	0.653606	1.195222	2.192512	0.15399474	1.224461	0.282311
4.5	1	1.258972	0.882076	1.196976	1.927405	0.11997872	1.151395	0.1898
4.5	1	1.128509	0.719867	1.107347	1.914308	0.11997872	1.14674	0.164887
4.5	1	1.245858	0.707399	1.157156	2.003662	0.11997872	1.202883	0.205982
4.5	1	1.220641	0.882076	1.100515	2.020223	0.12532405	1.303377	0.161343
4.5	1	1.277008	0.719867	1.116241	2.086289	0.10867465	1.257287	0.220383
4.5	1	1.329487	0.707399	1.186455	2.239633	0.11997872	1.252986	0.2014
4.5	1	1.373908	0.882076	1.175074	2.117934	0.11997872	1.359996	0.233114
4.5	1	1.297936	0.719867	1.159086	2.124537	0.12572045	1.322412	0.227995
4.5	1	1.141832	0.707399	1.104291	2.110084	0.11997872	1.244274	0.23721
6	1	1.289923	0.766442	1.101784	1.998695	0.09786705	1.199594	0.182112
6	1	1.215738	0.707399	1.110644	2.034682	0.14349666	1.288261	0.240694
6	1	1.352561	0.592196	1.133683	1.94838	0.08604473	1.284074	0.224371
6	1	1.172352	0.557894	1.088975	1.961453	0.08925775	1.105179	0.170019
6	1	1.167772	0.608381	1.10763	1.996033	0.10770302	1.117	0.152314
6	1	1.319614	0.608381	1.084514	1.953115	0.12376525	1.350919	0.23813
6	1	1.34981	0.592196	1.06861	2.030721	0.12989059	1.355513	0.253446
6	1	1.209783	0.575383	1.100922	2.010936	0.07966991	1.039119	0.138343
6	1	1.285368	0.623986	1.130199	2.074158	0.10732485	1.025455	0.14572
7.5	1	1.198465	0.667692	1.089001	1.952179	0.12765602	1.669366	0.433209
7.5	1	1.197225	0.608381	1.084295	1.744919	0.12121249	1.186103	0.24946
7.5	1	1.162696	0.667692	1.12053	1.891537	0.03754745	0.567417	0.088074
7.5	1	1.216973	0.707399	1.2479	2.069125	0.05117245	0.600186	0.099337

7.5	1	1.190673	0.694563	1.146035	1.954371	0.06256284	0.826456	0.100335
7.5	1	1.16214	0.719867	1.176641	2.089505	0.06852505	0.530041	0.094653
7.5	1	1.147082	0.78798	1.128419	2.159176	0.10181609	1.067551	0.189447
7.5	1	1.102797	0.707399	1.129064	2.137291	0.10167543	1.057332	0.151877
7.5	1	1.222472	0.846845	1.14739	2.149804	0.06438979	0.943851	0.146132
9	1	1.135164	0.681335	1.065692	1.893836	0.09622801	0.317613	0.04621
9	1	1.088483	0.766442	1.191012	1.758205	0.11103728	1.020434	0.179872
9	1	1.254949	0.766442	1.212596	1.82007	0.09622801	1.114392	0.163191
9	1	1.255557	0.681335	1.115323	1.740177	0.09622801	0.725824	0.101948
9	1	1.205713	0.608381	1.059243	1.885361	0.09622801	0.58886	0.071584
9	1	1.233372	0.653606	1.156268	1.903741	0.06965243	0.742734	0.09481
9	1	1.271368	0.667692	1.157943	1.891983	0.10287193	1.225881	0.194818
9	1	1.198811	0.608381	1.116156	2.026411	0.10022868	1.11264	0.156433
9	1	1.167719	0.766442	1.186174	1.977358	0.09622801	0.732659	0.125918
0	2	1.425129	0.667692	1.262097	2.085861	0.23668757	1.462494	0.381525
0	2	1.540604	0.78798	1.341391	2.201087	0.21963479	1.462494	0.064404
0	2	1.449455	0.855924	1.331307	2.137523	0.21963479	0.706037	0.11099
0	2	1.460848	0.818409	1.292851	2.33945	0.25522637	1.56799	0.397334
0	2	1.508351	0.798362	1.240231	2.298344	0.20056111	1.452829	0.34207
0	2	1.479009	0.78798	1.310016	2.350778	0.17297391	1.341627	0.356369
0	2	1.538348	0.828096	1.348906	2.059828	0.23469788	1.475922	0.367654
0	2	1.400853	0.777344	1.241686	2.129142	0.2126718	1.485902	0.307898
0	2	1.376871	0.623986	1.152153	2.136594	0.21963479	1.592221	0.410263
1.5	2	1.566343	0.714615	1.314162	2.159938	0.2023475	1.449564	0.390827
1.5	2	1.535127	0.650259	1.314372	2.198171	0.24237718	1.561845	0.439086
1.5	2	1.416883	0.643906	1.228646	2.392064	0.2023475	1.257387	0.118016
1.5	2	1.439779	0.464176	1.281748	2.392903	0.15052539	1.493145	0.31074
1.5	2	1.427643	0.518685	1.142121	2.418008	0.15078725	1.314546	0.142057
1.5	2	1.429374	0.617525	1.268297	2.315446	0.25460758	1.626551	0.479117
1.5	2	1.486356	0.603707	1.376108	2.209475	0.2023475	1.528048	0.446739
1.5	2	1.510279	0.412864	1.35443	2.123982	0.2023475	1.449755	0.385266
1.5	2	1.49536	0.59663	1.206113	2.078602	0.2023475	1.482874	0.417286
3	2	1.331756	0.755258	1.215536	2.177652	0.13130317	1.158754	0.251402
3	2	1.440541	0.743779	1.247914	2.187898	0.13229836	1.287762	0.242838
3	2	1.407447	0.882076	1.329651	2.098505	0.13229836	1.226951	0.241313
3	2	1.560763	1.065618	1.411165	2.359839	0.13229836	1.23704	0.254005
3	2	1.486685	0.98011	1.395169	2.385904	0.13229836	1.202582	0.227103
3	2	1.339047	0.808501	1.257293	2.406245	0.13229836	1.30394	0.238687
3	2	1.403091	0.755258	1.215224	2.249345	0.13329127	1.2397	0.233253
3	2	1.284813	0.743779	1.259734	2.155973	0.13229836	1.484037	0.297949
3	2	1.303805	0.78798	1.201136	2.19064	0.13229836	1.346729	0.278565
4.5	2	1.28649	0.681335	1.102729	2.074938	0.12849221	1.418438	0.336434
4.5	2	1.190173	0.667692	1.114857	2.007463	0.12849221	1.158221	0.175034
4.5	2	1.062363	0.592196	1.080549	1.988381	0.13577522	1.289678	0.25826
4.5	2	1.269638	0.681335	1.201641	2.091127	0.16976849	1.372697	0.293069
4.5	2	1.230236	0.608381	1.146184	2.11789	0.0966392	1.169173	0.209871
4.5	2	1.221115	0.743779	1.2389	2.254064	0.12849221	1.233874	0.264291
4.5	2	1.357863	0.755258	1.259741	2.125026	0.11683134	1.143211	0.206952
4.5	2	1.384471	0.719867	1.246832	2.053194	0.11998219	1.194522	0.224096
4.5	2	1.226027	0.592196	1.105928	2.088632	0.12849221	1.295378	0.279659

6	2	1.437937	0.603707	1.240229	2.311415	0.11943766	1.068302	0.194441
6	2	1.45162	0.464176	1.30671	1.85187	0.03902912	1.101189	0.123737
6	2	1.515322	0.574679	1.23395	2.184578	0.04512959	1.13047	0.088263
6	2	1.4485	0.378888	1.287055	2.157583	0.09172084	1.10931	0.179978
6	2	1.380844	0.680698	1.269885	2.143697	0.11434869	1.206449	0.234793
6	2	1.444956	0.567109	1.288358	2.147367	0.11434869	1.094542	0.234793
6	2	1.116189	0.287443	1.057629	1.941362	0.09172084	1.031045	0.165009
6	2	1.185211	0.444373	1.059401	2.092931	0.11005241	1.086637	0.229899
6	2	1.102156	0.329011	1.130337	1.979321	0.09172084	1.089436	0.219851
7.5	2	1.227192	0.719867	1.100395	2.123263	0.09724567	0.968732	0.167459
7.5	2	1.254801	0.653606	1.05935	1.963364	0.09724567	1.224232	0.222199
7.5	2	1.314736	0.719867	1.081849	1.880013	0.11862459	1.124236	0.20768
7.5	2	1.353744	0.707399	1.12788	2.010944	0.09724567	1.060635	0.194936
7.5	2	1.358007	0.731988	1.137144	1.908764	0.09912707	1.010832	0.164624
7.5	2	1.227122	0.694563	1.093234	2.002252	0.09724567	1.098175	0.176415
7.5	2	1.292733	0.798362	1.172839	1.952356	0.12250594	1.010832	0.114961
7.5	2	1.344434	0.731988	1.11994	1.931407	0.05919629	0.983504	0.138426
7.5	2	1.29028	0.639048	1.126894	2.040325	0.0836568	0.901629	0.169636
9	2	1.488034	0.492285	1.294272	2.141157	0.04935378	0.420388	0.103876
9	2	1.442579	0.444373	1.265004	1.829132	0.0728373	1.007349	0.134735
9	2	1.425005	0.401831	1.150244	1.938853	0.05587306	0.85827	0.109221
9	2	1.351613	0.624272	1.165407	1.845931	0.06852505	0.594003	0.092738
9	2	1.206693	0.354665	1.187976	1.900003	0.07556636	0.978065	0.180352
9	2	1.247024	0.444373	1.189471	2.00107	0.06852505	0.60349	0.048375
9	2	1.308594	0.423623	1.156443	1.936815	0.08155517	0.922135	0.105761
9	2	1.303689	0.390511	1.138141	1.89603	0.06181701	0.48282	0.097095
9	2	1.220696	0.329011	1.1058	1.898999	0.08154813	0.912853	0.130143

Microbial index	Plant N	Richness	Moisture	PH	EMF	Mason
0.810306967	0.428527	5	8.456513	7.05	-0.324887	22.71
0.435986775	0.488438	6	9.691756	7.12	0.1480468	21.76
1.137145292	0.413818	7	11.56808	7.4	0.1723901	31.77
1.295871979	0.412015	8	8.700251	7.39	-0.121094	NA
1.860193608	0.366943	7	8.700251	8.16	0.532705	NA
0.7209549	0.38347	10	9.623736	7.27	-0.268215	NA
1.195477272	NA	6	9.823949	7.09	0.201229	NA
1.255849414	NA	6	8.184455	8.22	0.1417794	NA
1.012228712	NA	6	7.828354	8.07	-0.90914	NA
0.359131257	0.400223	7	10.73698	8	-0.04964	18.28
0.364191505	0.482134	8	6.275834	7.18	0.4189267	11.63
0.716315629	0.463159	7	18.27747	7.06	0.2118911	13.69
0.603754241	0.457319	8	10.73698	6.95	0.4912155	NA
1.440656395	0.419679	7	6.275834	8.01	0.8213713	NA
0.610260023	0.42307	8	18.27747	7.15	0.4984331	NA
1.024661549	NA	5	10.73698	6.89	-0.0268	NA
0.744571231	NA	6	6.275834	7.05	-0.234038	NA
0.873205658	NA	6	18.27747	7.1	0.4116075	NA
0.294666259	0.429323	7	12.00332	8.23	0.4341047	12.25
0.699046444	0.480157	6	10.55013	7.54	0.4714804	27.45
0.90494545	0.50091	7	14.69306	7.04	0.2425025	19.04
0.660343647	0.482838	7	14.06681	8.04	0.7838649	NA
0.042623568	0.420391	6	7.73927	7.39	0.6317314	NA
0.287164323	0.420823	6	12.33942	6.94	1.1552362	NA
0.731533863	NA	6	10.5634	7	1.1515206	NA
0.257738709	NA	4	10.54189	6.91	0.4706136	NA
0.317174565	NA	5	11.28735	6.8	0.1660757	NA
-0.321509687	0.415914	6	9.588334	7.9	0.412896	14.06
-0.424055618	0.493564	8	7.43788	6.81	-0.726502	14.90
-0.196999345	0.479491	7	9.660303	7.08	0.0063513	19.49
-0.220643536	0.511291	4	12.03414	7.9	0.0707825	NA
-0.139496755	0.396872	6	9.159555	6.81	0.1246931	NA
-0.154973322	0.405751	4	9.140186	7.08	0.8400955	NA
0.096340534	NA	5	9.525423	7.9	1.0629157	NA
0.063789674	NA	4	10.76376	6.81	0.4367304	NA
-0.025983303	NA	4	6.129454	7.08	-0.356528	NA
-0.41817838	0.388105	7	7.243843	7.03	0.0400499	12.44
0.172369482	0.437139	8	4.368322	6.79	-0.223008	12.32
-0.219203881	0.492962	6	5.936993	7.21	-0.05944	13.15
-0.626468499	0.501862	7	10.29712	7.12	-0.885318	NA
-0.577555033	0.442837	5	8.908016	7	-0.662575	NA
0.126312199	0.476885	5	7.83271	8.2	-0.325579	NA
0.225862571	NA	5	6.109902	6.96	-0.176329	NA
-0.882612374	NA	5	8.794801	6.9	-0.586146	NA
-0.714725974	NA	4	7.930716	6.82	-0.003113	NA
2.243919227	0.428817	9	9.42545	6.88	-0.598288	10.10
-0.040862236	0.58732	7	7.829738	6.81	-1.121625	8.16
-1.878733716	0.526453	7	8.241745	6.86	-0.704335	17.60
-1.71912544	0.536542	5	8.613644	6.86	0.3932109	NA

-1.380850295	0.467664	6	12.8704	6.94	-0.339469	NA
-1.72360311	0.466089	6	8.279931	7.03	-0.012905	NA
-0.525185558	NA	4	9.146504	6.93	0.0072236	NA
-0.684438642	NA	4	12.29601	6.87	-0.338012	NA
-1.052032399	NA	4	10.15277	7.13	0.4343868	NA
-2.010228781	0.434139	7	4.838945	6.94	-0.984504	6.79
-0.566908741	0.641682	7	6.161221	6.81	-0.723224	9.17
-0.602848383	0.555358	5	3.753392	6.84	0.0351729	10.24
-1.305517989	0.603024	7	4.838945	7.46	-0.667083	NA
-1.587364246	0.519696	5	6.161221	7.2	-0.933491	NA
-1.462524412	0.510916	5	3.753392	6.96	-0.329975	NA
-0.309167446	NA	5	4.838945	7.05	-0.189941	NA
-0.608753911	NA	4	6.161221	6.94	-0.468326	NA
-1.204041911	NA	4	3.753392	6.94	-0.071701	NA
1.420899216	0.39307	7	8.454634	7.19	0.2511938	32.53
0.318970195	0.41096	8	11.23835	8.13	1.0760396	27.96
-0.473831718	0.43968	6	9.363605	8.13	0.8599408	25.38
1.710302396	0.404981	8	9.013975	8.18	1.0448977	NA
1.073062066	0.369889	8	10.399	8.33	0.9036025	NA
0.818844205	0.404688	7	11.86802	8.28	1.10162	NA
1.382116578	NA	6	9.360016	8.28	0.9265855	NA
1.076937999	NA	6	11.44597	8.23	0.380666	NA
1.573276821	NA	6	6.17305	7.25	-0.135311	NA
1.233544006	0.362797	12	12.94317	8.25	0.8778032	38.41
1.759534164	0.389194	10	13.58604	8.22	0.7768131	28.75
0.132502081	0.32645	11	10.80154	8.25	0.5968011	7.26
0.731730865	0.371546	13	11.28123	8.34	0.5181101	NA
-0.021805978	0.355031	8	10.87134	8.35	0.2338075	NA
2.03793677	0.378078	11	9.126005	8.29	0.5685184	NA
1.507784841	NA	5	9.919435	8.21	0.7915002	NA
1.216204442	NA	6	11.99662	8.2	0.355178	NA
1.358560619	NA	6	10.6187	8.33	0.1247649	NA
0.016314632	0.403642	8	6.93638	7.47	0.2092961	21.66
0.155380355	0.429113	7	9.174018	8.27	0.5235187	15.63
0.074990049	0.419679	6	8.83533	8.19	0.7451154	10.97
0.12764315	0.400125	9	10.34366	8.17	1.9849951	NA
-0.000204545	0.331877	5	8.418565	8.21	1.6987334	NA
0.162364674	0.436508	10	9.598423	7.91	0.7857646	NA
0.071162916	NA	6	8.410845	7.87	0.4719047	NA
0.573468579	NA	4	5.921442	7.96	0.1802599	NA
0.341573987	NA	5	8.128419	7.64	0.1821737	NA
0.591338401	0.383871	8	7.954838	8.4	-0.470484	16.80
-0.242139139	0.46493	6	7.810689	7.2	-0.766782	12.12
0.226820944	0.476684	6	5.136315	6.92	-1.272204	10.00
0.638659779	0.505977	5	10.01817	6.93	-0.209032	NA
-0.30457622	0.416819	5	8.876929	7.05	-0.510824	NA
0.133972967	0.443671	6	7.740522	6.96	0.1476523	NA
-0.228062048	NA	5	9.447734	8.16	0.3003483	NA
-0.091699099	NA	4	7.808974	8.28	0.1516519	NA
0.258975328	NA	4	5.682467	7	-0.70119	NA

-0.345458974	0.367425	11	12.36178	8.25	0.4821159	13.86
-0.997965235	0.424214	5	12.03333	8.36	-0.255502	14.60
-1.038043025	0.401719	5	8.884578	8.33	0.3789165	15.86
-0.50219031	0.422924	8	8.102592	8.16	0.0443207	NA
-0.075993688	0.380042	6	9.558102	8.26	0.2926258	NA
-0.215058066	0.425789	6	8.102592	8.09	0.3100711	NA
-0.646756623	NA	5	8.102592	6.95	-1.761037	NA
-0.265454638	NA	5	7.727374	7.27	-1.131214	NA
-0.400866847	NA	4	5.088269	7.11	-1.467392	NA
-0.684163718	0.400003	10	8.619108	7.45	-0.46448	15.13
-0.193648553	0.497542	9	9.083779	7.68	-0.876034	6.93
-0.238859349	0.463641	6	9.091556	8.26	-0.72244	0.30
-0.483113761	0.556854	5	10.12615	7.33	-0.324447	NA
-0.629809249	0.411037	5	8.782625	7.39	-0.416528	NA
-0.495000106	0.495139	5	8.508521	7.79	-0.716488	NA
-0.650143087	NA	4	7.448295	7.43	-0.28421	NA
-0.979928814	NA	4	9.273938	7.5	-0.455613	NA
-0.840085269	NA	4	8.63709	7.33	-0.51615	NA
-1.846420904	0.417565	6	11.47378	8.12	0.2923944	12.36
-0.882243835	0.4845	7	9.947806	8.06	-0.454955	7.49
-1.24727783	0.537838	4	8.29805	8.3	-0.694451	13.65
-1.553835562	0.575472	5	7.440471	8.28	-0.616796	NA
-0.758511466	0.511693	7	8.303975	7.56	-1.179953	NA
-1.682256021	0.511151	7	7.384936	8.14	-0.793672	NA
-1.02876059	NA	5	7.745247	8.13	-0.890195	NA
-1.717431577	NA	4	7.580667	8.15	-1.066119	NA
-0.963277177	NA	4	7.384936	7.31	-1.416199	NA

HLD(m g-2)
0.7935416
0.9008454
0.6297727
0.8624291
0.9332152
0.849692
0.9353428
0.9963758
0.7838735
0.8621152
0.8182022
0.9358731
0.7221579
0.8790521
0.749048
0.8503378
0.6297727
0.792437
0.7571208
0.9458273
0.7518906
0.5816242
0.7204207
0.5164685
0.728184
0.7080616
0.6424541
0.7607051
0.7724438
0.6971807
0.7724438
0.6971807
0.7607051
0.7724438
0.6971807
0.7607051
0.5875738
0.552515
0.7067163
0.687431
0.4756307
0.7979322
0.712516
0.7094027
0.5998086
0.7412373
0.6657714
0.648145
0.5550697

0.7178017
0.6361597
0.4740987
0.6532545
0.7816115
0.7116288
0.4167614
0.5763046
0.7583189
0.7116288
0.301057
0.4987101
0.3988858
0.5178583
0.3830907
0.5645185
0.5206247
0.5101588
0.5023203
0.6517279
0.6527463
0.5743755
0.5401702
0.5460615
0.5626451
0.7328608
0.6860202
0.7195494
0.6172621
0.4891805
0.7531031
0.5992338
0.8655558
0.7195494
0.6817599
0.7909598
0.8029992
0.778577
0.8047945
0.7587175
0.8421954
0.8483975
0.8856462
0.8461228
0.6393183
0.7164863
0.5975046
0.7857495
0.7315903
0.7751378

0.5267852
0.5122723
0.6100281
0.7559194
0.5881643
0.5986581
0.8438362
0.6846047
0.8175068
0.5707053
0.6324454
0.6335099
0.5613917
0.7353908
0.6100281
0.5335293
0.6512179
0.6803305
0.4389512
0.5288194
0.4671372
0.5016007
0.6105889
0.517164
0.5798234
0.5467112
0.3506859

EMF2	LRichness
-0.441328	-0.722694
-0.00345	0.075508
0.111595	0.766943
-0.238659	1.376832
0.167607	0.766943
-0.357331	2.415918
0.201229	0.148957
0.141779	-0.014028
-0.90914	0.321097
-0.321871	0.766943
0.140825	1.376832
-0.233596	0.766943
0.139927	1.376832
0.349095	0.766943
0.167437	1.376832
-0.0268	-0.997387
-0.234038	-0.014028
0.411608	0.178048
0.201043	0.766943
0.315705	0.075508
0.101129	0.766943
0.46915	0.766943
0.120335	0.075508
0.887318	0.075508
1.151521	-0.112806
0.470614	-1.345544
0.166076	-0.453643
0.118285	0.075508
-0.523495	1.376832
0.101904	0.766943
0.250925	-1.666768
-0.002637	0.075508
0.659041	-1.666768
1.062916	-0.696869
0.43673	-1.316427
-0.356528	-1.230044
-0.234719	0.766943
-0.256189	1.376832
-0.20019	0.075508
-0.790329	0.766943
-0.754832	-0.722694
-0.333003	-0.722694
-0.176329	-0.988295
-0.586146	-1.006495
-0.003113	-1.394441
-0.636979	1.922396
-0.731069	0.766943
-0.51005	0.766943
0.67817	-0.722694

-0.393208	0.075508
0.14791	0.075508
0.007224	-1.374827
-0.338012	-1.287472
0.434387	-1.625508
-0.887511	0.766943
-0.45575	0.766943
0.328461	-0.722694
-0.108111	0.766943
-0.533471	-0.722694
-0.052463	-0.722694
-0.189941	-1.043089
-0.468326	-1.646097
-0.071701	-1.258678
0.137526	0.37188
0.996765	0.817158
0.575575	-0.132936
0.71754	0.817158
0.454519	0.817158
0.66793	0.37188
0.926585	-0.079311
0.380666	-0.198306
-0.135311	0.046368
0.544625	2.207341
0.736408	1.575794
0.529257	1.90474
0.446869	2.487507
0.094171	0.817158
0.373225	1.90474
0.7915	-0.916255
0.355178	-0.198306
0.124765	-0.058072
0.106656	0.817158
0.527193	0.37188
0.77353	-0.132936
1.705294	1.215474
1.268483	-0.715702
0.539545	1.575794
0.471905	-0.270424
0.18026	-1.170444
0.182174	-0.519269
-0.481791	0.817158
-0.460433	-0.132936
-0.911603	-0.132936
0.044756	-0.715702
-0.577426	-0.715702
-0.021099	-0.132936
0.300348	-0.696847
0.151652	-1.149185
-0.70119	-1.086117

0.187752	1.90474
-0.239173	-0.715702
0.454121	-0.715702
0.216064	0.817158
0.218288	-0.132936
0.345548	-0.132936
-1.761037	-0.909617
-1.131214	-0.922905
-1.467392	-1.206143
-0.434048	1.575794
-0.235845	1.215474
-0.315516	-0.132936
0.036453	-0.715702
-0.266416	-0.715702
-0.511625	-0.715702
-0.28421	-1.191823
-0.455613	-1.128045
-0.51615	-1.374845
0.189162	-0.132936
0.28192	0.37188
-0.196937	-1.404969
0.023805	-0.715702
-0.70401	0.37188
-0.424204	0.37188
-0.890195	-0.949622
-1.066119	-1.389877
-1.416199	-1.107023