Multi-diversity strengthens multifunctionality in grasslands with intensive grazing pressure

Ruiyang Zhang[1], Dashuan Tian[2], Han Chen[3,4], Eric Seabloom[5], Guodong Han[6], Shaopeng Wang[7], Guirui Yu[8], and Shuli Niu[1]

[1]Institute of Geographic Sciences and Natural Resources Research Chinese Academy of Sciences
[2]Institute of Geographic Sciences and Natural Resources Research, CAS
[3]Lakehead University Faculty of Law
[4]Lakehead University
[5]University of Minnesota
[6]Inner Mongolia Agricultural University
[7]Peking University
[8]Information Management Group for the Synthesis Center of Chinese Ecosystem Research Network (CERN)

July 31, 2020

Abstract

Livestock grazing strongly affects biodiversity and ecosystem functioning in grasslands. However, it remains unclear how different grazing impact multiple biodiversity, ecosystem multifunctionality (EMF), and their relationship with the interactions of grazing duration, livestock type and climatic factors. Here, we conducted a global synthesis from 104 published studies. Our results showed that light and moderate grazing improved multi-diversity, but heavy grazing significantly decreased multi-diversity and EMF. The grazing-induced decrease of EMF intensified with grazing duration, and the reduction of multi-diversity and EMF under intensive grazing was stronger in more arid climates. The response of EMF increased linearly with that of multi-diversity under all grazing intensities. Moreover, grazing intensity reduced EMF largely via decreasing multi-diversity, whereas a shift of livestock type from small to large size promoted EMF by increasing multi-diversity. This study provides first empirical evidence and new insights into the relationship between multi-diversity and EMF under grazing in global grasslands.

Introduction

Many grassland ecosystems are subjected to livestock grazing, and these grazing systems provide up to a third of global food consumption and support the livelihoods of more than one billion people in the world(Suttie *et al.* 2005; Kemp *et al.* 2013). Increasing demand for livestock products has driven a global increase in grazing (Tilman *et al.* 2011; Kemp *et al.* 2013; Fetzel *et al.* 2017), which is threatening grassland biodiversity and ecosystem functioning (Schönbach *et al.* 2011; Eldridge *et al.* 2016). Yet, understanding how grazing impacts biodiversity, ecosystem functioning, and their relationship is still a major challenge in the context of climate change at broader spatial and temporal scales.

Biodiversity at multiple trophic levels (i.e., plants, animals, or microbes)and dimensions (i.e., taxonomic and functional diversity) respond differently to grazing due to their differential biological response mechanism(Fischer *et al.*2019; Wang & Tang 2019; Filazzola *et al.* 2020), which makes it difficult to estimate the overall grazing effects on biodiversity and its relationship with ecosystem functioning. Therefore, recent studies have acknowledged using multi-diversity by integrating different dimensions of diversity across multiple trophic levels simultaneously to reflect the overall effects of grazing on total local biodiversity(Allan *et al.* 2014; Wang *et al.* 2019). In addition, biodiversity becomes more important in maintaining multiple ecosystem functions (hereafter ecosystem multifunctionality, EMF) (Byrnes *et al.* 2013; Lefcheck *et al.* 2015; Gamfeldt & Roger 2017) than individual functions of productivity (Ma & Chen 2016; Zhang *et al.* 2018), stability (Loreau & Mazancourt 2013; Hautier *et al.* 2015), carbon storage (Yang *et al.* 2019), or nutrient availabilities(Komarov *et al.* 2018; Wang *et al.* 2020) based on a common positive biodiversity–ecosystem functioning (BEF) relationship in natural grasslands (Tilman*et al.* 2001; Zhang *et al.*2018). Furthermore, evidence is also mounting that the positive BEF relationship can be facilitated by intermediate environmental stress (Baert *et al.* 2018; Guo *et al.* 2019). However, how grazing affects multi-diversity, EMF, and their relationships in managed ecosystems still remain poorly understood and a systematic assessment at the global scale is lacking.

Grazing effects on biodiversity and ecosystem functioning are highly dependent on intensity quantified by stocking rate or density (Schönbach *et al.* 2011; Herrero-Jáuregui & Oesterheld 2018), and grazing duration (Porensky *et al.*2017). For example, previous studies suggested that species diversity and aboveground net primary productivity (ANPP) is maximized at moderate grazing intensity due to reduced competitive exclusion and increased compensatory growth in the plant community compared with non-grazing condition(McNaughton 1983; Milchunas *et al.* 1988), whereas high-intensity grazing with long duration decreases plant diversity and community productivity by reducing abundance of annuals and several weedy species in the plant community (Porensky *et al.* 2017; Zhang *et al.* 2018), as well as soil water-holding capacity and nutrient availability (Zhang *et al.* 2017; Sitters *et al.* 2020). Moreover, the magnitude and direction of grazing intensity effects on biodiversity vary across the wide range of ecological contexts(Olff & Ritchie 1998; Gao & Carmel 2020). In relatively humid and productive grasslands, moderate grazing may increase plant species diversity through reducing the dominance of palatable species and improving the availability of limited resources (i.e., light and nutrients) to rare species colonization (Olff & Ritchie 1998; Gao & Carmel 2020). In relatively arid and low productive grasslands, intermediate grazing may reduce species diversity by increasing dominance of grazing-tolerant species and aggravating resources stress (i.e., water and nutrients) to rare palatable species (Herrero-Jauregui & Oesterheld 2018; Zhang *et al.*2018). Collectively, these disparities of grazing effect not only depend on grazing intensity, but also are driven by environmental gradients.

In addition, different domestic herbivores (e.g., cattle and sheep) may have differential impacts on biodiversity due to their different grazing behavior (i.e., distinct diet of selectivity) (Grant *et al.* 1985; Dumont *et al.* 2011; Bremm *et al.* 2012; Toth *et al.* 2016). For example, compared to cattle, sheep are more likely to reduce taxonomic and functional diversity by reducing the amount of forbs at light or intermediate grazing intensities, but differences in selectivity between sheep and cattle may decrease with increasing grazing intensity(Toth *et al.* 2016). Overgrazing and the use of inappropriate livestock may lead to grassland degradation and desertification (Toth*et al.* 2016; Gao & Carmel 2020). Therefore, understanding how grazing intensity interacts with livestock type in changing grassland multi-diversity and EMF are essential for determining sustainable grazing management strategies.

Here, we conducted a global meta-analysis from 138 grazing intensity studies to evaluate grazing effects on the multiple biodiversity and ecosystem functioning in grassland ecosystems worldwide. Together, 16 biodiversity metrics across 5 groups (i.e., plant species diversity, functional group diversity, functional diversity, insect and soil microbial diversity) and 12 individual ecosystem functions (i.e., above- and belowground biomass, temporal stability of plant community, soil nutrients and moisture, net ecosystem productivity, ecosystem respiration and gross ecosystem productivity) were aggregated to estimate the multi-diversity and EMF, respectively, by weighted-averaging the natural log-transformed response ratio (lnRR) of each variable. In particular, we examine how the relationship between multi-diversity and EMF changes with intensifying grazing disturbance by incorporating the regulation of livestock types and grazing duration across a wide range of the aridity index.

Materials and Methods

Data preparation. To investigate the integrative effect of grazing intensity, duration, livestock type and climatic factor on multiple biodiversity and ecosystem functioning, we searched peer-reviewed publications during 1900–2019 using Google Scholar, Web of Science, and China Knowledge Resource Integrated Database with the search terms: (grazing) AND (diversity or richness) AND (ecosystem functioning) OR (productivity/stability/soil properties /soil nutrients/carbon exchange).

We examined the identified publications according to the following criteria: (a) field-manipulated experiments included a control (no grazing treatment), which had similar conditions to the grazing plots, such as microclimatic factors, vegetation and soil types. (b) Grazing intensity was clearly quantified in terms of vegetation utilization rate or stocking rate. (c) Experimental duration, livestock type and climatic characteristics (i.e., mean annual temperature and precipitation) were clearly indicated. (d) The means, standard deviation, and the number of replicates were explicitly provided. We obtained the table-form data directly and extracted graphical data using Getdata software (GetData Pty Ltd, Kogarah NSW, Australia) from the original publications. In total, 104 publications that investigated the effects of grazing intensity on biodiversity and individual ecosystem functions were used to establish a global dataset containing 494 independent observations (Fig. S1).

In this dataset, mean annual precipitation (MAP) ranged from 76 to 1834 mm and mean annual temperature (MAT) ranged from -3degC to 26.6degC. Aridity index was calculated as mean annual evaporation (provided by the original literatures or local weather records of the experimental site) /MAP to quantify dry conditions. Livestock type was categorized as small herbivores (i.e., sheep and goats in 62 publications), and large herbivores in 35 publications, including cattle, yak, horse (1 publication), bison (1 publication) and wildebeest (1 publication), while both cattle and sheep were used in 7 publications. Grazing duration was represented by experimental duration and ranged between 1 and 75 years, which was calculated from the establishment of the control (grazing exclusion treatment), because there is usually an untraceable long-term grazing history on natural grasslands. In addition, three grazing intensities were classified (light, moderate and heavy grazing) according to the description in the original publications. We also calculated the percentage change in aboveground biomass (AGB) from the 73 publications containing AGB in the dataset to verify the level of grazing intensity (Tang *et al.*2019). Our results showed that the percentage decline in AGB gradually increased with rising grazing intensity, indicating that the grazing intensity estimates in the original publications were reliable (Fig. S2).

Our dataset collected 5 biodiversity components (i.e., plant species diversity, diversity of plant functional group, plant functional diversity, insect diversity and soil microbial diversity). Among them, plant species diversity included 5 metrics: species richness, Shannon-Wiener, Margalef's, Pielou's and Simpson index. Diversity of plant functional groups was indicated by Shannon-Wiener, Margalef's and Pielou's index. Plant functional diversity was indicated by Rao's quadratic entropy's, evenness and dispersion index. Insect diversity (including herbivores and predators) was indicated by richness and Shannon-Wiener index. Soil microbial diversity (represented by bacteria diversity) was indicated by richness, Shannon-Wiener and Pielou's index. In addition, 12 individual ecosystem functions were collected in our dataset, including aboveground biomass (AGB), belowground biomass (BGB), temporal stability of vegetation productivity (TS), soil organic carbon (SOC), soil total nitrogen (STN), soil available nitrogen (SAN), soil total phosphorus (STP), soil available phosphorus (SAP), soil moisture (SM), net ecosystem productivity (NEP), ecosystem respiration (ER) and gross ecosystem productivity (GEP). For each publication, AGB and BGB were measured at the same period of peak vegetation biomass, and soil properties were surveyed at 0-30 cm depth.

Data analysis. We employed the natural log-transformed response ratio (lnRR) to evaluate grazing effects on all biodiversity metrics and individual ecosystem functions, which was calculated as

$$\ln(\mathrm{RR})=\ln(\mathrm{X}_{\mathrm{grazing}} / \mathrm{X}_{\mathrm{control}})$$

where $X_{grazing}$ and $X_{control}$ represent the observed values of the selected variables in grazed and control plots, respectively(Hedges *et al.*1999; Tang *et al.* 2019).

We weighted each observation using its sample size as in previous studies (Ma & Chen 2016; Tian *et al.*

2018; Chen & Chen 2019):

Weighting = $N_{grazing}$ x $N_{control}/(N_{grazing} + N_{control})$

Where $N_{grazing}$ and $N_{control}$ indicate the number of replications for the response variables in grazed and control plots, respectively.

We employed a linear mixed effect model to analyze the overall effects of grazing intensity on multiple biodiversity groups and individual ecosystem functions and their 95% confidence intervals (Fig. S3). We examined the links between plant species diversity and other biodiversity groups (Fig. S4), the relationships between aboveground biomass of plant community with other individual functions (Fig S5), as well as the relationship between plant species diversity and individual functions (Fig. S6) under grazing using the linear regression analysis, because most of the studies in our database have species diversity and aboveground biomass of plant community that can match other indicators. Then, we found that these individual biodiversity and ecosystem functions had the consistent negative responses to increasing grazing intensity (Fig.S3), and there were no possible trade-offs among different biodiversity groups, individual ecosystem functions and the BEF relationship (Fig. S4-S6). Moreover, although EMF had more significant correlations with plant diversity (including species diversity, functional groups diversity and functional diversity) than insect and soil microbial diversity (Fig. S9), the slope of the BEF relationship significantly increased with increasing number of biodiversity groups or individual functions, and so is the R value of correlations (Fig. S10). These results provide a key motivation for further exploration of multi-diversity and EMF in response to grazing intensity.

We calculated multi-diversity (including 5 biodiversity groups) and EMF (including 12 ecosystem functions) using the averaging approach(Manning *et al.* 2018; Wang *et al.* 2019), with each variable naturally log transformed (lnRR) and weighted according to the number of indicators provided before averaging in each study. Then, we analyzed the effects of grazing intensity and its interactions with grazing duration, livestock type and aridity index on multi-diversity and EMF, with all these factors taken as fixed effects, and each "study" set as a random effect to account for possible autocorrelation among observations in each study (Fig. 2). As a supplementary method, we took the classified indicators of different biodiversity groups and individual ecosystem functions as the random effects, and nested them into "study" using linear mixed effect model to avoid the possible autocorrelation among biodiversity groups or individual functions, and then we detected the similar results as the averaging approach (Fig. S7, S8). For the analysis, all variables were examined for normality and homogeneity. The treatment effects were considered significant at $\alpha = 0.05$, or if the 95% CIs does not cover zero. Linear regression was used to examine the relationships between lnRRs of individual biodiversity or multi-diversity and EMF under different grazing intensities, and the interaction term "grazing intensity×lnRR (multi-diversity)" specifically tests whether the effects of grazing intensity on EMF are dependent on multi-diversity. These analyses were conducted using the linear mixed effect model of lme4 package (Bates *et al.* 2015), and the correlations between multiple biodiversity and ecosystem functioning also were checked using model II regression of lmodel2 package.

Structural equation model. We employed a structural equation model (SEM) to evaluate the simultaneous effects of grazing intensity, duration, livestock type, aridity index and their interactions on the lnRRs of EMF directly and indirectly via lnRRs of multi-diversity (conceptual model), and then we selected the final model by excluding the insignificant factors (i.e., aridity index as well as the interactive effects of grazing intensity and other factors) based on goodness-of-fit statistics and lowest AIC value. The SEM was implemented using the "piecewiseSEM 1.2.1" package to account for the random effects of "Study" (Lefcheck, 2016). All statistical analyses were performed in r 3.5.2 (R Core Team, 2018).

Results and Discussion

Our synthesis provides global-scale evidence that both multi-diversity and ecosystem multifunctionality (EMF) are significantly altered by intensified grazing disturbance in grasslands. However, multi-diversity and EMF responded differently to grazing intensity. Specifically, light and moderate grazing increased multi-diversity, but heavy grazing reduced multi-diversity (Fig. 1). The similar results were found for the grazing effects on individual biodiversity, where light and moderate grazing intensity had slightly positive effects on diversity of plant species and soil microbes, and heavy grazing decreased the diversity of plant species and functional groups as well as functional diversity (Fig.S3). This result is different from the previous meta-analysis that included a much smaller sample size than ours and showed little effect of grazing intensity on plant species diversity(Herrero-Jáuregui & Oesterheld 2018).

The EMF decreased consistently with increasing grazing intensity, and the reduction of EMF response under heavy grazing (-19.3%) was significantly stronger than that under light (-5.8%) and moderate grazing (-11.1%) (Figs. 1, 2). Moreover, increasing grazing intensity had significant negative effects on individual ecosystem functions (Fig. S3). Compared to no grazing, all grazing intensities significantly reduced above- and belowground biomass, net ecosystem productivity (NEP), ecosystem respiration (ER) and gross ecosystem productivity (GEP). In addition, heavy grazing further decreased soil moisture, organic carbon and total phosphorus content, but had a non-significant effect on soil nitrogen content (Fig. S3). This is because overgrazing decreases aboveground plant biomass, leading to less plant litters inputs into the soil and thereby less carbon and phosphorus storage, but the loss of nitrogen can be mitigated by increases in nitrogen inputs through N-fixation of legumes and herbivore dung and urine(He *et al.* 2011; Martinsen *et al.* 2011; Sitters *et al.* 2020).

The negative effect of grazing intensity on multi-diversity becomes stronger over time (grazing duration) (Fig. 2). On the one hand, long-term grazing disturbance may facilitate a shift in plant community composition from weedy and annual plants to grazing-tolerant species, thereby leading to a limited decline in plant species richness and functional diversity (Marriott *et al.* 2009; Lyseng *et al.* 2018; Fischer *et al.* 2019). On the other hand, the accumulation of herbivores trampling and removal of aboveground biomass by grazing may reduce carbon and nitrogen inputs through litters into the belowground processes, and promote the evaporation of soil moisture by increasing bare land area, leading to lower soil microbial activity and plant regrowth rates(Liu *et al.* 2016; Sitters *et al.* 2020). Furthermore, even low-intensity grazing may also aggravate biodiversity loss and grassland degradation with the accumulation of grazing years. This result suggests that the magnitude of grazing effects estimated on multi-biodiversity and EMF may be underestimated when only short experimental durations are considered.

The shift in livestock type from small livestock (e.g., sheep and goat) to large livestock (e.g., cattle and yak) had a significantly positive effect on multi-diversity (Fig. 2). Moreover, a similar tendency towards a positive effect was also found in the interaction between grazing intensity and larger livestock type (Fig. 2). This is likely because of the distinctive diet selectivity and grazing behavior of large and small livestock, which leads to differences in vegetation structure and soil properties (Tóth *et al.* 2016; Wang *et al.* 2019; Gao & Carmel 2020). Previous research has found that cattle are likely to select the dominant perennial grasses that are higher and have greater aboveground biomass(P *et al.* 2014) and thereby alleviate competitive exclusion by alleviating ground-level light limitation(Hautier *et al.* 2009; Borer *et al.* 2014), leading to increased abundance of subordinate species and prevent rare species extinctions(Olff & Ritchie 1998). Compared with cattle grazing, sheep grazing is more likely to threaten plant species and functional diversity by increasing extinction of rare palatable species due to their greater selective preference for forbs with high abundance in the short-grass community (Tóth *et al.* 2016; Zhang *et al.* 2018).

Additionally, increasing aridity index had a significantly negative effect on the grazing-induced responses of multi-diversity and EMF (Fig. 2). This result suggests that increasing grazing intensity reduces the biodiversity of arid grasslands more strongly than that of humid grasslands, as reported previously for plant species diversity (Herrero-Jáuregui & Oesterheld 2018; Gao & Carmel 2020). Importantly, we found a significant negative interaction effect between grazing intensity and aridity on multi-diversity index (Fig. 2), indicating a negative synergistic effect of grazing intensity and aridity. This may be attributed to the idea that herbivores may further aggravate water stress and limitation of nutrient resources of dry grasslands, causing decreases of plant and soil microbial diversity (Ren *et al.* 2018; Gao & Carmel 2020; Zhang *et al.* 2020). Therefore, our results suggest that the predicted increasing drought events might aggravate the negative effect of grazing disturbance in thefuture.

Compared with the single biodiversity-ecosystem function relationship, there was a stronger positive relationship between multi-diversity and EMF responses when integrated a great number of biodiversity groups and functions (Fig. S10). Further, we found that the slope of the multi-diversity and EMF relationship increased significantly by 66.6% from light grazing to heavy grazing (P =0.005) (Fig. 3). The underlying mechanism may be attributable to increased abiotic facilitation under a certain extent of increased stress of disturbances, as predicted by the "stress gradient hypothesis"(Baert *et al.* 2018). On the one hand, the environmental stress caused by increasing grazing intensity may strengthen the positive BEF relationship by promoting the dominance effects that high functional adaptive species increasingly replace low functional vulnerable species(Baert *et al.* 2018; Guo *et al.* 2019). On the other hand, although extremely high environmental stress was predicted to weaken the BEF relationship by inhibiting the functioning of all species(Baert *et al.* 2018), we did not detect this under any grazing intensities, which may be due to that the levels of heavy grazing in most studies are not sufficient to cause extreme environmental stress. Overall, our results suggest that increasing grazing intensity strengthens the dependence of EMF on multi-diversity globally.

The structural equation modeling reveals that an increase in grazing intensity decreased EMF not only directly, but also indirectly via reducing multi-diversity (Fig. 4). Grazing duration had a direct negative effect on the response ratio of EMF, and the changing livestock type from small to large size mainly had an indirect positive effect on EMF by increasing multi-diversity. In contrast, rising aridity index had an indirect negative effect on the response ratio of EMF via decreasing multi-diversity (Fig. 4). These findings established a unique and critical role of multi-diversity in mediating EMF under the integrative impacts of grazing intensity, duration, livestock type and climatic factors at the global scale, which expands our understanding based on the regulation of single-trophic biodiversity on ecosystem functions under land use and environmental changes at a local scale, as shown by previous studies(Allan *et al.* 2015; Hautier *et al.* 2015).

In conclusion, this study provides new insights into the effects of grazing intensity interacting with livestock type, grazing duration and aridity on the multi-diversity, EMF, and their relationship. We found that intensifying grazing disturbance strengthens the dependence of EMF on multi-diversity, and reduces ecosystem functioning through extensively decreasing biodiversity. Moreover, the negative grazing effects are stronger in drier grasslands with smaller livestock and longer grazing duration. The findings extend our current understanding on the grazing management practices in promoting biodiversity conservation and sustainability of ecosystem services (Schönbach *et al.* 2011; Kemp *et al.* 2013; DeLonge & Basche 2018). We strongly suggest to carefully modify the grazing duration and select proper livestock types while optimizing the grazing intensity. Establishing optimal adaptive management strategy based on biodiversity conservation is critical for preventing grassland degradation and promoting sustainable development of global pastoral areas, especially when extreme drought events are predicted to occur more intensively and frequently under global climate change.

ACKNOWLEDGMENTS

This study was supported by the National Natural Science Foundation of China (31988102, 31625006), the CAS international collaboration program (131A11KYSB20180010),and the Postdoctoral Science Foundation of China.

References

Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tscharntke, T. *et al.* (2014). Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the National Academy of Sciences of the United States of America* 111, 308-313.

Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N. *et al.* (2015). Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecology letters* , 18, 834-843.

Baert, J.M., Eisenhauer, N., Janssen, C.R. & De laender, F. (2018). Biodiversity effects on ecosystem functioning respond unimodally to environmental stress. *Ecology Letters* , 21, 1191-1199.

Bates, D., Maechler, M., Bolker, B.M. & Walker, S.C. (2015). Fitting linear mixed-effects models using lme4.*arXiv preprint arXiv* , 1406, 5823.

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M. *et al.* (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* , 508, 517-520.

Bremm, C., Laca, E.A., Fonseca, L., Mezzalira, J.C., Elejalde, D.A.G., Gonda, H.L. *et al.* (2012). Foraging behaviour of beef heifers and ewes in natural grasslands with distinct proportions of tussocks. *Applied Animal Behaviour Science* , 141, 108-116.

Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A. *et al.* (2013). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology & Evolution* , 5, 111-124.

Chen, X.L. & Chen, H.Y.H. (2019). Plant diversity loss reduces soil respiration across terrestrial ecosystems. *Global Change Biology* , 25, 1482-1492.

DeLonge, M. & Basche, A. (2018). Managing grazing lands to improve soils and promote climate change adaptation and mitigation: a global synthesis. *Renewable Agriculture And Food Systems* , 33, 267-278.

Dumont, B., Carrère, P., Ginane, C., Farruggia, A., Lanore, L., Tardif, A. *et al.* (2011). Plant–herbivore interactions affect the initial direction of community changes in an ecosystem manipulation experiment. *Basic & Applied Ecology* , 12, 187-194.

Eldridge, D.J., Poore, A.G., Ruiz-Colmenero, M., Letnic, M. & Soliveres, S. (2016). Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. *Ecological Applications* , 26, 1273-1283.

Fetzel, T., Havlik, P., Herrero, M., Kaplan, J., Kastner, T., Kroisleitner, C. *et al.* (2017). Quantification of uncertainties in global grazing systems assessment.*Global Biogeochemical Cycles* , 31, 1089-1102.

Filazzola, A., Brown, C., Dettlaff, M.A., Batbaatar, A., Grenke, J., Bao, T. *et al.* (2020). The effects of livestock grazing on biodiversity are multi-trophic: a meta-analysis. *Ecology Letters* , Online: https://publons.com/publon/10.1111/ele.13527.

Fischer, F.M., Bonnet, O.J., Cezimbra, I.M. & Pillar, V.D. (2019). Long-term effects of grazing intensity on strategies and spatial components of functional diversity in subtropical grassland. *Applied Vegetation Science* , 22, 39-47.

Gamfeldt, L. & Roger, F. (2017). Revisiting the biodiversity–ecosystem multifunctionality relationship.*Nature ecology & evolution* , 1, 0168.

Gao, J. & Carmel, Y. (2020). Can the intermediate disturbance hypothesis explain grazing-diversity relations at a global scale? *Oikos* , 129, 493-502.

Grant, S.A., Suckling, D.E., Smith, H.K., Torvell, L., Forbes, T.D.A. & Hodgson, J. (1985). Comparative Studies of Diet Selection by Sheep and Cattle: The Hill Grasslands.*Journal of Ecology* , 73, 987-1004.

Guo, Y., Schob, C., Ma, W., Mohammat, A., Liu, H., Yu, S. *et al.* (2019). Increasing water availability and facilitation weaken biodiversity-biomass relationships in shrublands. *Ecology* , 100, e02624.

Hautier, Y., Niklaus, P.A. & Hector, A. (2009). Competition for Light Causes Plant Biodiversity Loss After Eutrophication. *Science* , 324, 636-638.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T. & Reich, P.B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity.*Science* , 348, 336-340.

He, N.P., Zhang, Y.H., Yu, Q., Chen, Q.S., Pan, Q.M., Zhang, G.M. *et al.* (2011). Grazing intensity impacts soil carbon and nitrogen storage of continental steppe.*Ecosphere* , 2, 304-316.

Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology* , 80, 1150-1156.

Herrero-Jauregui, C. & Oesterheld, M. (2018). Effects of grazing intensity on plant richness and diversity: a meta-analysis. *Oikos* , 127, 757-766.

Herrero-Jauregui, C. & Oesterheld, M. (2018). Effects of grazing intensity on plant richness and diversity: a meta-analysis. *Oikos* , 127, 757-766.

Kemp, D.R., Han, G., Hou, X., Michalk, D.L., Hou, F., Wu, J. *et al.* (2013). Innovative grassland management systems for environmental and livelihood benefits.*Proceedings of the National Academy of Sciences of the United States of America* , 110, 8369-8374.

Komarov, A., Priputina, I., Zubkova, E. & Shanin, V. (2018). Plant biodiversity and soil nitrogen and carbon pools changes as a result of nitrogen deposition at permanent pine plots in Central Russia. *Chemosphere* , 199, 168-173.

Lefcheck, J.S., Byrnes, J.E., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N. *et al.* (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature communications* , 6, 6936.

Liu, N., Kan, H.M., Yang, G.W. & Zhang, Y.J. (2016). Changes in plant, soil, and microbes in a typical steppe from simulated grazing: explaining potential change in soil C.*Ecological Monographs* , 85, 269-286.

Loreau, M. & Mazancourt, C.D. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* , 16, 106-115.

Lyseng, M.P., Bork, E.W., Hewins, D.B., Alexander, M.J., Carlyle, C.N., Chang, S.X. *et al.* (2018). Long-term grazing impacts on vegetation diversity, composition, and exotic species presence across an aridity gradient in northern temperate grasslands. *Plant ecology* , 219, 649-663.

Ma, Z.L. & Chen, H.Y.H. (2016). Effects of species diversity on fine root productivity in diverse ecosystems: a global meta-analysis. *Glob. Ecol. Biogeogr.* , 25, 1387-1396.

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G. *et al.* (2018). Redefining ecosystem multifunctionality. *Nature ecology & evolution* , 2, 427-436.

Marriott, C.A., Hood, K., Fisher, J.M. & Pakeman, R.J. (2009). Long-term impacts of extensive grazing and abandonment on the species composition, richness, diversity and productivity of agricultural grassland. *Agriculture Ecosystems & Environment* , 134, 190-200.

Martinsen, V., Mulder, J., Austrheim, G. & Mysterud, A. (2011). Carbon storage in low-alpine grassland soils: effects of different grazing intensities of sheep. *European Journal of Soil Science* , 62, 822-833.

McNaughton, S.J. (1983). Compensatory plant growth as a response to herbivory. *Oikos* , 40, 329-336.

Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* , 132, 87-106.

Olff, H. & Ritchie, M.E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* , 13, 261-265.

P, T., Orsolya, V., Balazs, D., Andras, K., Bela, T. & Regina, L. (2014). Traditional Cattle Grazing in a Mosaic Alkali Landscape: Effects on Grassland Biodiversity along a Moisture Gradient. *Plos One* , 9, e97095.

Porensky, L.M., Derner, J.D., Augustine, D.J. & Milchunas, D.G (2017). Plant Community Composition After 75 Yr of Sustained Grazing Intensity Treatments in Shortgrass Steppe. *Rangeland Ecology & Management* , 70, 456-464.

Ren, H., Eviner, V.T., Gui, W., Wilson, G.W., Cobb, A.B., Yang, G. *et al.* (2018). Livestock grazing regulates ecosystem multifunctionality in semi-arid grassland.*Functional ecology* , 32, 2790-2800.

Schonbach, P., Wan, H., Gierus, M., Bai, Y., Muller, K., Lin, L. *et al.* (2011). Grassland responses to grazing: effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. *Plant and Soil* , 340, 103-115.

Sitters, J., Wubs, E.R.J., Bakker, E.S., Crowther, T.W., Adler, P.B., Bagchi, S. *et al.* (2020). Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands. *Global Change Biology* , 26, 2060-2071.

Suttie, J.M., Reynolds, S.G. & Batello, C. (2005). *Grasslands of the world* . FAO.

Toth, E., Deak, B., Valko, O., Kelemen, A., Miglecz, T., Tothmeresz, B. *et al.* (2016). Livestock type is more crucial than grazing intensity: Traditional cattle and sheep grazing in short-grass steppes. *Land Degradation & Development* , 231-239.

Tang, S.M., Wang, K., Xiang, Y.Z., Tian, D.S., Wang, J.S., Liu, Y.S. *et al.* (2019). Heavy grazing reduces grassland soil greenhouse gas fluxes: A global meta-analysis.*Science Of the Total Environment* , 654, 1218-1224.

Tian, D.S., Xiang, Y.Z., Wang, B.X., Li, M.L., Liu, Y.S., Wang, J.S. *et al.* (2018). Cropland abandonment enhances soil inorganic nitrogen retention and carbon stock in China: A meta-analysis. *Land Degradation & Development* , 29, 3898-3906.

Tilman, D., Balzer, C., Hill, J. & Befort, B.L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United States of America* , 108, 20260-20264.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science* , 294, 843-845.

Wang, C. & Tang, Y. (2019). A global meta-analyses of the response of multi-taxa diversity to grazing intensity in grasslands. *Environmental Research Letters* , 14, 114003.

Wang, L., Delgado-Baquerizo, M., Wang, D., Isbell, F., Liu, J., Feng, C. *et al.* (2019). Diversifying livestock promotes multidiversity and multifunctionality in managed grasslands. *Proceedings of the National Academy of Sciences of the United States of America* 116, 6187-6192.

Wang, L., DelgadoBaquerizo, M., Zhao, X., Zhang, M., Song, Y., Cai, J. *et al.* (2020). Livestock overgrazing disrupts the positive associations between soil biodiversity and nitrogen availability. *Functional Ecology* , Online: https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2435.13575.

Yang, Y., Dou, Y.X., Cheng, H. & An, S.S. (2019). Plant functional diversity drives carbon storage following vegetation restoration in Loess Plateau, China. *J. Environ. Manage.* , 246, 668-678.

Zhang, J., Zuo, X.A., Zhou, X., Lv, P., Lian, J. & Yue, X.Y. (2017). Long-term grazing effects on vegetation characteristics and soil properties in a semiarid grassland, northern China. *Environ. Monit. Assess.* , 189, 216.

Zhang, R., Wang, Z., Han, G., Schellenberg, M.P., Wu, Q. & Gu, C. (2018). Grazing induced changes in plant diversity is a critical factor controlling grassland productivity in the Desert Steppe, Northern China. *Agriculture Ecosystems & Environment* , 73-83.

Zhang, Y.T., Gao, X.L., Hao, X.Y., Alexander, T.W., Shi, X.J., Jin, L. *et al.* (2020). Heavy grazing over 64 years reduced soil bacterial diversity in the foothills of the Rocky Mountains, Canada. *Applied Soil Ecology* , 147, 103361.

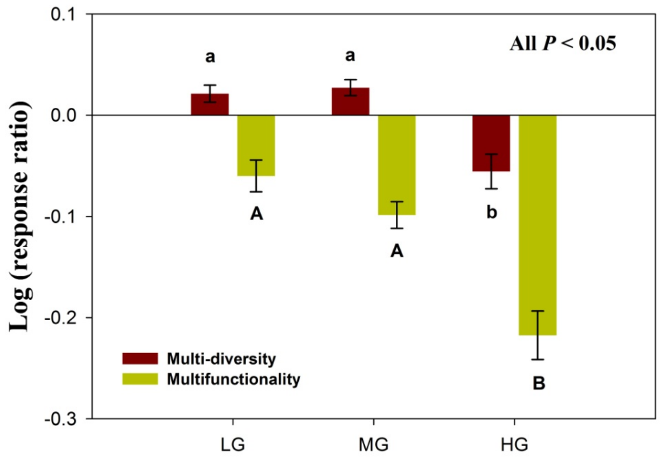


Figure 1 Grazing-induced responses of multi-diversity and ecosystem multifunctionality under light grazing (LG), moderate grazing (MG) and heavy grazing (HG). Significant differences (P <0.05) among different grazing intensities are indicated by different lower case letters (for multi-diversity) and capital letters (for multifunctionality).Error bars represent ±SE.

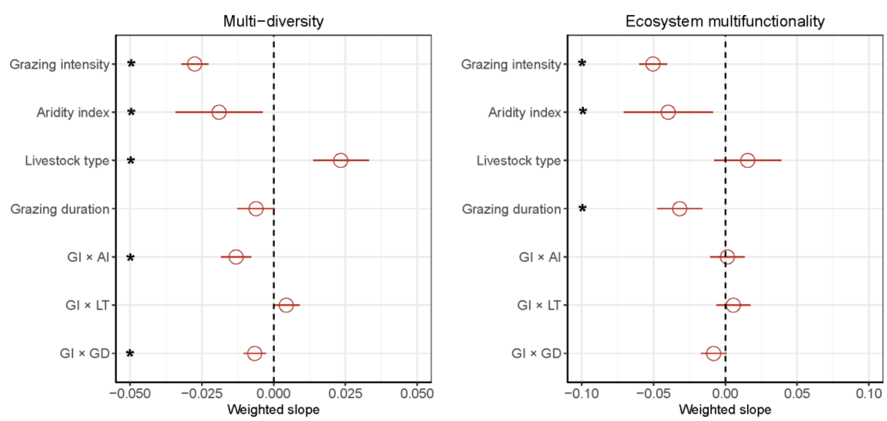


Figure 2 Effects of grazing intensity (GI), aridity index (AI), livestock type (LT), grazing duration (GD) and their interactions on multi-diversity and ecosystem multifunctionality. Circles represent mean weighted response ratios with their 95% confidence intervals (CI). If the 95% CI does not cover the dashed line, this indicates a significant effect (represented by *).

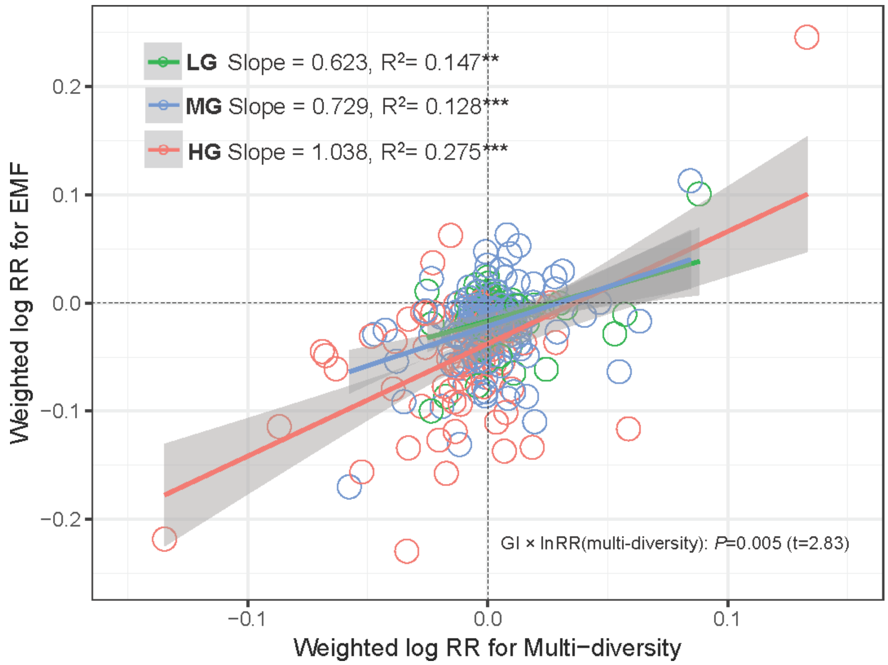


Figure 3 The linear relationships between the relative changes in multi-diversity and ecosystem multifunctionality (EMF) under light grazing (LG), moderate grazing (MG) and heavy grazing (HG), respectively. The shade represents confidence intervals (CI). The significance indicated as ****P* <0.001 ***P* <0.01 and **P* <0.05. The interactive effect of grazing intensity (GI) and multi-diversity on EMF obtained from the linear mixed effect model are shown.

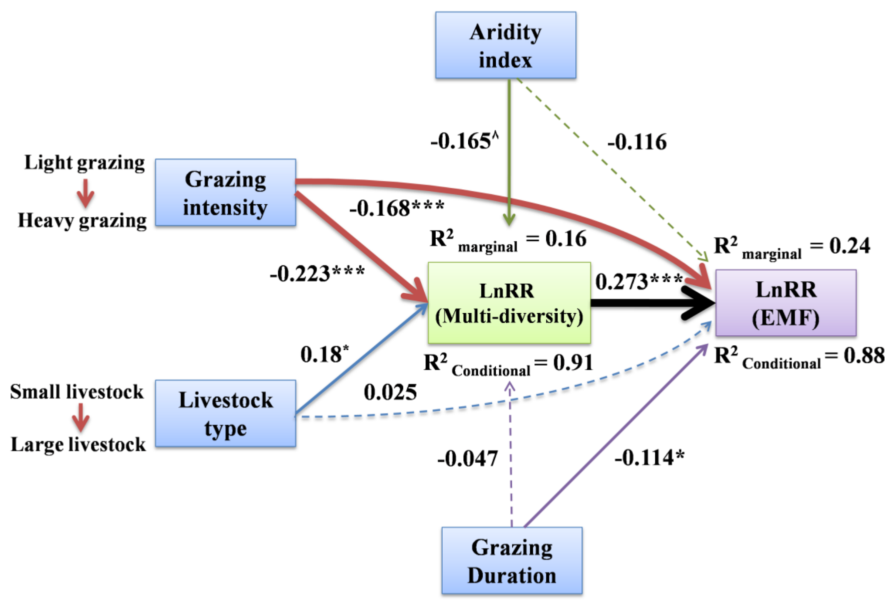
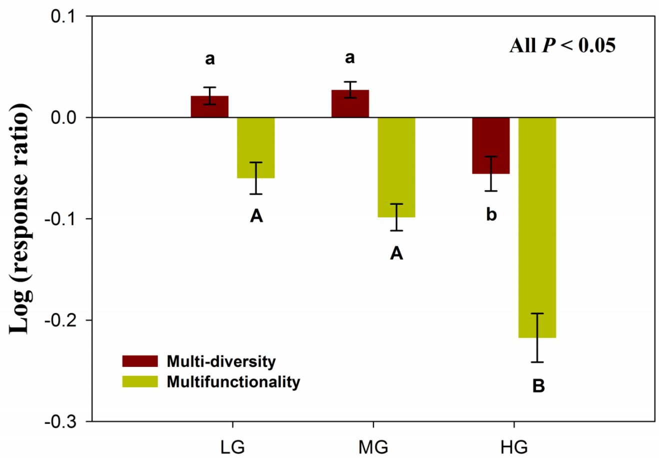
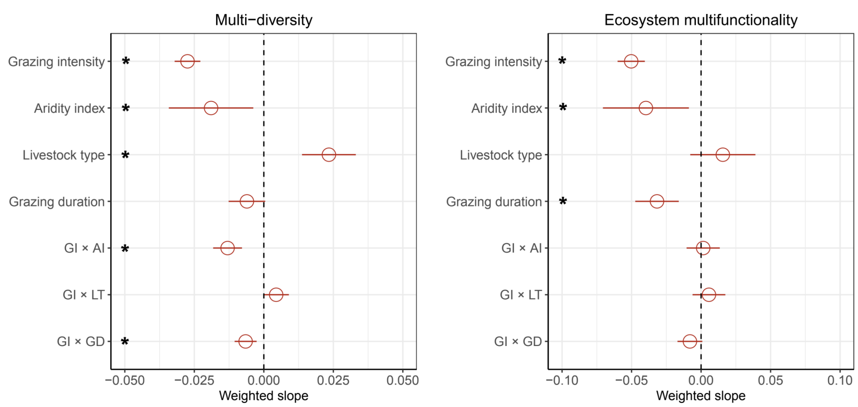
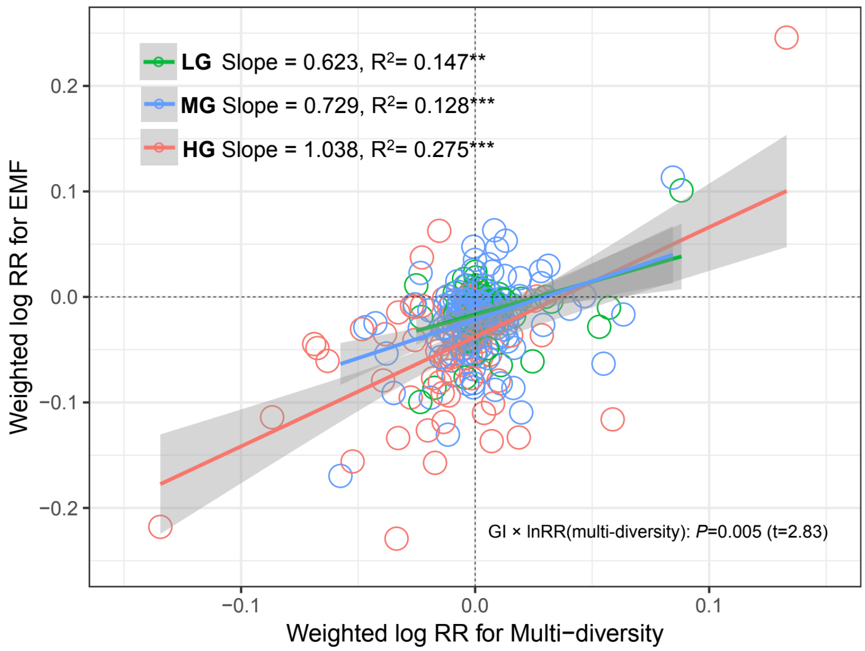


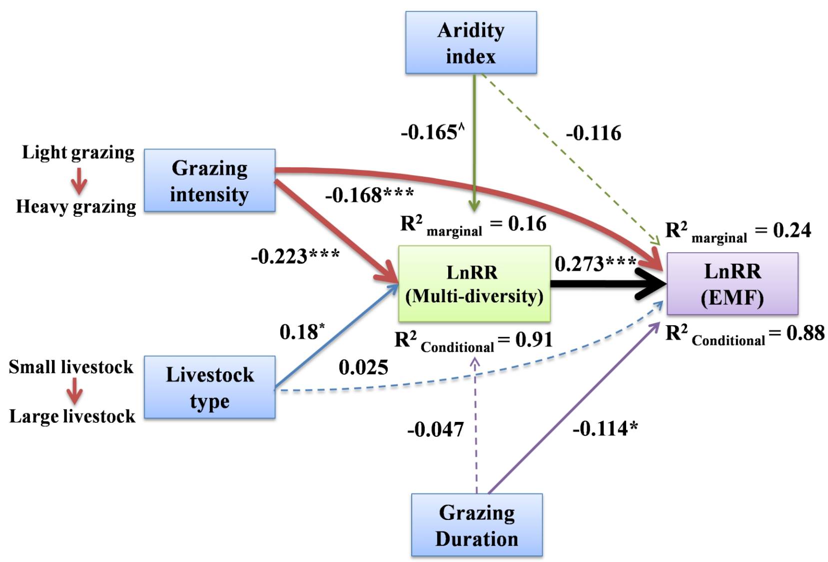
Figure 4 Structural equation model describing the effects of grazing intensity, grazing duration, livestock type and aridity index on relative changes in ecosystem multifunctionality (EMF) through the relative changes in multi-diversity. Numbers adjacent to arrows indicate the effect size of the relationship, and solid

arrows represent standardized path coefficients with significance indicated as ***P <0.001 **P <0.01 and *P <0.05. Non-significant paths are indicated by dashed arrows (P >0.05).$R^2_{marginal}$and $R^2_{conditional}$ represent the level of deviance of the variable explained by all paths from the fixed effects, and both the fixed and random effects ("study"),respectively.






LG Slope = 0.623, R²= 0.147**
MG Slope = 0.729, R²= 0.128***
HG Slope = 1.038, R²= 0.275***
GI × lnRR(multi-diversity): P=0.005 (t=2.83)
Weighted log RR for EMF
Weighted log RR for Multi−diversity
0.2
0.1
0.0
−0.1
−0.2
−0.1
0.0
0.1


Aridity index
Light grazing
Heavy grazing
Grazing intensity
Small livestock
Large livestock
Livestock type
Grazing Duration
LnRR (Multi-diversity)
LnRR (EMF)
-0.165^
-0.116
-0.168***
-0.223***
0.18*
0.025
0.273***
-0.047
-0.114*
R² marginal = 0.16
R² Conditional = 0.91
R² marginal = 0.24
R² Conditional = 0.88